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LARGE-SCALE DIVERSITY PATTERNS OF CEPHALOPODS IN THE ATLANTIC OPEN OCEAN AND DEEP SEA

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Abstract. Although the oceans cover 70% of the Earth's surface and the open ocean is by far the largest ecosystem on the planet, our knowledge regarding diversity patterns of pelagic fauna is very scarce. Here, we examine large-scale latitudinal and depth-related patterns of pelagic cephalopod richness in the Atlantic Ocean in relation to ambient thermal and productive energy availability. Diversity, across 17 biogeochemical regions in the open ocean, does not decline monotonically with latitude, but is positively correlated to the availability of oceanic resources. Mean net primary productivity, determined from ocean color satellite imagery, explains 37% of the variance in species richness. Outside the poles, the range in NPP explains over 40% of the variability. This suggests that cephalopods are well adapted to the spatial patchiness and seasonality of open-ocean resources. Pelagic richness is also correlated to sea surface temperature, with maximum richness occurring around 15°C and decreasing with both colder and warmer temperatures. Both pelagic and benthos-associated diversities decline sharply from sub-littoral and epipelagic regions to the slope and bathypelagic habitats and then steadily to abyssal depths. Thus, higher energy availability at shallow depths seems to promote diversification rates. This strong depth-related trend in diversity also emphasizes the greater influence of the sharp vertical thermal gradient than the smoother and more seasonal horizontal (latitudinal) one on marine diversity.

Key words: cephalopods; deep-sea ecology; diversity patterns; open ocean ecology; species–energy relationships.

INTRODUCTION

Oceans cover 70% of the Earth's surface and provide a volume of living space 168 times that of terrestrial habitats (Cohen 1994). Since life originated in and was restricted to the oceans for the first 3 billion years of evolution, it is not surprising to see that biodiversity of higher taxa is greater in marine than in terrestrial ecosystems. Marine habitats contain 29 of the 34 metazoan phyla on the planet, including 14 phyla that are endemic (Rupert et al. 2004). However, only 12 are present in the open ocean and none of those are endemic (Pierrot-Bults 1997). This disparity highlights the evolutionary difficulties of the transition from benthos to pelagic life strategies (Angel 1993). Although richer in higher taxonomic levels, the oceanic environment is assumed to sustain much lower species diversity than terrestrial ecosystems, comprising only ~2% of the global diversity. The number of known marine taxa, about 200 000, contrasts sharply with the 12 millions species of terrestrial plants and animals (~80% are insects [Briggs 1994]). There are also markedly fewer

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species in the open ocean than in coastal regions (e.g., phytoplankton and fish diversity) and much greater diversity in the benthic than in the pelagic realm (Grassle and Maciolek 1992). Speciation is considered to be much slower in the open ocean due to the higher dispersal abilities and fewer relevant geographical barriers to gene flow (Pierrot-Bults and van der Spoel 1979, Norris 2000). However, some of these long-standing concepts may be artificially driven by the developed cryptic biodiversity in the open ocean. Molecular phylogenetic analyses suggest that the traditional species identifications based on morphological features may have greatly underestimated oceanic species richness (Bucklin 1986, Gibbs 1986, Bucklin et al. 1996, Miya and Nishida 1997).

As in coastal marine ecosystems, there is no consensus whether the most conspicuous ecological pattern on Earth, the poleward decline in diversity, is a pervasive feature in the open ocean. While some studies demonstrate that tropical regions sustain more pelagic diversity than temperate and polar regions (Bé 1977, Angel 1993, 1997, McGowan and Walker 1993, Dodge and Marshall 1994, Macpherson 2002), others show that species richness is greater at temperate latitudes (McGowan and Walker 1985, Boltovskoy et al. 1999, Rutherford et al. 1999, Brayard et al. 2005). Latitudinal gradients of

species richness (LGSR) have been relatively well examined on land for the past decades and are highly correlated with environmental energy availability (Gaston 2000, Hawkins et al. 2003, Mittelbach et al. 2007). The species–energy relationships are currently assumed to be driven by two primary mechanisms: climate and productivity. Several climate-based hypotheses have been formulated, including the "physiological tolerance hypothesis" and the "evolutionary rates hypothesis." The former states that diversity varies according to the species' tolerance to different climatic conditions (Currie et al. 2004) and the later that high-energy areas accelerate rates of evolution and speciation by shortening generation times and increasing mutation and physiological rates (Rohde 1992, Allen et al. 2002, Gillooly et al. 2005, Mittelbach et al. 2007).

The classic unimodal relationship of maximal diversity at intermediate levels of productivity was, until recently, the most widely documented pattern (Huston 1979, Tilman 1982, Rosenzweig 1995). The available evidence now shows that this hump-shaped relationship is one of many patterns (including U-shaped, positive, and negative) and that none of them predominate (Waide et al. 1999, Mittelbach et al. 2001). Furthermore, patterns are know to change under the influence of spatial scale (Chase and Leibold 2002), history of community assembly (Fukami and Morin 2003), disturbance (Kondoh 2001), and consumers (Worm et al. 2002), among others. The most cited ecological explanation for the positive relationship between productivity and diversity is the "more individuals hypothesis" (Wright 1983, Srivastava and Lawton 1998), that suggests that more productive areas can support larger populations, which lower extinction rates and promotes speciation. The way that these mechanisms may explain the broad-scale diversity patterns in the open ocean is unclear.

The three-dimensional nature of the oceans, with an average depth of 3.8 km and maximum around 11 km, set them apart from the primarily two-dimensional terrestrial ecosystems. There is no terrestrial equivalent to the extensive, cold, and dark deep-sea habitats. Its distinctiveness has many ecological implications (e.g., bioluminescence is the primary source of light and communication) and may hold the key to understanding global diversity patterns. Diversity typically shows a parabolic pattern with depth, i.e., it peaks at intermediate depths (e.g., Sanders 1968, Rex 1973, 1981, Pineda and Caswell 1998). Both in pelagic (Angel 1993, 1997) and benthic communities (especially of soft sediments), this unimodal trend is attributed to an eventual diversifying effect of the more stable nutrient input at intermediate depths, compared to scarcity of food resources in the abyss and the increased seasonality at shallower depths (Rex et al. 2005). Several other causal factors are thought to shape local deep-sea diversity, such as sediment heterogeneity, oxygen availability, deep-sea currents, and catastrophic physical disturbance

(see Levin et al. 2001). The mid-domain effect (also known as "boundary constraints model") has also been advocated. That is, an increased tendency of species ranges to overlap toward the midpoint if there is a random placement of ranges within a spatial domain (Colwell and Lees 2000). The depth-related patterns are not well understood because the data sets available are too scarce to make generalizations and do not clearly show whether the bathyal depths have higher and lower diversity than coastal systems (Gray 2001).

