**RESEARCH PAPER**

# Ecological biogeography of cephalopod molluscs in the Atlantic Ocean: historical and contemporary causes of coastal diversity patterns

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## ABSTRACT

**Aim**  One of the most recognized ecological paradigms on earth is the increase in species richness from the poles towards the equator. Here we undertake a comprehensive survey of the latitudinal gradients of species richness (LGSR) of coastal cephalopod fauna in the western (WA) and eastern margins (EA) of the Atlantic Ocean, and test climate and non-climate theories to explain the variation in diversity.

**Location**  The coastal Atlantic Ocean.

**Methods**  The diversity and geographical ranges of coastal cephalopods were investigated by means of an exhaustive survey of the primary literature, reports and on-line data bases. In order to test the productivity, ambient energy and area hypotheses, we investigated the relationship between diversity and net primary production (NPP), sea surface temperature (SST; measure of solar energy input) and continental shelf area, respectively.

**Results**  LGSR of cephalopod molluscs are present at both Atlantic coasts, but are quite distinct from each other. Historical processes (rise of the Central American Isthmus, formation of 'Mare Lago' and glaciations) explained much of the shape and the zenith of LGSR. Contemporary climate and non-climate variables also each explained over 83% and 50% of the richness variation in WA and EA, respectively, and the best fitted models accounted for > 92% of the variance. By combining latitude with depth a strong Rapoport effect was observed in WA but not in EA.

**Main conclusions**  Besides the evolutionary history, we demonstrate that the contemporary environmental gradients (SST and NPP), shelf area and extent of coral habitat can predict many of the diversity patterns. The longitudinal difference in Rapoport's bathymetric rule is attributed to western fauna specialization to shallow coral reef habitats and greater ecological tolerance of eastern fauna to upwelling ecosystem dynamics. A combined approach of historical biogeography and species–area–energy theories was essential to fully understand broad-scale variation in cephalopod biodiversity.

**Keywords**

**Coastal Atlantic Ocean, coastal ecology, historical processes, latitudinal gradients, Rapoport's rule, species–area, species–energy.**

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## INTRODUCTION

The most recognized ecological pattern on our planet is the increased richness in biological diversity from polar to equatorial regions (Rohde, 1992; Brown & Lomolino, 1998). Understanding the causes of this pattern is still one of greatest contemporary challenges for ecologists. This paradigm has been widely scrutinized in the terrestrial biosphere over the last decades and several factors have been hypothesized to explain it, such as competition and predation, spatial heterogeneity, 'Rapoport's rule', environmental stability, ambient energy, productivity, biome area, evolutionary time, energetic equivalents, Milankovitch

oscillations and geometric constraints, among other possible causes (the total exceeds 30; for reviews see Rohde, 1992; Rosenzweig, 1995; Willig *et al.*, 2003). Though there have been few efforts to reduce the number of explanations, the best documented contenders for a short-list of explanations are the climate-based hypotheses (see Currie *et al.*, 2004).

While several studies with marine groups have described the negative association between diversity and latitude (Steele, 1988; Stevens, 1996; Roy *et al.*, 1998, 2000; Rex *et al.*, 2000, 2005; Macpherson, 2002; Smith & Gaines, 2003), many others have failed to find such a relationship (Clarke, 1992; Lambshead *et al.*, 2000; Mokievsky & Azovsky, 2002). Therefore, whether the former causal hypotheses apply to the large spatial scales in the marine biosphere remains unclear. Since cephalopod molluscs are a very diverse group of marine organisms found in all marine habitats from the polar regions to the tropics, here we examine their latitudinal gradients of species richness (LGSR) in the coastal margins of the western (WA) and eastern Atlantic (EA) and test several of the previous hypotheses to explain the modern diversity patterns, namely the biome area, ambient energy and productivity (formerly just known as species–energy hypothesis) and Rapoport's latitudinal and bathymetric rules. Briefly, the biome area hypothesis states that the tropics support more species because they comprise more area than the other regions (promoting higher speciation rates and lower extinction rates; Rosenzweig, 1995). The ambient energy hypothesis argues that diversity is a result of the effect of climate (namely its energetic elements) on the organism's physiology (Turner *et al.*, 1987), while the productivity hypothesis claims that the rate of photosynthetically active radiation governs the diversity of primary producers and, as a consequence, all the other trophic levels in the food chain (Wright, 1983). Rapoport's rule attributes the latitude (or depth)–diversity gradient to a reduction in the size of distributional ranges of species towards the equator, resulting in a progressively larger number of species along this trend (Stevens, 1989). We also discuss the role of historical processes (large-scale geological and climatic events) on ecological and evolutionary patterns of cephalopod fauna.

## METHODS

The data base for the latitudinal distributions of coastal (neritic) cephalopod fauna (i.e. species that are associated with continental shelves) in the Atlantic Ocean was constructed by means of a comprehensive search of the primary literature (e.g. Voss *et al.*, 1998; Jereb & Roper, 2005), regional faunal compilations (e.g. Rosa & Sousa Reis, 2004), expedition reports and CephBase (an on-line data base that is part of the Census of Marine Life: http://www.cephbase.utmb.edu/). Furthermore, an additional search was carried out in several journals that publish papers on the taxonomy and biogeography of cephalopod species. The description of cephalopod fauna from the Southern Ocean was based on the recent review by Collins & Rodhouse (2006). Species richness (the number of species) was used as the measure of diversity and determined as the sum of all species whose ranges crossed a given 5° of latitude band. The depth of occurrence for

each species was also recorded. In order to test the productivity, ambient energy and area hypotheses, we investigate the relationship between diversity and net primary production (NPP), sea surface temperature (SST; measure of solar energy input) and continental shelf area, respectively. Ocean productivity was estimated from the Vertically Generalized Production Model (Behrenfeld & Falkowski, 1997) with a temperature-dependent description of chlorophyll-specific photosynthetic efficiency applied to satellite-derived chlorophyll and SST from the MODIS Aqua sensor. On-line *Standard Products* were downloaded as monthly, global NPP gridded 18-km data from November 2002 to October 2006 (Oregon State University, 2006). Because NPP follows a logarithmic distribution, the geometric mean was calculated for 5° latitudinal increments along the western and eastern Atlantic shelves. Monthly SST was derived from MODIS Aqua imagery processed with the 4-μm night-time algorithm. For these SST data, the arithmetic mean was calculated for each of the defined bins. Continental shelf area was determined using satellite-derived ocean bathymetry resampled at a 1° resolution (USDC, 2006).

