Environmental determinants of latitudinal size-trends in cephalopods

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ABSTRACT: Understanding patterns of body size variation is a fundamental goal in ecology, but although well studied in the terrestrial biota, little is known about broad-scale latitudinal trends of body size in marine fauna and much less about the factors that drive them. We conducted a comprehensive survey of interspecific body size patterns in coastal cephalopod mollusks, covering both hemispheres in the western and eastern Atlantic. We investigated the relationship between body size and thermal energy, resource and habitat availability and depth ranges. Both latitude and depth range had a significant effect on maximum body size in each of the major cephalopod groups (cuttlefishes, squids and octopuses). We observed significant negative associations between sea surface temperature (SST) and body size. No consistent relationships between body size and either net primary productivity (NPP), habitat extent (shelf area) or environmental variation (range of SST and NPP) were found. Thus, temperature seemed to play the most important role in structuring the distribution of cephalopod body size along the continental shelves of the Atlantic Ocean, and resource availability, seasonality or competition only played a limited role in determining latitudinal body size patterns.

KEY WORDS: Body size · Ectotherms · Cephalopods · Thermal energy · Resource availability · Latitude · Temperature-size rule

INTRODUCTION

Animal body size has an important influence on many physiological and ecological traits (Atkinson & Hirst 2007, Seibel 2007, Rosa et al. 2009), community growth and abundance (Blackburn & Gaston 1999, White et al. 2007) and ecosystem-scale energy flux and storage (Peters 1986). As a result, considerable effort has been devoted to the study of spatial patterns in body size, especially across large environmental gradients, to understand the organization of ecological communities. Bergmann (1847) was the first to propose a biogeographic 'rule' stating that smaller endotherms should, in general, abound in warmer areas, while larger-bodied species would inhabit colder climates. Underlying this hypothesis was the idea that a reduced surface to volume ratio at larger sizes facilitates greater heat conservation, allowing a lower mass-specific metabolic rate, whereas larger ratios in smaller individuals facilitate heat loss.

In the same context, but for ectothermic animals, a 'temperature-size rule' was postulated (Atkinson 1994), which argues that at lower temperatures (higher latitudes), ectotherms generally exhibit lower growth rates and delayed maturation but also grow to a larger body size. At higher temperatures, they tend to grow faster and mature at smaller sizes, but their adult body size is reduced. Although both

hypotheses suggest that ambient energy (temperature) is the best environmental explanatory variable for the latitudinal-size trends, both lack a convincing mechanistic explanation. The resource availability (primary productivity) hypothesis assumes that body mass must be maintained by a sufficient food supply and predicts greater body sizes in more productive areas (Rosenzweig 1968). However, it is worth noting that cephalopods are voracious carnivores with many different feeding strategies that enable them to feed opportunistically on a wide range of prey (Rosa et al. 2004), and their growth seems to be primarily limited by predation rather than food shortages (Wood & O'Dor 2000).

Some also argue that species adopt smaller body sizes in more equatorial areas because of increased inter- and intra-specific competition for resources (McNab 1971, Ashton et al. 2000). Because the feeding, behavior and reproduction of neritic cuttlefish, octopuses and squids are closely associated with seabed characteristics, one may argue that the larger continental shelves near the poles (i.e. greater habitat availability) could affect cephalopod body size variation by reducing competition. Moreover, variation in oxygen availability has been suggested to explain polar gigantism (Chapelle & Peck 1999) and size increase in the deep sea (McClain & Rex 2001, but also see Spicer & Gaston 1999 for a rebuttal of this idea). Seasonality (or fasting endurance) has also been advocated to explain latitudinal size clines in both endo- and ectotherms, with large-bodied species being favored in colder and more variable environments because they can store more energy reserves (namely fat) to enhance survival during seasonal shortages of resources (Lindsey 1966, Boyce 1979). In marine systems, some argue that coastal animals tend to be bigger than deeper living counterparts (see the 'size-structure hypothesis' by Thiel 1975, 1979). Yet, the generality of this phenomenon is not convincing because body size has been reported to decrease, increase or show no association with depth (see reviews by Gage & Tyler 1991, Rex & Etter 1998).

Although body size has been well studied in terrestrial biota, large-scale marine surveys of body size have been conducted only for fish (Lindsey 1966, Macpherson & Duarte 1994), amphipods (Poulin & Hamilton 1995, Chapelle & Peck 1999), gastropods (Frank 1975, Olabarria & Thurston 2003) and bivalve mollusks (Roy & Martien 2001). Only 2 of these studies have covered both hemispheres (Poulin & Hamilton 1995, Chapelle & Peck 1999). In fact, while bathymetric variations in body size have been fairly well documented (Rex & Etter 1998, Rex et al. 1999, 2006, McClain & Rex 2001, McClain 2004, McClain et al. 2006), very little is known about broad-scale latitudinal trends in body size in marine fauna, and much less about the factors that drive them.

Here, we provide a comprehensive survey of large-scale interspecific body size patterns for cephalopod mollusks along the continental shelves on both sides of the Atlantic. Furthermore, we investigate the relationship between latitudinal size trends and sea surface temperature (SST, an indicator of energy availability), net primary productivity (NPP, an indicator of resource availability), SST and NPP range (a proxy of seasonality) and shelf area (habitat availability, as a surrogate for competition), with depth ranges taken into account.