Cephalopod mollusks are found from polar to equatorial oceanic regions and from the surface to 5000 m depth. Here we examine the latitudinal and bathymetric gradients of cephalopod species richness in the Atlantic open ocean and deep sea. We test both climate and productivity hypotheses to explain the large-scale spatial patterns obtained.

METHODS

The diversity and geographical ranges of pelagic and deep-sea cephalopod off the Atlantic Ocean were investigated by means of an exhaustive survey of primary literature, expedition reports and on-line databases. A more detailed description of data sources is given in a previous study regarding coastal cephalopod diversity (Rosa et al., *in press a*). Pelagic diversity (i.e., number of species) was grouped into large faunal regions and provinces based on Backus et al. (1977; Fig. 1). This spatial approach has been already applied by Voss et al. (1998) to describe the biogeography of some pelagic squid families. Backus and collaborators carried out an extensive biogeographical study of lantern fish (myctophids) throughout the Atlantic Ocean. This group of pelagic fish accounts for much of the biomass responsible for the oceanic deep scattering layer, and plays a key role as prey for many oceanic and deep-sea cephalopods (Boyle and Rodhouse 2005; Rosa et al., *in press b*).

The depth of occurrence for each species was also recorded and divided in large-scale bathymetric ranges: littoral and sub-littoral (0–200 m), upper bathyal (200–1000 m), lower bathyal (1000–3000 m), and abyssal (3000–5000 m) for benthos-associated species and epi-(0–200 m), meso-(200–1000 m), bathy-(1000–3000 m), and abyssopelagic (3000–5000 m) for oceanic species.

Ocean net primary productivity (NPP) was estimated from the vertically generalized production model (Behrenfeld and Falkowski 1997) with a temperature-dependent description of chlorophyll-specific photosynthetic efficiency applied to satellite-derived chlorophyll and sea surface temperature from the MODIS Aqua sensor. Online *Standard Products* were downloaded as monthly, global NPP, gridded, 18-km data from November 2002 through October 2006 (data *available online*).[6] Because NPP follows a logarithmic distribu-

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[6] ⟨http://web.science.oregonstate.edu/ocean.productivity/⟩
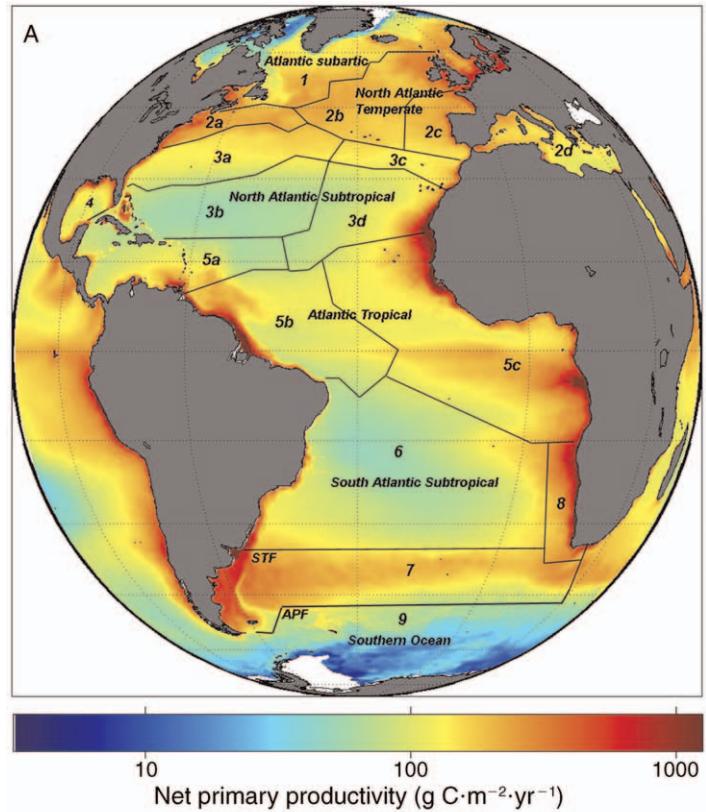
FIG. 1. (A) Zoogeographic areas used for the description of oceanic cephalopod fauna (adapted from Backus et al. 1977) and mean net primary productivity averaged over all months (NPP) in the Atlantic Ocean. (B) Mean sea surface temperature (SST) average over all months. Regions are 1, Atlantic Subarctic Province; 2, North Atlantic Temperate Region (2a, Slope water; 2b, Northern Gyre, Azores, and Britain Province; 2c, Mediterranean Outflow; 2d, Mediterranean Sea); 3, North Atlantic Subtropical Region (3a, North Sargasso Sea; 3b, South Sargasso Sea; 3c, North African Subtropical Sea; 3d, South North African Subtropical Sea); 4, Gulf of Mexico; 5, Atlantic Tropical Region (5a, Caribbean Sea and Lesser Antillean Province; 5b, Amazonian Province; 5c, Guinean-Namibian Province); 6, South Atlantic Subtropical Sea; 7, Southern Convergence (between subtropical front, STF, and Antarctic Polar Front, APF); 8, Benguela Current Coastal Province; 9, Southern Ocean.
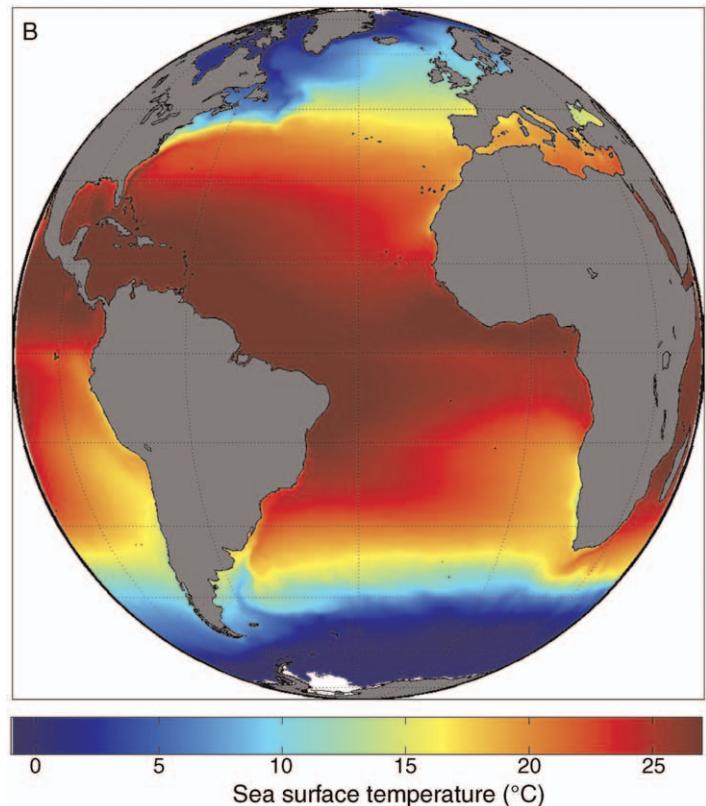
TABLE 1. Mean and ranges (difference between maximum and minimum observation from monthly mean values between November 2002 and October 2006) of satellite-derived net primary productivity (NPP) and sea surface temperature (SST), area size, and pelagic cephalopod richness (number of species) for each of zoogeographic region (for identification, see Fig. 1).