The statistical analysis of the data was carried out in SAS (version 9.1). As the coastal data were binned in latitudinal bands there was the concern of spatial dependency in the observations. Descriptive analysis and tests of autocorrelation indicated a lack of independence in the variables, hence the need to account for it in the modelling. The spatial dependency in these data was in one dimension; hence, methods that apply to time-series data could be used for statistical analysis (Cressie, 1993, p. 200).

Ordinary regression analysis requires that errors in the variables are independent of each other. In the analysis of species richness, this particular assumption was violated, thus causing tests of significance and confidence intervals to be incorrect. Another consequence was that the estimated regression coefficients were not as efficient as they would have been if autocorrelation had been taken into account. Generalizations of the Durbin and Watson test were used to detect the presence of autocorrelation of order up to four (results not reported). Hence, we used autoregressive (AR) models in the analysis of the data.

In the context of this paper, a simple linear regression model with first-order autoregressive errors (AR(1)) can be defined as

$$y_l = \beta_0 + \beta_1 x_l + \varepsilon_l$$

$$\varepsilon_l = \rho \varepsilon_{l-1} + a_l$$

where $y_l$ and $x_l$ are the observations on the response (diversity) and regression variables (i.e. SST, area, etc.) respectively, at latitude $l$, $\varepsilon_l$ is the error term in the model at latitude $l$, $a_l$ is a normally and independently distributed (NID) (0, $\sigma_a^2$) random variable, and $\rho$ is the autocorrelation parameter. This model can easily be extended to a multiple regression model with $p$ independent variables and an autoregressive error of order $k$ (AR($k$)) by adding additional terms to the model given above.

The AUTOREG procedure in SAS was used in parts of the analysis to account for autocorrelation in the residuals when present. In the cases where there was no dependency in the

residuals, standard multiple regression analysis was used. The goodness of fit statistics reported are the total $R^2$ and the Akaike information criterion (AIC) where

$$R^2_{tot} = 1 - (SSE/SST)$$

SST is defined as the corrected sum of squares total for the response variable (different from the variable sea surface temperature, SST) and SSE is the final error sum of squares. The AIC information criterion is defined as

$$AIC = -2\ln(L) + 2k$$

where $L$ is the value of the likelihood function evaluated at the parameter estimates and $k$ is the number of estimated parameters.

Analysis of covariance (ANCOVA) was used to fit models that allowed for a different linear association between species richness and area, at different latitudes (i.e. coral regions). That is, ANCOVA allowed us to fit two different regression lines within a single model by using an interaction term between a quantitative (area) and a qualitative variable (coral indicator variable). The described ANCOVA model can be written as

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2 + \varepsilon$$

where $x_1$ is the variable area, $x_2$ an indicator variable taking the value of 1 if the observation belongs to the coral region and 0 otherwise, and $x_1 x_2$ is the interaction term. In the model above, the parameter $\beta_2$ allows us to test for differences in intercepts and $\beta_3$ for differences in slopes in the two regression lines.

## RESULTS

### Latitudinal diversity gradients

The association between latitude and diversity of shallow-living cephalopods on the continental shelves of the western (WA) and eastern Atlantic (EA) is shown in Fig. 1. After accounting for the positive autocorrelation in the residuals there was a significant curvilinear association between the two variables in both Atlantic coasts (Tables 1 & 2). The negative coefficient associated with the quadratic component indicated that species richness is smaller at the poles and higher at lower latitudes. Though it corroborated the current paradigm (negative association between taxonomic richness and latitude), there were other interesting features. The most salient was the asymmetric diversity pattern with the peak occurring at north tropical (in WA) and temperate (in EA) latitudes rather than at the equator. Also, the two north Atlantic diversity profiles were noticeably different from each other due to the greater gradient steepness in WA, from subtropical to subarctic waters, related to the striking lower diversity of sepiolids, neritic octopods and absence of sepiids. The diversity peak at 40° N in EA was partially due to the contribution of endemic sepiolid fauna of the Mediterranean Sea (30–45° N). Another notable difference between the two Atlantic coasts is the octopod diversity.
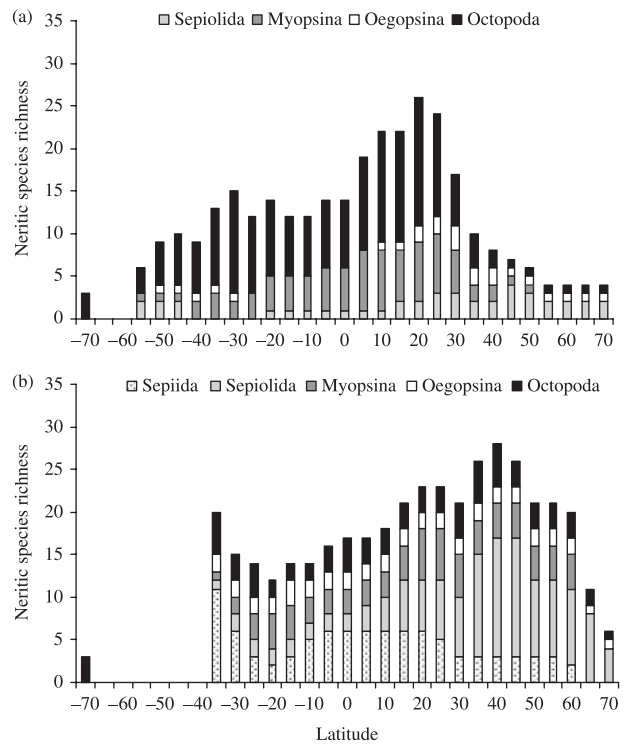