Zone	Cephalopod richness	SST(°C)		NPP (g C·m^{-2}·yr^{-1})		Area (1 × 10^6 km^2)
		Mean	Range	Mean	Range	
1	14	4.63	4.65	142.24	361.13	8.01
2a	74	14.03	14.69	223.27	307.08	1.38
2b	63	14.37	8.40	185.69	126.53	5.24
2c	70	16.36	2.80	212.77	66.07	1.20
2d	33	19.64	1.01	156.79	97.48	1.98
3a	68	22.45	7.88	124.33	294.49	3.05
3b	48	25.78	8.33	68.65	306.57	2.73
3c	61	20.72	1.89	132.98	42.11	1.45
3d	72	23.28	3.06	111.67	96.19	2.45
4	43	25.58	5.91	170.05	228.72	1.09
5a	42	27.30	13.09	107.70	116.84	2.78
5b	44	26.90	8.95	126.13	149.58	3.52
5c	77	24.95	5.70	168.12	57.31	7.28
6	47	22.33	5.20	89.75	36.60	9.56
7	80	11.21	7.34	194.19	140.22	10.74
8	84	18.41	8.46	304.48	317.54	1.72
9	22	0.51	4.68	44.61	71.40	4.62

tion, the geometric mean was calculated within each of the defined zoogeographic zones in Fig. 1. Monthly sea surface temperature (SST) was derived from MODIS Aqua imagery processed with the 4-μ nighttime algorithm. For SST data, the arithmetic mean was calculated for each of the defined regions. For this analysis, four-year average NPP and SST were calculated for each region from the monthly mean values from November 2002 through October 2006. Since adaptations to temporal variation in temperature and primary production have been implicated in theories of species diversity, we also determined the range of NPP and SST (a measure of variability in the data calculated as the difference between maximum and minimum observation during the studied period) for each oceanic region. All relationships between environmental variables and oceanic diversity were adjusted for area (km^2), i.e., area was included as a covariate in each of the models. Area was calculated as the total area of every pixels assigned to each zone in the remote sensing imagery. All environmental data and area sizes are shown in Table 1.

Assessing associations between species richness and sea surface temperature and net primary productivity, after adjusting for the effect of area, was done within the framework of general linear models. The likelihood ratio test for comparing models was used to test for spatial dependency in each of the fitted models. Most of the P values associated with the chi-square tests were around 0.10, indicating lack of spatial dependency in the residuals at the 5% level of significance. Hence, the use of general linear models in all analyses. The statistical analysis of the data was carried out in SAS (SAS Institute 2003). The GLM procedure was used to fit the general linear models and the MIXED procedure to fit the spatial models.

The goodness of fit statistics reported are the total-R^2 and the Akaike's information criterion (AIC) were

$$R_{tot}^2 = 1 - (ESS/TSS)$$

where TSS is defined as the corrected sum of squares total for the response variable and ESS is the final error sum of squares. The Alkaike information criterion (AIC) 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.

RESULTS

Patterns of diversity in open ocean

Of the 43 cephalopod families surveyed in the Atlantic Ocean, only five (12%) are found along the Atlantic continental shelves (none of them endemic), while 34 (79%) are exclusively present in the open ocean. Yet, the oceanic families tend to be less speciose. Given the difficulties of sample collection in the open ocean and the expected cryptic diversity present there, the pelagic contribution to the overall diversity may be greater than the present results indicate. The diversity is dominated by two major taxonomic groups, the sub-orders Oegopsina and Incirrina. The former is the largest group with 118 species. Of those, most are oceanic squids of the families Cranchidae, Histioteuthidae, Onychoteuthidae, Mastigoteuthidae, and Enoploteuthidae (Fig. 2). The later group consists primarily of pelagic octopuses (e.g., Argonautidae, Bolitaenidae, Tremoctopodidae, Ocythoidae, and Vitreledonellidae).
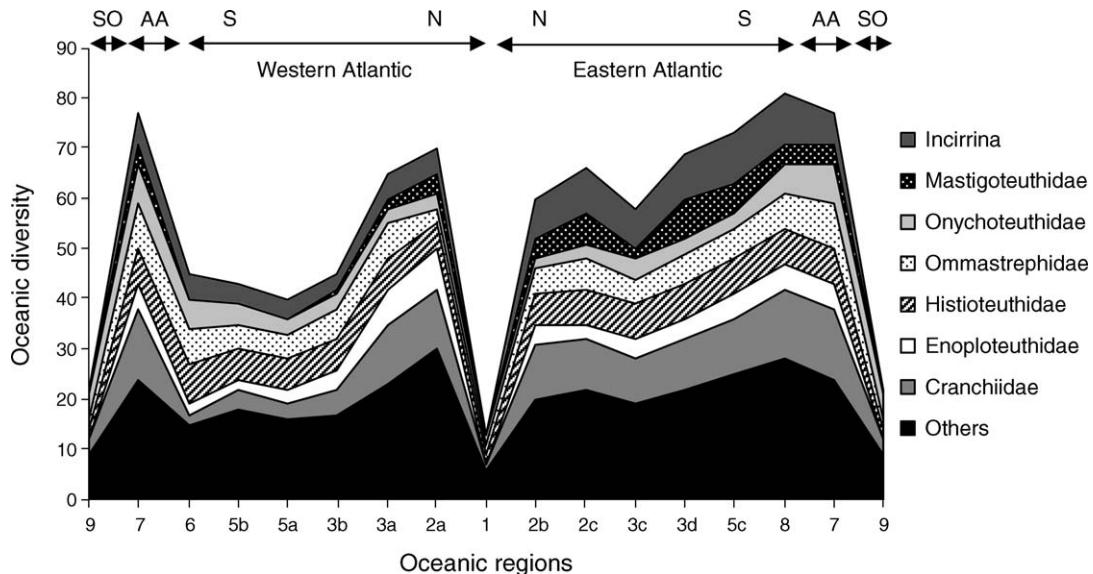
FIG. 2.   Diversity of oceanic cephalopods in the different zoogeographic regions of the Atlantic Ocean (for abbreviations, see Fig. 1). The most diverse taxonomic groups are Oegopsida (major families shown) and Octopoda Incirrina. SO, Southern Ocean; AA, amphi-atlantic zone; S, south; N, north. Note: the enclosed regions of Gulf of Mexico (zone 4, 43 species) and Mediterranean Sea (zone 2d, 33 species) are not included in the panel.