Figure 1 Latitudinal diversity gradient of neritic cephalopods on the western (a) and Eastern (b) Atlantic. Species richness (the number of species) was used as the measure of diversity and determined as the sum of all species whose ranges crossed a given 5° of latitude band.
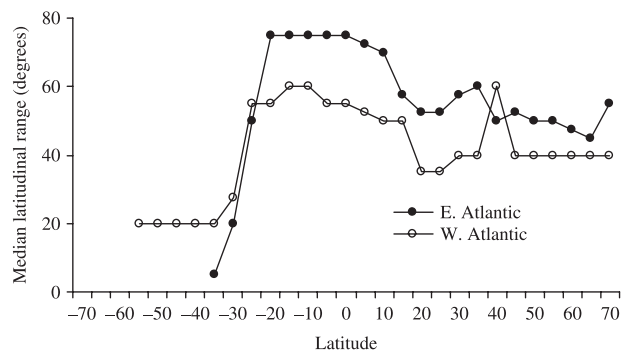


Figure 2 Median latitudinal ranges of western and eastern Atlantic neritic cephalopods (based on all species ranges that intersect each particular bin).

The order Octopoda represents almost 60% of the species richness in WA, while in EA it only represents 13%.

### Rapoport's latitudinal and bathymetric rules

When median latitudinal ranges of WA and EA neritic cephalopods at each latitudinal bin were determined (Fig. 2), it was evident that the size of distributional ranges of the species does not decrease towards the equator, which may imply that Rapoport's

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**Table 1** Relationships between species richness and latitude, sea surface temperature (SST), net primary productivity (NPP) and continental shelf area in the western Atlantic Ocean. The columns on the left give estimates without taking into consideration the correlation structure in the data. The columns on the right give the same information but after the autocorrelation is taken into account in the estimation of the parameters. The Akaike information criterion (AIC) is also given, with smaller values indicating a better fit. Restricted maximum likelihood was used to estimate the parameters of each of the models.

| | No autocorrelation in model | | | | | Autocorrelation in model | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Coefficient | $t$-ratio | $P$-value | Total $R^2$ | AIC | Coefficient | $t$-ratio | $P$-value | Total $R^2$ | AIC |
| **Latitude** | | | | | | | | | | |
| Latitude | −0.04 | −1.62 | 0.1198 | 62.71% | 149.80 | −0.03 | −0.76 | 0.4579 | 87.40% | 126.86 |
| Latitude$^2$ | −0.00 | −6.01* | < 0.0001 | | | −0.00 | −3.68* | 0.0014 | | |
| AR(1) | | | | | | 1.09 | 5.56* | < 0.0001 | | |
| AR(2) | | | | | | −0.45 | −2.28* | 0.0329 | | |
| **Sea surface temperature** | | | | | | | | | | |
| SST | 0.55 | 7.62* | < 0.0001 | 70.75% | 141.48 | 0.52 | 4.53* | 0.0002 | 86.38% | 126.48 |
| AR(1) | | | | | | 0.91 | 4.58* | 0.0001 | | |
| AR(2) | | | | | | −0.37 | −1.87† | 0.0753 | | |
| **Net primary productivity** | | | | | | | | | | |
| NPP | 0.01 | 1.53 | 0.1396 | 8.87% | 171.03 | 0.01 | 2.36* | 0.0274 | 86.91% | 126.90 |
| AR(1) | | | | | | 1.39 | 7.88* | < 0.0001 | | |
| AR(2) | | | | | | −0.56 | −3.10* | 0.0053 | | |
| **Area** | | | | | | | | | | |
| Area | −0.00 | −1.91† | 0.0690 | 13.66% | 162.48 | 0.00 | 0.64 | 0.5315 | 82.93% | 128.07 |
| AR(1) | | | | | | 1.30 | 6.66* | < 0.0001 | | |
| AR(2) | | | | | | −0.41 | 2.22* | 0.0374 | | |

*Indicate statistical significance at the 5% level of significance.
†Indicate statistical significance at the 10% level of significance.
AR refers to first-order (AR(1)) and second-order (AR(2)) autoregressive models.

**Table 2** Relationships between species richness and latitude, sea surface temperature (SST), net primary productivity (NPP) and continental shelf area in eastern Atlantic Ocean. The columns on the left give estimates without taking into consideration the correlation structure in the data. The columns on the right give the same information but after the autocorrelation is taken into account in the estimation of the parameters. The Akaike information criterion (AIC) is also given, with smaller values indicating a better fit. Restricted maximum likelihood was used to estimate the parameters of each of the models.

| | No autocorrelation in model | | | | | Autocorrelation in model | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Coefficient | $t$-ratio | $P$-value | Total $R^2$ | AIC | Coefficient | $t$-ratio | $P$-value | Total $R^2$ | AIC |
| **Latitude** | | | | | | | | | | |
| Latitude | 0.03 | 1.01 | 0.3263 | 36.73% | 132.85 | −0.01 | −0.31 | 0.7583 | 65.66% | 121.78 |
| Latitude$^2$ | −0.00 | −3.16* | 0.0051 | | | −0.00 | −2.42* | 0.0261 | | |
| AR(1) | | | | | | 0.56 | 2.86* | 0.0104 | | |
| **Sea surface temperature** | | | | | | | | | | |
| SST | 0.17 | 0.89 | 0.3826 | 33.71% | 133.87 | 0.38 | 1.66 | 0.1136 | 78.94% | 111.68 |
| SST$^2$ | −0.07 | −2.42* | 0.0259 | | | −0.08 | −2.93* | 0.0090 | | |
| AR(1) | | | | | | 0.80 | 5.70* | < 0.0001 | | |
| **Net primary productivity†** | | | | | | | | | | |
| NPP | −0.01 | −3.56* | 0.0023 | 50.81% | 115.82 | | | | | |
| NPP$^2$ | 0.00 | 4.00* | 0.0008 | | | | | | | |
| **Area** | | | | | | | | | | |
| Ln(Area) | 2.14 | 2.87* | 0.0097 | 30.29% | 121.14 | 1.48 | 1.62 | 0.1237 | 54.48% | 114.45 |
| AR(1) | | | | | | 0.48 | 2.35* | 0.0304 | | |

*Indicates statistical significance at the 5% level of significance.
†Excluding latitude 70° N.
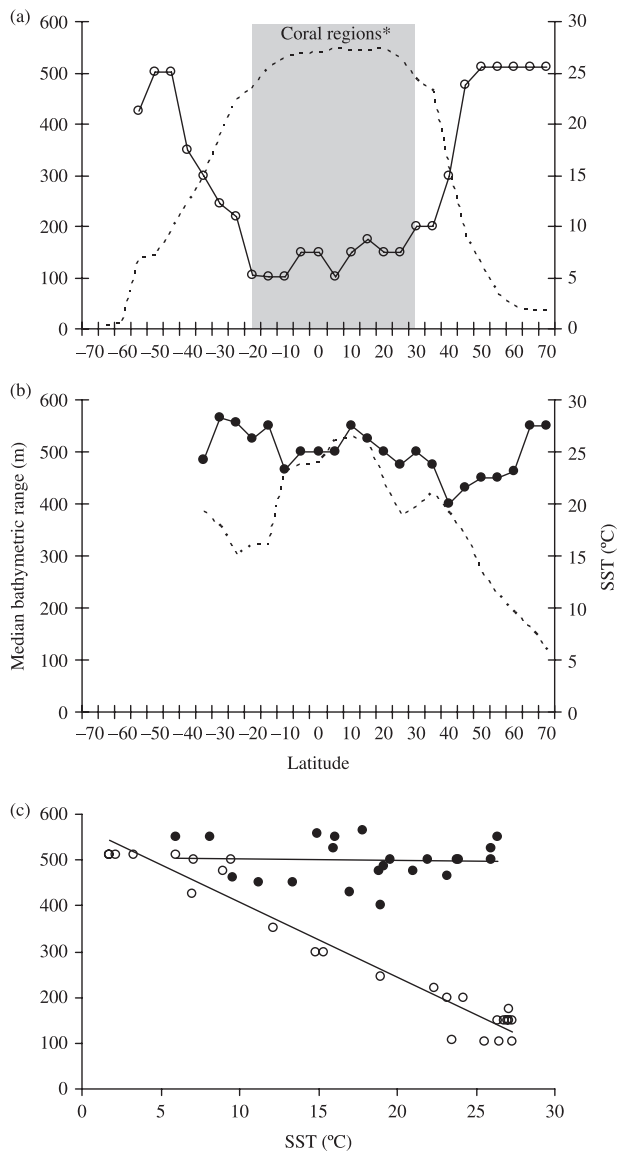AR refers to first-order (AR(1)) and second-order (AR(2)) autoregressive models.

Figure 3 (a), (b) Latitudinal gradients of sea surface temperature (SST, °C, broken line) and bathymetric ranges (m) of neritic cephalopods in the western (W, open circles) and eastern (E, closed circles) Atlantic Ocean. (c) Linear relationships between bathymetric ranges and SST (W: $r^2 = 0.95$; $P < 0.0001$; E: $r^2 = 0.00$; $P > 0.05$). Since autocorrelation was not taken into account, the statistics are only used for comparative purposes. Coral regions* (grey zone) are from the Florida to Abrolhos region (Brazil) latitudes.

latitudinal rule cannot explain the LGSR in Figure 1. However, this conclusion would be premature if bathymetry, a key component in marine distributions, were not tested. Stevens (1996) verified that Rapoport's rule can be generalized to any gradient existing in nature, such as altitude and depth. When both latitude and depth are included in the analysis, the western neritic cephalopod fauna increases its median bathymetric range size with increasing latitude, and it is strongly associated with the SST gradient and the extension of coral reef regions (Fig. 3). Nevertheless, Rapoport's bathymetric rule was not observed for the EA neritic fauna.

**Table 3** Analysis of covariance between species richness and area in latitudes where coral habitats are found (latitudes –20 to 30) and the poles (all others) in the western Atlantic Ocean.

| Analysis of covariance | Coefficient | *t*-ratios | *P*-value | Total $R^2$ | AIC |
|---|---|---|---|---|---|
| Area | −0.00 | −4.50* | 0.0002 | 88.37% | 116.37 |
| Coral | −1.05 | −0.62 | 0.5410 | | |
| Interaction term : Area × Coral | 0.00 | 7.39* | < 0.0001 | | |

*Indicates statistical significance at the 5% level of significance.

### Ambient energy, area and productivity hypotheses

In both Atlantic coasts, SST showed a significant relationship with neritic diversity. The relationship was linear in WA (Fig. 4d, Table 1), especially outside the tropical coral reef regions, and curvilinear in the EA (Fig. 4d, Table 2), where the highest values of diversity were found at intermediate temperatures. Since the residuals were positively autocorrelated, the dependence structure was modelled with an autoregressive process of order 2 (AR(2)) for the WA and of order 1 for the EA (Tables 1 & 2). Although the strength of association between diversity and SST decreased in WA (*t* ratio of 4.53 vs. 7.62), the results were still significant in both margins. SST explains 86% and 79% of the variance in species richness in WA and EA, respectively.

The relationship between continental shelf area and diversity was quite distinct between Atlantic margins. While significant and curvilinear in EA (Fig. 4c, Table 2), it was non-significant in WA (Table 1). Yet, by subdividing the western analysis into two distinct regions, outside and within the latitudinal extent of coral reef regions [from Florida (30° N) to the Abrolhos region in Brazil (20° S)], important spatial patterns arose (Fig. 4c). By fitting an ANCOVA (Table 3), the coefficient associated with area indicated that the association between diversity and area towards the poles was negative (area increased and species richness decreased). The coefficient associated with the variable labelled 'Coral' indicated that the intercepts of the two regression equations did not differ ($P = 0.54$). There was a significant interaction term indicating that the slopes of the two regression lines were different. The slope of the regression line associated with the coral regions was 0.00003 (= −0.00001 + 0.00004) indicating that in the latitudes –20 to 30, when area increases, species richness also increases.

After accounting for the dependency in the data with an autoregressive process of order two, NPP was significantly associated with species richness in WA but the association was not as strong as the associations of the other variables. A *t*-value of 2.36 with an associated *P*-value of 0.02 (Table 1) indicated a significant positive association between the variables. In the EA, there was no need of correcting for the dependence in the observations, and a significant polynomial trend was observed (Table 2).