The highest levels of pelagic diversity are observed in the southern hemisphere (Fig. 2, Table 1), namely in the Bengela Current System (zone 8) and the Southern convergence (amphi-atlantic zone between sub-tropical front [STF] and Antarctic Polar Front [APF]; zone 7). In the Northern hemisphere, higher levels of diversity are observed in the western Slope water region (zone 2a) and North Sargasso Sea (zone 3a), North African Subtropical Sea (zone 3d), Mediterranean outflow (zone 2c), and Azores Province (zone 2b). The lowest diversity is observed in the polar zones (zones 1 and 9). However, the most evident large-scale biogeographic pattern is the diversity impoverishment in some western oceanic regions. From the South Sargasso Sea (zone 3b) to the South Atlantic Subtropical (zone 6), the richness is below 50 species. This biogeographic trend seems to be coupled with lower net primary productivity (NPP) of those regions (illustrated in Fig. 1). In fact, mean NPP is positively associated with oceanic species richness and explains, after adjusting for area, 37% of the variance with all the regions included (Fig. 3C, Table 2). Cephalopod diversity in the open ocean is also significantly associated with the quadratic component of mean sea surface temperature (SST; Table 2, $r^2 = 49.7\%$; to avoid multicollinearity in polynomial regression, SST was centered around its mean [Montgomery et al. 2001:226]). That is, when SST is either low or high, species richness is also low but when SST is in the middle of the range, oceanic richness reaches a maximum (Fig. 3A). When the same association is assessed outside the polar regions, this relationship follows a negative linear trend (Fig. 3A, explaining 31% of the variance) and NPP

becomes the most important explanatory variable, explaining 44% of the variance (Table 2).

We also looked at the relationship between oceanic diversity and the range of SST and NPP (Table 3). Quadratic polynomials were used for assessing associations between oceanic richness and range of STT and NPP when all oceanic regions are included and linear associations when the Polar Regions are excluded (Fig. 3B, D). Though the association between oceanic diversity and variability of STT showed a similar pattern to the association displayed with respect to the mean level (Fig. 3A, B), none of the components was statistically significant (Table 3). On the other hand, the relationship between species richness and the mean and range of NPP displayed similar patterns, both statistically significant, when poles were excluded (dashed lines in Fig. 3C, D), and in both cases the linear associations were statistically important (Table 3). However, when the polar regions were included, a linear association (total $R^2 = 37.46\%$) gave a better fit than did a curvilinear association (total $R^2 = 35.81\%$) for the association between oceanic diversity and mean NPP (solid line Fig. 3C), and a nonsignificant pattern was observed for NPP range (solid line in Fig. 3D). It is important to note that area was not statistical significant in any of the regression models, but because "diversity" is in general associated with larger "areas," the covariate "area" was left in the models to remove potential effects on species richness.

Bathymetric gradients of diversity

The diversity of benthos-associated cephalopods, i.e., species that live in the bottom floor or that spend part of
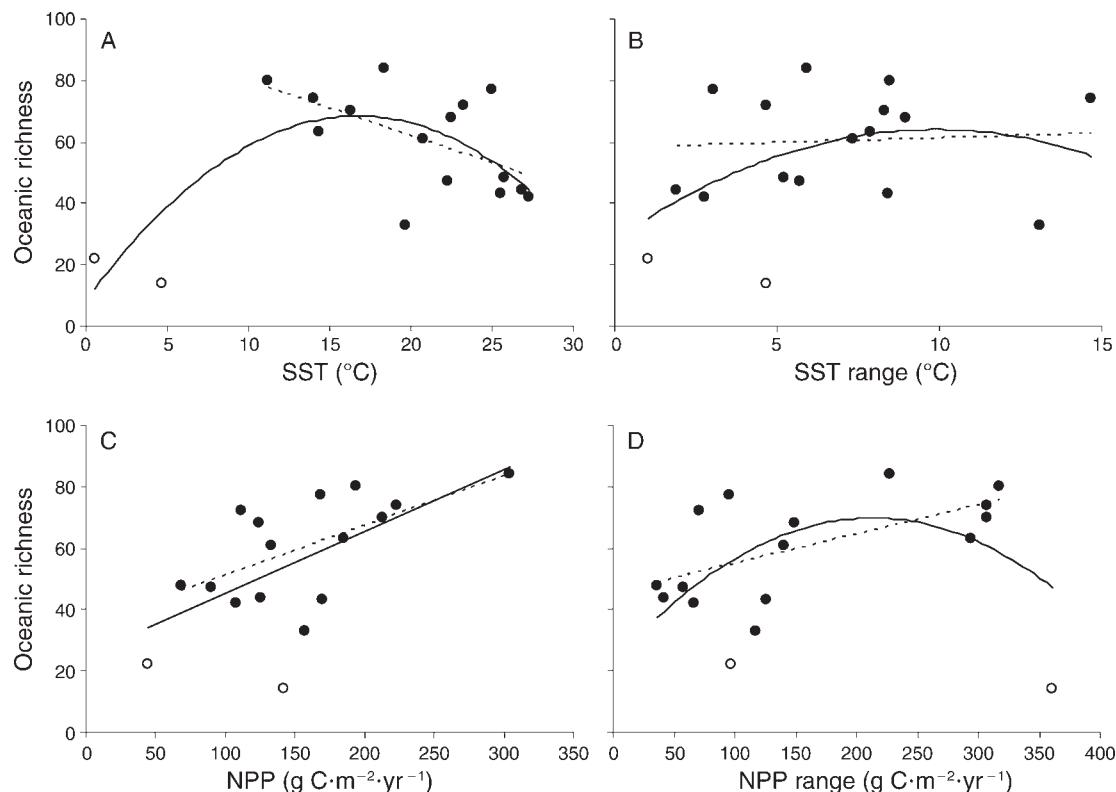
FIG. 3. Relationships between oceanic diversity of cephalopods (number of species) within the Atlantic zoogeographic regions and (A) sea surface temperature (SST); (B) SST range; (C) net primary productivity (NPP); (D) range of NPP. Solid lines represent the best fit for all regions and dotted lines represent the best fit excluding the Artic and Southern Ocean (regions 1 and 9 represented with open circles). All regressions are adjusted for area of each region and the statistics on goodness of fit in panels A and C are presented in Table 1, and the statistics on goodness of fit in panels B and D are shown in Table 2.