We also constructed multiple regression models that included all the environmental variables (Table 4). In the WA, after adjusting
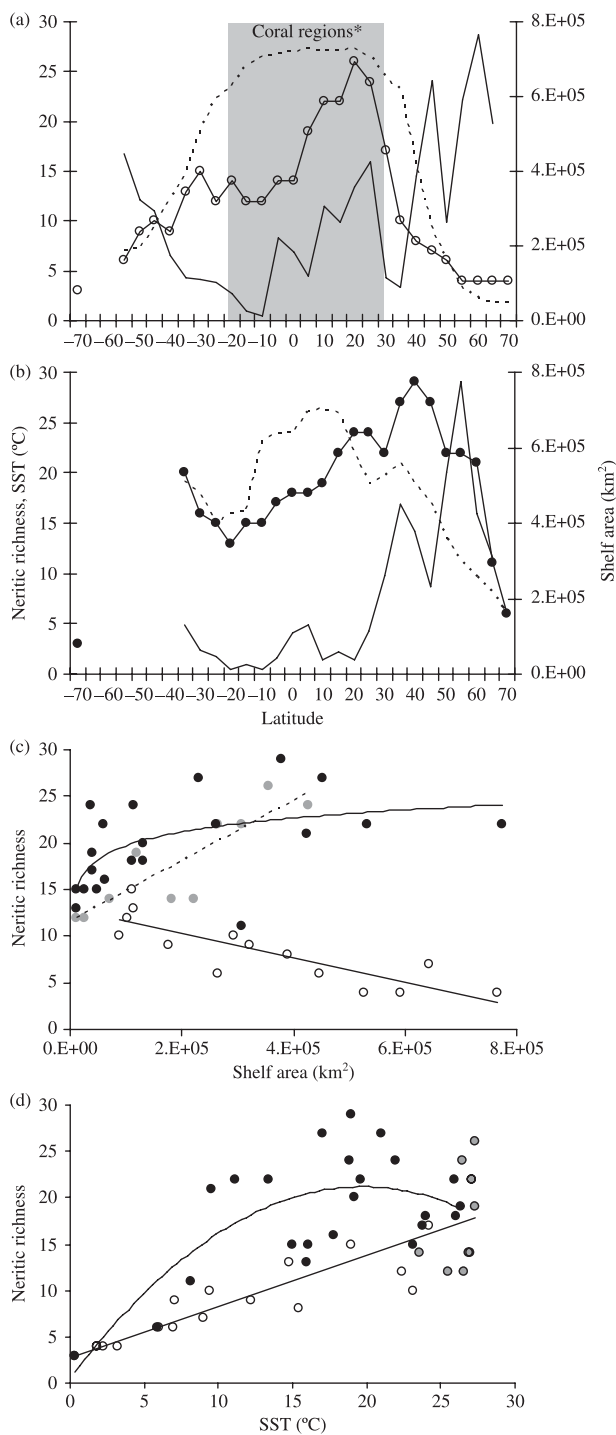
**Figure 4** (a), (b) Latitudinal gradients of shelf area (km²; solid line), sea surface temperature (SST, °C, broken line) and neritic species richness in the western (W, open circles) and eastern (E, closed circles) Atlantic Ocean. (c) Relationship between diversity and shelf area (W non-coral regions: $r^2 = 0.69$; $P < 0.001$; W coral regions: $r^2 = 0.73$; $P < 0.001$; E: $r^2 = 0.30$; $P < 0.05$). (d) Relationship between neritic diversity and SST (all W: $r^2 = 0.71$; $P < 0.0001$; only W coral regions: $r^2 = 0.18$; $P > 0.05$; E: $r^2 = 0.54$; $P < 0.01$). Since autocorrelation was not taken into account, the statistics are only used for comparative purposes. Coral regions* (grey zone) are from the Florida to Abrolhos region (Brazil) latitudes. Filled grey circles in (c) and (d) indicate WA (coral regions).

**Table 4** Models assessing the importance of sea surface temperature (SST), net primary productivity (NPP) and area in predicting species richness in the western (Models 1 and 2) and eastern Atlantic (Models 3 and 4).

| | Coefficient | *t*-ratios | *P*-value | Total $R^2$ | AIC |
|---|---|---|---|---|---|
| Western Atlantic | Model 1 (autocorrelation in model) | | | | |
| SST | 0.59 | 6.04* | < 0.0001 | 91.25% | 114.89 |
| NPP | 0.01 | 3.56* | 0.0021 | | |
| Area | 0.00 | 2.02 | 0.0579 | | |
| AR(1) | 1.08 | 6.23* | < 0.0001 | | |
| AR(2) | −0.64 | −3.73* | 0.0014 | | |
| | Model 2 (Interaction term in model) | | | | |
| SST | 0.13 | 1.28 | 0.2165 | 92.68% | 106.79 |
| NPP | 0.00 | 3.31* | 0.0035 | | |
| Area | −0.00 | −1.39 | 0.1811 | | |
| Interaction term : Area × Coral | 0.00 | 6.35* | < 0.0001 | | |
| Eastern Atlantic | Model 3 | | | | |
| SST | 0.40 | 3.40* | 0.0040 | 80.33% | 102.57 |
| SST² | −0.05 | −2.61* | 0.0196 | | |
| NPP | −0.00 | −0.85 | 0.4087 | | |
| NPP² | 0.00 | 2.75* | 0.0148 | | |
| Log(Area) | 2.84 | 3.68* | 0.0022 | | |
| | Model 4 | | | | |
| Latitude | 0.11 | 3.90* | 0.0013 | 93.59% | 96.76 |
| SST | 0.52 | 4.95* | 0.0001 | | |
| SST² | −0.10 | −5.43* | < 0.0001 | | |
| Log(Area) | 1.51 | 2.37* | 0.0307 | | |

*indicate statistical significance at the 5% level of significance.
AR refers to first-order (AR(1)) and second-order (AR(2)) autoregressive models.

for autocorrelation in the data, the most important variable in explaining the variation in species richness was SST, followed by NPP and lastly by area (Model 1). Interestingly, when we allowed area to have different associations with diversity depending on the region (within and outside coral regions), then area became the most important covariate in the modelling of diversity, followed by NPP (Model 2). It is important to note that the interaction model did not display dependency due to the fact that the positive autocorrelation of species richness was accounted for by area. This explains the non-inclusion of auto-regressive components in the interaction model. Moreover, when the interaction term for area was included in the model, SST became non-significant. Latitude and its square were not included in either of the models since they were highly non-significant in the presence of all other variables. Of the two models given above, the interaction model (Model 2) gave the smaller AIC, indicating a closer fit to the observed species richness, and explained 93% of the variance in diversity.