their time in the water column but also dwell on the bottom (benthic and nektobenthic life strategies, respectively), declines sharply from continental shelves to the slope of both Western Atlantic (WA) and Eastern Atlantic (EA) coasts, and then decreases gradually toward the abyssal plains (Fig. 4). The greatest difference between the two Atlantic bathymetric gradients occurs within the first 500 m depth due to the exclusive presence of sepiids and higher sepiolid diversity in the EA shelves and upper slopes (see historical explanations in Rosa et al., *in press a*). The diversity–depth pattern of oceanic species richness differs from the benthic ones since the sharp decline in the upper layers does not occur (Fig. 4C). Instead, pelagic diversity is fairly similar at epi- and mesopelagic depths, decreasing abruptly only at bathypelagic depths.

TABLE 2. Relationships between oceanic species richness and mean sea surface temperature (SST) and mean net primary productivity (NPP) in the Atlantic Ocean, after adjusting for the effect of area (i.e., included as a covariate in each of the models).

	All regions included					Outside the poles				
Variables	Coefficient (SE)	t	P	Total R^2	AIC	Coefficient (SE)	t	P	Total R^2	AIC
Sea surface temperature (adjusting for area)										
Area	0.36 (1.41)	0.26	0.7999	49.67%	146.66	0.30 (1.29)	0.23	0.8191	30.96%	125.58
SST	−0.82 (0.73)	−1.12	0.2838			−1.73 (0.79)	−2.20	0.0482		
SST^2	−0.22 (0.00)	−3.29	0.0058							
Net primary productivity (adjusting for area)										
Area	0.17 (1.45)	0.12	0.9078	37.46%	148.35	1.45 (1.15)	1.26	0.2303	44.04%	122.43
NPP	0.20 (0.07)	2.87	0.0123			0.17 (0.06)	2.96	0.0119		

Notes: The statistical analyses were done in two separate regression models: (1) the panel on the left gives estimated coefficients with associated standard errors, t ratios and P values for models including all oceanic regions, (2) the panel on the right gives the same information when the poles are excluded from the analysis. Total R^2 are given in the fourth column and AIC values in the fifth column of each panel for each of the models.

TABLE 3. Relationships between oceanic species richness and range (difference between maximum and minimum observation during the studied period) of sea surface temperature (SST) and mean net primary productivity (NPP) in the Atlantic Ocean, after adjusting for the effect of area (i.e., included as a covariate in each of the models).

Variables	All regions included					Outside the poles				
	Coefficient (SE)	t	P	Total R^2	AIC	Coefficient (SE)	t	P	Total R^2	AIC
Sea surface temperature (adjusting for area)										
Area	−0.34 (1.79)	−0.19	0.8538	17.53%	155.05	1.07 (1.53)	0.70	0.4958	4.39%	130.47
SST	2.37 (1.59)	1.49	0.1612			0.53 (1.33)	0.40	0.6983		
SST^2	−0.38 (0.32)	−1.18	0.2580							
Net primary productivity (adjusting for area)										
Area	−0.83 (1.78)	0.23	0.8180	21.24%	154.27	0.79 (1.18)	0.67	0.5139	39.74%	123.54
NPP	0.05 (0.05)	1.72	0.1092			0.09 (0.03)	2.70	0.0193		
NPP^2	−0.00 (0.00)	−1.57	0.1407							

Notes: The statistical analyses were done in two separate regression models: (1) the panel on the left gives estimated coefficients with associated standard errors, t ratios and P values for models including all oceanic regions, (2) the panel on the right gives the same information when the poles are excluded from the analysis. Each of the regression models adjusts for the effect of area. Total R^2 are given on the fourth column and AIC values on the fifth column of each panel for each of the models.

The distribution of pelagic cephalopods along a gradient of depth reveals a linear increase in median bathymetrical range size with increasing depth (Fig. 5). However, the benthos-associated species show a curvilinear trend, with species showing identical size ranges of distribution below 2500 m.

DISCUSSION

Diversity in the open ocean

As in other ecosystems, the maintenance and functioning of the open ocean relies on photosynthetic production, which determines the maximum amount of energy expenditure and sets constrains on the oceanic food web complexity. Outside the polar regions (region 1 and 9), mean NPP explains 44% of the variance in pelagic diversity of cephalopods. The highest large-scale diversity levels are located in two very energetic frontal regions of the Southern and Atlantic Oceans (zone 7), namely the Brazil/Malvinas Confluence and the Agulhas Current and its retroflection along with the upwelling area of the Benguela Current (zone 8). An equivalent subtropical convergence zone is found across the North Atlantic subtropical gyre (at 30°–35° N), forming the southern limit to winter-mixing regions of the westerly wind biome. These frontal systems show intense mesoscale activity and exhibit high levels of NPP (Fig. 1). Also, diversity is continually higher than 60 species in oceanic regions adjacent to eastern coastal provinces that are strongly controlled by upwelling dominate phytoplankton ecology (Canary, Guinea, and Benguela Current Coastal Provinces; see Longhurst [2007:214–273]). On the other hand, diversity is markedly lower in the poles, Caribbean Sea (zone 5a), Amazonian Province (zone 5b), and along the western regions of subtropical gyres, namely South Sargasso Sea (zone 3b) and Subtropical South Atlantic (zone 6). In these oligotrophic subtropical zones there is a strong vertical stratification of the water column that limits the supply of nutrients from below the thermocline to the euphotic layer. Carbon fixation by autotrophs is low (NPP is <90 g C·m^{-2}·yr^{-1}; Fig. 1), but since subtropical gyres cover globally >60% of the total ocean surface area, they have a large impact on biogeochemical budgets, accounting for >30% of the total marine primary production (Longhurst 1995).

Some studies suggest that the latitudinal increase in species richness from high to low latitudes (see Fig. 3 in Angel 1993), followed by a decrease of species dominance, are associated with low productivity and lack of seasonality (Margalef 1989, Angel 1997). At oligotrophic regions, primary and second productions are assumed to be closely coupled and their cycles have generally lower seasonal amplitudes, which favors diversification rates (Longhurst and Pauly 1987). On the other hand, in the westerlies biome, the seasonal cycles of production and consumption are uncoupled and more variable, which does not promote specialization and, thus diversity.

We did not find a latitudinal gradient of species richness in the open ocean. Rather, we report higher diversities at middle (temperate) latitudes, and lower diversities in oligotrophic regions of the Trade biome (Fig. 2). Similar distributional patterns were also obtained by Cheung et al. (2005:19) for commercially important cephalopods. Greater diversification at middle transitional (and more seasonal) latitudes is also observed in many other pelagic groups, such as foraminiferans (Rutherford et al. 1999, Brayard et al. 2005), chaetognaths, euphausiids, pteropods, salpids, and ostracods (McGowan and Walker 1985, Boltovskoy et al. 1999). These latitudinal patterns have been attributed to differences in upper-ocean thermal structure (Fig. 6), with middle latitudes exhibiting a weaker permanent thermocline that favors vertical niche partitioning and greater diversification rates. At the poles and equator, the thermocline is either absent or very sharp, respectively (Fig. 6), not favoring niche separation and high number of species (Rutherford et al. 1999). The negative effect of high SST on species' eco-
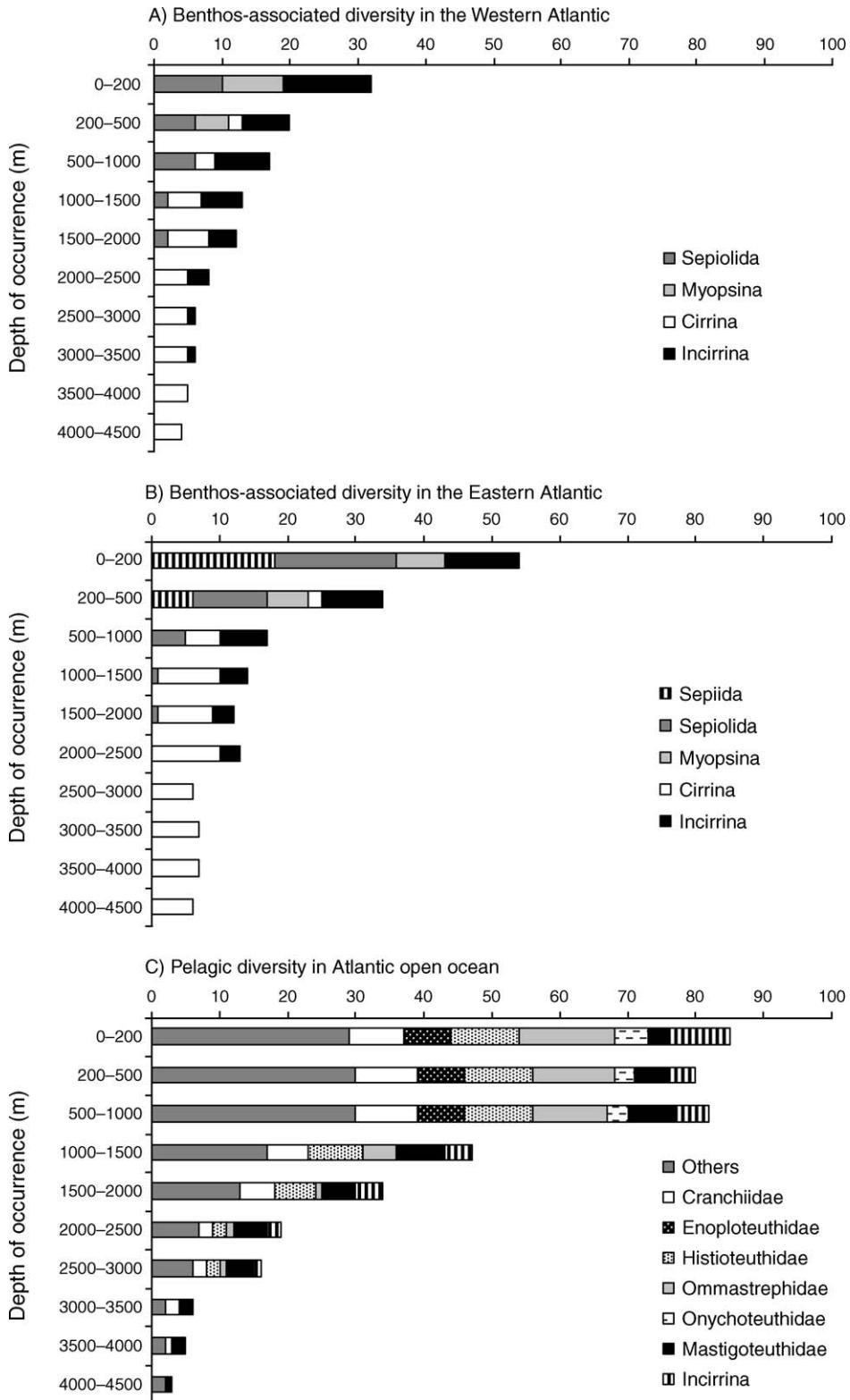
FIG. 4. Bathymetric gradient of: benthos associated species diversity in the (A) western and (B) eastern Atlantic coasts, and (C) pelagic species diversity in Atlantic open ocean. Diversity is estimated as the number of coexisting species ranges in pre-defined depth increments.
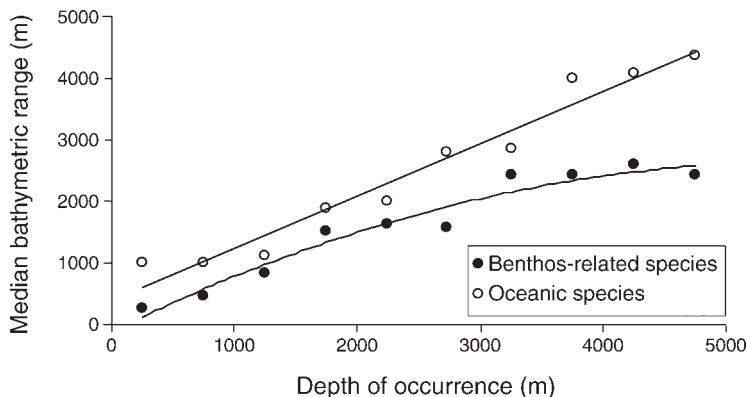
FIG. 5. Relationship between the median bathymetrical range of benthos-associated and oceanic cephalopods and depth of occurrence (in pre-defined depth intervals). The linear regression gives a significant relationship for oceanic species ($r^2 = 0.96$, $P < 0.0001$) and a second order polynomial regression gives a significant relationship for benthos-associated species, $r^2 = 0.95$, $P = 0.0000$.