In EA, when all the variables and the associated quadratic components were considered as independent variables, there was concern with the level of collinearity as indicated by three variance inflation factors (VIF) being larger than 10. Two of these large VIFs were associated with the linear and quadratic

components on latitude. In an attempt to remove collinearity, latitude and its quadratic component were excluded from the analysis (Model 3). It can then be concluded that the most important variable in explaining the variation in the EA diversity is the second-order polynomial in SST (with a contribution to the sum of squares of $112.52 = 70.76 + 41.76$), followed by log(Area) (with a contribution of 83.07) and lastly by the second-order polynomial in NPP (with a contribution of $50.82 = 4.42 + 46.40$). The individual variable that contributed the most to the sum of squares associated with model was log(Area). No autocorrelation was present in the residuals, indicating that the correlation structure in diversity was accounted for by the variables in the model that were also highly correlated. An alternative (Model 4) excluded the quadratic component on latitude and the linear and quadratic components on NPP to remove the collinearity among the independent variables. In assessing the importance of the contributions of the rest of the variables it can be concluded that the polynomial in SST was the most important variable in explaining the variability in diversity (a contribution of $258.24 = 117.39 + 140.85$), followed by latitude (with a contribution of 72.84) and lastly log(Area) (with a contribution of 26.86). Note the reduction in AIC and the increment in the total $R$-square from Model 3 to Model 4 (80% to 94%).

## DISCUSSION

### Historical biogeography

To understand the contemporary LGSR of cephalopods it is important not only to relate them to contemporary environmental gradients but also to evolutionary processes that have occurred throughout geological time. For instance, the extinction of cuttlefish (sepiids) in WA is thought to have occurred in the Caribbean province as a consequence of the sea surface cooling in the WA equatorial region during the Eocene to Oligocene transition (Emiliani, 1966). This hypothesis is corroborated by the exclusive presence of sepiids in post-Eocene strata of the EA (Büllow-Trummer, 1920, quoted in Khromov, 1998). Another key historical event for cephalopod biogeography occurred around 5 Ma, when the North and South American, and Caribbean plates converged, and the rise of the Central American Isthmus restricted the exchange of water between the Atlantic and Pacific oceans (Haug & Tiedemann, 1998). The eventual closure of the Central American Seaway, around 1.9 Ma, may have led to the formation of geographically isolated octopod populations by vicariance and then to allopatric speciation in the tropical WA (Voight, 1988), where higher diversity is currently found (Fig. 1). In fact, many faunal turnover events (i.e. the evolutionary appearance and disappearance of a large proportion of a biota) took place in the Late Pliocene in the WA due to a decline in nutrients (and so in marine productivity) associated with closure of the Central American Seaway and change of ocean circulation (Allmon, 2001). Yet, the emergence of Central American Isthmus also set the stage for glaciation in the Northern Hemisphere at 2.7 Ma (Haug *et al.*, 1999). In fact, one of the most dominant

features of the Earth's past climate are the ice ages in the Quaternary period, which involve repeated global cooling and expansion of the continental and polar ice sheets and mountain glaciers. Average temperatures seem to have changed by 7–15 °C over 5–10 years and lasted for periods of hundreds of years (Hewitt, 1999) and the sea levels fluctuated dramatically on both global and regional scales, strongly affecting the distribution and diversity of biotas (Brown & Lomolino, 1998). These ice age events are believed to have caused mass species extinctions in the WA as far south as Florida and the Bahamas and confined most species in the Caribbean region (Stanley, 1986). During the most recent glacial maximum (LGM) in North America, the ice sheets extended to about 42° N (Riggs *et al.*, 1996). Under this faunal turnover scenario, the shallow-living cephalopod species may also have been subject to localized extinction by Pleistocene glaciation or forced from their typical habitat to refugia beyond the southern-most extent of the glaciers at Long Island Sound. Extinction or geographical range contraction seem coherent with the lower diversity in WA from 35° N towards the pole (Fig. 1), and contrasts with the EA where the ice sheets appear to have extended south to 52° N in the LGM and caused fewer extinctions and displacements (Vermeij, 1991). The abrupt decrease in western diversity is also noticeably different from the Southern Hemisphere gradient and contradicts Hillebrand's (2004) concept of common gradient strength and slope between hemispheres. In fact, the changes in the extension of the ice sheets in the Southern Hemisphere during the Cenozoic were much smaller in comparison with the Northern Hemisphere (see Fig. 1 in Mercer, 1983). As a result, the effects of the glaciations on the south WA fauna were far less severe. In the Southern Ocean, however, the continental shelves around Antarctica were covered by ice over the last 30 Myr (Barrett *et al.*, 1989), which led to the reduction of available coastal habitats and the loss of some taxonomic groups. At present, although some marine fauna are diverse and abundant in shallow Antarctic waters (e.g. sponges, bryozoans, polychaetes, amphipods and isopods; Clarke & Crame, 1989; Clarke, 1992), with numbers comparable to lower latitudes, other groups have markedly lower diversity, namely teleost fish, crustacean decapods and bivalve, gastropod (Clarke & Crame, 1992) and cephalopod molluscs (restricted exclusively to the order Octopoda, Fig. 1). The loss of some and the success of others seems to be the effect of historical contingency (Gould, 1989).