physiology has also been put forward to explain the drop in equatorial diversity (illustrated in Fig. 3A with the negative trend), but this explanation does not seem plausible since many cephalopod species can reproduce successfully at these temperatures or, on the other hand, can avoid the warmer near-surface temperatures during the daytime by undertaking vertical migrations to deeper waters.

Acknowledging the expected scale dependence in diversity–productivity relationships, our study reveals that there is a significant positive relationship between mean NPP and oceanic richness at regional scales. Other studies have also shown that, at larger scale, species richness increases monotonically with productivity, contrasting with the hump-shaped pattern at smaller scales (Waide et al. 1999, Mittelbach et al. 2001, Chase and Leibold 2002). The larger amount of energy in highly productive regions may enable a greater number of predatory species to occur (Evans et al. 2005),

especially cephalopods. In order to support their high growth rates, short lifespan, semelparity, and high metabolic rates, epipelagic squid (Group 1, definition is given previously) are highly mobile, voracious, and opportunistic predators that are well adapted to the seasonality and spatial patchiness of food resources in the open ocean. For instance, many are known to make extensive migrations to exploit the latitudinal differences in productivity (Rodhouse and Nigmatullin 1996). The richness of other groups (e.g., 2 and 3) can also be positively affected by the greater energy availability because it is also associated with environmental heterogeneity (including in productivity itself), which can increase species dissimilarities (Kerr and Packer 1997, Chase and Leibold 2002). In fact, there is experimental evidence that seasonal fluctuations in availability of limiting resources can favor biological diversity by the coexistence of different ecotypes via frequency-dependent competition (Spencer et al. 2007). Environments in
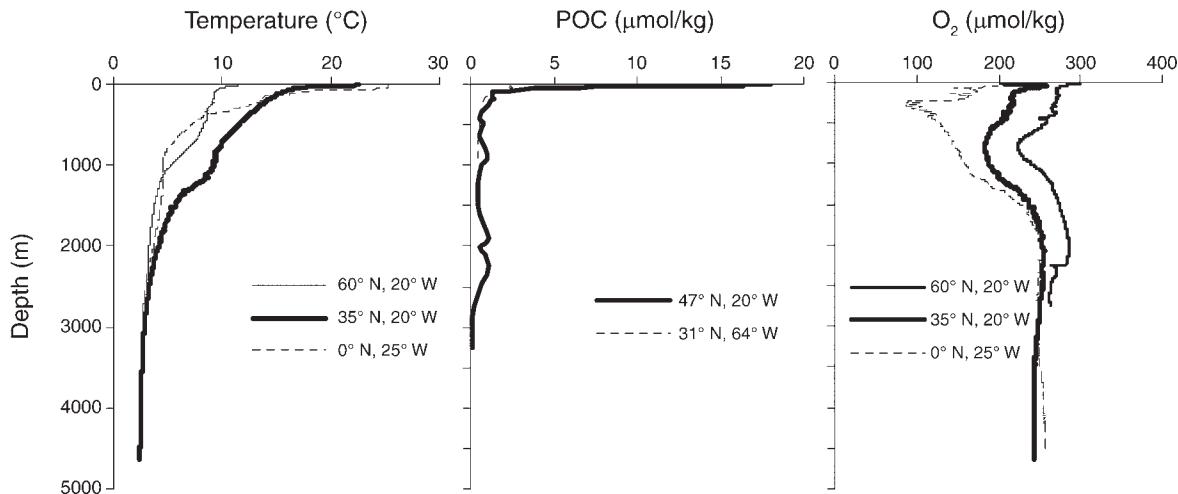
FIG. 6. Patterns of temperature gradient, particulate organic carbon (POC), and oxygen concentration (O_2) in the North Atlantic Ocean (from the Comprehensive Ocean Atmosphere Data Set [COADS] ⟨http://dss.ucar.edu/pub/COADS_intro.html⟩). POC is used as a food availability indicator.

which resources occur in pulses facilitate the coexistence of subdominant species with competitively dominant species and, therefore, tend toward higher species richness (Sommer 1984, 1985, Grover 1988). Outside the poles, the significant positive relationship between the range in NPP and cephalopod oceanic richness (Fig. 3D) supports this idea. Additionally, increased productivity also results in different resource types that can sustain a larger number of more specialist species (DeAngelis 1994, Abrams 1995).

The more productive and seasonally variable regions in the Atlantic Ocean support the largest cephalopod populations (northern and southern Atlantic regions represent 84% of total fishery catches while central regions represent only 16% [Fishstat 2004]). These figures may be indicative of higher diversity because higher resource availability enables larger populations, which buffer extinction and promotes species richness ("more individuals hypothesis" [Wright 1983, Srivastava and Lawton 1998]). Underlying this hypothesis is the concept that abundance and energy availability are closely linked (Hurlbert 2004, Evans et al. 2005, Pautasso and Gaston 2005) and that the number of species arising per unit time is positively related to the number of individuals in the metacommunity (see "neutral theory of biodiversity" [Hubbell 2001]).

Depth–diversity gradients

Cephalopod diversity is highest above the first 200 m, namely in sub-littoral and epipelagic regions (Fig. 4) and declines with depth. The vast majority (~60%) of benthic and nektobenthic diversity (e.g., cuttlefishes and loliginids) is restricted to the upper 500 m of depth and to the upper 1000 m for oceanic fauna. This greater spread in the pelagic biota is associated with diel vertical migrations of the most abundant oegopsid squids, between epi- and mesopelagic zones (e.g., Hunt and Seibel 2000, Watanabe et al. 2006). A continuous decrease in diversity with depth has also been observed in pelagic fishes (Smith and Brown 2002). Although it is expected that the distributional range of the lesser known bathyal and abyssal fauna is underestimated, such limitations are not expected to change the observed decrease of biodiversity with depth.

Though it's difficult to compare the almost two-dimensional terrestrial area to the three-dimensional aquatic domain, we don't believe there is an effect of water volume on diversity ("biome area hypothesis" [Rosenzweig 1995]), because the majority of cephalopod species avoids the immense deep-sea biome and is restricted to the smaller volume of shallower productive waters. For example, the continental shelf only represents 3% of the global ocean area and even less of the ocean's volume. While the greater environmental stability of the deep sea has not permitted extensive niche diversification ("environmental stability hypothesis" [Sanders 1968]), the higher energy availability at coastal and shallow waters may enhance speciation

("more individuals hypothesis," see *Diversity in the open ocean*). Additionally, since feeding, behavior and reproduction of the neritic cephalopods are closely associated with the seabed characteristics, the greater spatial heterogeneity along the continental shelves may explain the higher faunal diversification rates ("habitat heterogeneity hypothesis" [Grassle and Sanders 1973]).

Cephalopods do not show smaller bathymetric range sizes toward the "spatial boundaries" and larger ranges at the intermediate depth (mid-domain effect). Instead, they show a linear (pelagic species) or a polynomial (benthos-related species, with range uniformity below 2500 m; Fig. 5) increase in range size with depth. The different patterns between these two groups may reflect the distinct locomotory abilities of the two different life strategies. Mid-domain effects also do not seem to account for diversity-depth patterns in other invertebrate groups (McClain and Etter 2005) and fish (Kendall and Haedrich 2006). It is also known that depth-related trends may vary between regions (Kendall and Haedrich 2006), but the present knowledge of cephalopod deep-sea biogeography does not allow us to make a smaller-scale approach. Although it is expected that the distributional range of the lesser known bathyal and abyssal fauna is underestimated, such limitations are not expected to change the distinct decrease of biodiversity with depth.

The inverse relationship between depth and diversity in both benthos-related and pelagic cephalopods strongly indicates the influence of the same causal mechanisms. In fact, the vertical gradients in the physical environment are pronounced (Fig. 6). In the pelagic realm, they dictate pervasive behavioral (e.g., bioluminescence and sit-and-wait predation strategies), locomotory (e.g., fin or medusoid swimming instead of inefficient high-jet-speed propulsion) and morphological adaptations (e.g., reduced high-density musculature; coelomic chambers and ammonium chloride retention as buoyancy mechanisms), leading to a strong depth-related decline in metabolism, above and beyond the effect of temperature. The general decrease in pelagic cephalopod metabolic rates with depth has been attributed to a reduced need for locomotory capabilities associated with visually cued predator/prey interactions in the light-limited deep sea ("the visual interaction hypothesis" [Childress 1995, Seibel et al. 1997, Seibel 2007, Seibel and Drazen 2007]), while the possible influences of hydrostatic pressure, reduced food availability, and oxygen levels have been ruled out. This pattern is not evident in benthic organisms, including cephalopods (Seibel and Childress 2000), where lifestyles and temperature-normalized metabolic rates are similar across the depth range. Nevertheless, temperature has been hypothesized to influence the abundance and diversity of organisms via its effects on biochemical processes (Allen et al. 2002, 2006), mutation rates (Gillooly et al. 2005), and lifestyles ("metabolic niche hypothesis" [Clarke and Gaston 2006]). Contrary to the

patterns observed in soft-sediment benthic diversity, the cephalopod richness decreases along the permanent thermocline and becomes more stable at lower bathyal and abyssal regions (compare Figs. 4 and 6). In fact, of the several possible environmental factors influencing the depth distributions of benthos-related and pelagic cephalopods (some illustrated in Fig. 6), food availability (measured as particulate organic carbon) and temperature (independent of metabolism) seem to be the best causal predictors for depth-related patterns. However, given the differential responses of pelagic and benthic cephalopod lifestyles and metabolism to depth, these environmental influences must mediate diversity via some mechanism other than biochemical rate processes or lifestyles. Although not quantified, temperature–species relationships should be stronger with depth than with latitude, emphasizing the stronger influence of the sharp vertical thermal gradient than the smoother and more seasonal horizontal (latitudinal) one.

CONCLUSIONS

Cephalopod mollusks are a special case of success among metazoans in the colonization of the pelagic realm, with high levels of endemism and with the majority of the families restricted to it. Contrary to the coastal environment (Rosa et al., *in press a*), no classical latitudinal gradient in species richness is found in the open ocean, since higher diversity levels are found at middle latitudes. While coastal patterns of cephalopod diversity can be robustly predicted by climate (sea surface temperature) and non-climate (spatial area) variables (Rosa et al., *in press a*), pelagic richness follows the spatial changes in surface ocean net primary productivity. The significant linear increase in cephalopod diversity with mean productivity and the occurrence of higher population densities (fisheries data) in more productive regions of the Atlantic Ocean are consistent with the "more individuals" hypothesis. At the same time, the positive response of species richness with NPP range outside the Polar Regions also supports the idea that diversity can be favored by seasonal fluctuations in availability of limiting resources. Both benthos-related and pelagic cephalopod diversity does not increase at bathyal and mesopelagic depths, which has been described in several macrofaunal groups, including bivalves and gastropod mollusks (Rex et al. 2005). Our findings clearly show that diversity peaks along the continental shelves and in the epipelagic zone (<200 m), and decreases with depth. It suggests that higher environmental energy availability and productivity in shallow and surface waters promotes diversification rates.

ACKNOWLEDGMENTS

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