In the EA, the major historical event impinging on cephalopod neritic diversity was closure of the Mediterranean Sea during the 'Messinian salinity crisis' into an isolated hyperhaline lake about 5.5 Ma ('Mare Lago'), with the consequent isolation, extinction of stenohaline species and arise of endemism (Taviani, 2002). Therefore, it becomes evident that historical geological and climatic events influence the contemporary latitudinal gradients of cephalopod diversity in the Atlantic Ocean.

### Latitudinal-diversity gradients

The neritic cephalopod diversity is distributed heterogeneously across the Atlantic coasts, with the north-western tropical

and north-eastern temperate coastal areas peaking in species richness, while the Arctic and Southern oceans clearly show diminished biological variation. As already noted above, large-scale historical events in both WA and EA have a major influence on the location of the contemporary peaks of diversity. Contrary to the theory that species boundaries become more densely packed towards the equator ('Rapoport's latitudinal rule'; Stevens, 1989), there was no evidence for a reduction in neritic cephalopod ranges at lower latitudes (Fig. 3). When Stevens (1989) formulated this rule he argued that the exceptions occurred in species that also did not show LGRS (e.g. migratory birds). Also, he stated that Rapoport's phenomenon has a climate-based explanation, with tropical organisms having narrower climatic tolerances in opposition to broad tolerance of organisms inhabiting high latitudes where seasonal variation is greater (known as 'the climatic hypothesis' or 'the seasonal variability hypothesis'; Stevens, 1996). However, because tropics are the largest of the world's major bioclimatic zones, it is not surprising to find that cephalopod tropical clades are able to occupy larger areas than lower-latitude ones (the largest median latitudinal ranges occur between 20° S and 20° N; Fig. 2). Species with planktonic life stages, such as many cephalopods, tend to have wider geographical distributions than species lacking such stages (Vermeij et al., 1990), and these differences in dispersal ability may indeed explain the coexistence of clades with narrow and large latitudinal ranges in the tropics (Rohde, 1998). It has also been argued that the Rapoport's rule is a local phenomenon that cannot be generalized, because it is found with more consistency at high latitudes in the Northern Hemisphere (above approximately 30–40° N), where the extinction of species adapted to narrow temperature ranges has occurred during the glaciations (Brown, 1995; Rohde, 1996; Gaston et al., 1998). Interestingly, when we combined the depth component with latitude a strong Rapoport effect was observed in WA. Though the 'bathymetric Rapoport's rule' (a species increase its median bathymetric range size with increasing latitude) holds true for neritic WA fauna, it does not for EA, which suggests that this effect cannot be dismissed but cannot be generalized either as a rule. The increased depth ranges in north-western neritic fauna may be explained by the conditions of Quaternary glaciations, with the ice sheets preventing the existence of low-tolerance, shallow-living stenobathic species and favouring species capable of living in a wide range of depths (eurybathic species). This 'differential extinction hypothesis' (see Brown, 1995) is supported by the bathymetric distributions of cephalopod species living in the non-glaciated eastern shelves but, on the other hand, is refuted by the existence of the exact same Rapoport phenomenon in the Southern Hemisphere, where the effects of glaciation were far less severe (as pointed out above). Alternatively, the loss of shallow coral reef habitats in high latitudes has been put forward to explain the Rapoport effect in shallow-living fish (Smith & Gaines, 2003). Our findings corroborate this explanation in two ways. First, the narrow bathymetric ranges of neritic cephalopods follow closely the latitudinal extent of the shallow Caribbean and Brazilian coral faunal regions (isolated due to enormous outflow of the Amazon riverine system) with the inflection points

coincidental with two major biogeographical boundaries (noticed above). These boundaries definitely have an important restraining impact on coral reef biogeography due to the significant decrease in SST (Fig. 3) and restricted light penetration associated with water turbidity (especially in the Southern Hemisphere). Second, the non-occurrence of a Rapoport effect in EA is probably associated with the absence of these shallow tropical habitats and the greater influence of upwelling systems. In fact, the dynamics of these coastal ecosystems (e.g. seasonal variations in enrichment and mixing processes; upwelling-driven nearshore hypoxia) may explain why the majority of the EA neritic species are not strictly restricted to the continental shelves and overlaps to deeper slope waters (median bathymetric range greater than 400 m along the entire latitudinal gradient). Indeed, the increased environmental dynamics and broader ecological tolerance (i.e. non-specialization) of neritic eastern fauna seem to be causally linked to: (1) the lack of association between bathymetric range and SST (Fig. 3c), (2) the weaker and curvilinear species–temperature relationship (Fig. 4d, Table 2), and (3) the lower species turnovers along the EA subtropical and tropical regions (data not shown). These assumptions are supported by quite the opposite scenario in WA, where SST is the most important environmental predictor for LGSR (Model 1, Table 4), especially in extratropical latitudes (Fig. 4c) and for bathymetric ranges (Fig. 3c). Western tropical regions contain more species because increased energy availability (and stability) promotes the occurrence of more viable populations of specialized species (e.g. shallow-living reef octopod and loliginid fauna). Though higher levels of solar radiation (and therefore higher temperatures) may induce faster evolutionary rates due to faster biochemical processes (Allen et al., 2006), mutation rates (Gillooly et al., 2005) and shorter generation times ('evolutionary rates hypothesis'; Rohde, 1992), eastern tropical coasts do not present higher cephalopod diversities than temperate ones (Fig. 1b), which clearly demonstrates that diversity patterns in EA are not solely governed by temperature. In Model 3 (Table 4), shelf area contributed the most to the sum of squares associated with the model. In fact, the EA shelf area increases towards northern temperate latitudes and, consequently, a positive correlation with cephalopod richness is found (Fig. 4c). Larger shelf areas should imply higher habitat diversity, higher colonization and speciation rates and lower extinction rates ('geographical area hypothesis'; Rosenzweig, 1995). Yet, since the greater Patagonia and Newfoundland–Labrador shelf areas in WA did not favour higher diversification rates compared to the tropical regions, our findings seem at a first glance contradictory in relation to this already controversial concept (see Rohde, 1998, and Rosenzweig & Sandlin, 1997). However, by predicting that the complexity and diversity of coral reef regions have a determinant influence on the neritic cephalopod biogeography in WA (Johnson et al., 2007) and by restricting the analysis to their latitudinal extent, we observe that the higher tropical levels of diversity are indeed closely associated with the greater shelf areas in the tropics (grey circles in Fig. 4c) and higher coverage of reef habitats. While SST can explain the majority of the variance outside the tropics (< 25 °C), it fails within these regions (grey circles in Fig. 4d)

*to date*. FAO species catalogue for fishery purposes, N4, Vol. 1. FAO, Rome.

Johnson, K.G., Todd, J.A. & Jackson, J.B.C. (2007) Coral reef development drives molluscan diversity increase at local and regional scales in the late Neogene and Quaternary of the southwestern Caribbean. *Paleobiology*, **33**, 24–52.

Khromov, D.N. (1998) Distribution patterns of Sepiidae. *Smithsonian Contributions to Zoology*, **586**, 191–206.

Lambshead, P.J.D., Tietjen, J., Ferraro, T. & Jensen, P. (2000) Latitudinal diversity gradients in the deep sea with special reference to North Atlantic nematodes. *Marine Ecology Progress Series*, **194**, 159–167.

Macpherson, E. (2002) Large-scale species-richness gradients in the Atlantic Ocean. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 1715–1720.

Mercer, J.H. (1983) Cenozoic glaciation in the Southern Hemisphere. *Annual Review of Earth Planetary Science*, **11**, 99–132.

Mokievsky, V. & Azovsky, A. (2002) Re-evaluation of species diversity patterns of free-living marine nematodes. *Marine Ecology Progress Series*, **238**, 101–108

Oregon State University (2006) *Ocean productivity*. http://web.science.oregonstate.edu/ocean.productivity/ (acessed 10 May 2007).

Rex, M.A., Stuart, C.T. & Coyne, G. (2000) Latitudinal gradients of species richness in the deep-sea benthos of the North Atlantic. *Proceedings of the National Academy of Sciences USA*, **97**, 4082–4085.

Rex, M.A., Crame, J.A., Stuart, C.T. & Clarke, A. (2005) Large-scale biogeographic patterns in marine molluscs: a confluence of history and productivity? *Ecology*, **86**, 2288–2297.

Riggs, S.R., Snyder, S.W., Hine, A.C. & Mearns, D.L. (1996) Hardbottom morphology and relationship to the geologic framework: mid-Atlantic continental shelf. *Journal of Sediment Research*, **66**, 830–846.

Rohde, K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, **65**, 514–527.

Rohde, K. (1996) Rapoport's rule is a local phenomenon and cannot explain latitudinal gradients in species diversity. *Biodiversity Letters*, **3**, 10–13.

Rohde, K. (1998) Latitudinal gradients in species diversity. Area matters, but how much? *Oikos*, **82**, 184–190.

Rosa, R. & Sousa Reis, C. (2004) *Cephalopods of the Portuguese coast*. Prémio do Mar Rei D. Carlos, Câmara Municipal de Cascais, Cascais [in Portuguese].

Rosa, R., Dierssen, H.M., Gonzalez, L. & Seibel, B.A. (2008) Large-scale diversity patterns of cephalopods in the Atlantic open ocean and deep-sea. *Ecology*. Accepted pending revision.

Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.

Rosenzweig, M.L. & Sandlin, E.A. (1997) Species diversity and latitudes: listening to area's signal. *Oikos*, **80**, 172–176.

Roy, K., Jablonski, D., Valentine, J.W. & Rosenberg, G. (1998) Marine latitudinal diversity gradients: tests of causal hypotheses. *Proceedings of the National Academy of Sciences USA*, **95**, 3699–3702.

Roy, K., Jablonski, D. & Valentine, J.W. (2000) Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 293–299.

Smith, K.F. & Gaines, S.D. (2003) Rapoport's bathymetric rule and the latitudinal species diversity gradient for Northeast Pacific fishes and Northwest Atlantic gastropods: evidence against a causal link. *Journal of Biogeography*, **30**, 1153–1159.

Stanley, S.M. (1986) Anatomy of a regional mass extinction: Plio-Pleistocene decimation of the western Atlantic bivalve fauna. *Palaios*, **1**, 17–36.

Steele, D.H. (1988) Latitudinal variations in body size and species diversity in marine decapod crustaceans of the continental shelf. *International Review of Hydrobiology*, **73**, 235–246.

Stevens, G.C. (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist*, **133**, 240–256.

Stevens, G.C. (1996) Extending Rapoport's rule to pacific marine fishes. *Journal of Biogeography*, **23**, 149–154.

Stevens, R.D. (2006) Historical processes enhance patterns of diversity along latitudinal gradients. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 2283–2289.

Taviani, M. (2002) The Mediterranean benthos from late Miocene up to present: ten million years of dramatic climatic and geologic vicissitudes. *Biologia Marina Mediterranea*, **9**, 445–463.

Turner, J.R.G., Gatehouse, C.M. & Corey, C.A. (1987) Does solar energy control organic diversity? Butterflies, moths and the British climate. *Oikos*, **48**, 195–205.

USDC (2006) *2-minute gridded global relief data* (ETOPO2v2). US Department of Commerce, National Oceanic and Atmospheric Administration, National Geophysical Data Center. http://www.ngdc.noaa.gov/mgg/fliers/06mgg01.html (accessed 10 May 2007).

Vermeij, G.J. (1991) Anatomy of an invasion: the trans-Arctic interchange. *Paleobiology*, **17**, 281–307.

Vermeij, G.J., Palmer, A.R. & Lindberg, D.R. (1990) Range limits and dispersal of molluscs in the Aleutian Islands, Alaska. *Veliger*, **33**, 346–354.

Voight, J.R. (1988) Trans-Panamanian geminate octopods (Mollusca: Octopoda). *Malacologia*, **29**, 289–294.

Voss, N.A., Vecchione, M., Toll, R.B. & Sweeney, M.J. (1998) Systematics and biogeography of cephalopods. *Smithsonian Contributions to Zoology*, **586**, 1–599.

Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution*, **19**, 639–644.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution and Systematics*, **34**, 273–309.

Wright, D.H. (1983) Species–energy theory: an extension of species–area theory. *Oikos*, **41**, 496–506.

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