METHODS

Species data

After the assemblage of a species diversity database of cephalopods in the continental shelves (Rosa et al. 2008a), here, we present the latitudinal ranges and body sizes of coastal cephalopod fauna, i.e. species that are associated with, but not restricted to, continental shelves and depths shallower than 200 m in the Atlantic Ocean (Fig. 1). The body size database was constructed based on a comprehensive search of primary literature (e.g. Voss et al. 1998, Jereb & Roper 2005), regional faunal compilations (e.g. Rosa & Sousa Reis 2004) and expedition reports. Furthermore, an additional search was carried out in several journals that publish papers on the taxonomy and biogeography of cephalopod species (see Appendix 1 for more details). To examine the relationship between body size and latitude, we divided the western and eastern Atlantic corridors into 5° latitudinal bins. Existing information on cephalopod biogeography did not permit finer resolution. We used the geometric mean of maximum length as a measure of size (here as maximum mantle length, MML). Although it is not the most common measure used to define latitudinal size patterns, MML is the most common standard measure (and sometimes the only available) for cephalopod species. The body size variable for each of the assemblages in each of the latitudinal bins had maximum skewness of 2.18 on the eastern side and 1.89 on the western side. The geometric mean is a useful measure of center when the distribution of the log-transformed original variable is made more symmetrical (Dallal 2007), and because the geometric
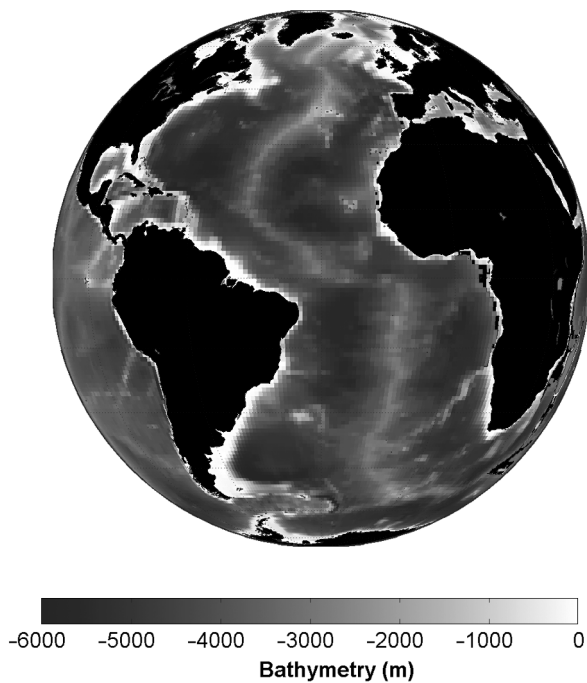
Fig. 1. Bathymetry in the Atlantic Ocean. White areas along the Atlantic coastal margins represent the continental shelves under study in the present investigation

mean is defined as the exponential of the average of the natural logs, it also has the advantage that the results are in the original scale of the data. Moreover, the geometric mean of body size is the metric most commonly used to investigate interspecific latitudinal patterns of body size, by providing some degree of standardization of shape differences among species (Hawkins & Lawton 1995, Roy & Martien 2001, Olabarria & Thurston 2003). It is important to note that there are cases where the median of body size could be a better measure of center than the geometric mean (Meiri & Thomas 2007). The bathymetric range for each species was also recorded.

Effects of phylogeny

Phylogenetic effects are known to influence spatial trends in body size (de Queiroz & Ashton 2004). We tested these effects indirectly (in the absence of a well-resolved cladogram) by comparing the latitudinal patterns of body size at the class level (Cephalopoda) to those at the order level, namely Sepiida and Sepiolida (cuttlefishes), Teuthida (squids) and Octopodida (octopods). We also used the geometric mean of MML as a representative measure of body size within the orders.

Environmental and spatial predictors

Ocean NPP 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 sea surface temperature data from the MODIS Aqua sensor. Online Standard Products were downloaded as monthly, global 18 km gridded NPP data from November 2002 through October 2006 (OSU 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 nighttime algorithm. For SST data, the arithmetic mean was calculated for each of the defined bins. We also determined the range of NPP and SST, a measure of variability (seasonality) in the data, calculated as the difference between maximum and minimum observations during the studied period. Habitat availability, i.e. continental shelf area extent, was determined using satellite-derived ocean bathymetry resampled at 1° resolution (USDC 2006).

Statistical analyses

The statistical analyses were carried out in SAS (version 9.1.3) and run separately for the western and eastern margins and for the different cephalopod groups. Pearson's correlation coefficients were used to identify the relationships among all of the potential explanatory variables for latitudinal size patterns (Table 1). For subsequent analyses, because the data were binned in latitudinal bands, there was the concern of spatial dependency in the residuals; thus, lack of independency was accounted for when testing for associations between latitudinal size and other environmental variables. The spatial dependency in the data is in 1 dimension; hence, methods that apply to time series data can be used for statistical analysis (Cressie 1993, p. 200).

Simple and multiple regression analyses were used to test for associations among variables, and generalized Durbin-Watson statistics were used to check the order of autocorrelation present in the data (see Gujarati 1995). When autocorrelation was present, autoregressive models (AR models) were used to test for associations of variables. In the present study, the highest level of autocorrelation detected was of order 2, and the largest number of variables included in a

Table 1. Pearson correlation coefficients between sea surface temperature (SST), SST range, net primary productivity (NPP), NPP range, shelf area and depth range of Cephalopoda in western and eastern margins of the Atlantic Ocean. Significance levels are corrected for spatial autocorrelation. *p < 0.05, **p < 0.01, #: excluding Eastern sepiolids

	SST	SST range	NPP	NPP range	Shelf area
Western					
SST	1				
SST range	−0.34	1			
NPP	0.23	0.28	1		
NPP range	−0.29	0.40*	0.72**	1	
Shelf area	−0.66**	0.18	−0.35	0.13	1
Depth range	−0.97**	0.37	−0.23	0.27	0.68**
Eastern					
SST	1				
SST range	−0.32	1			
NPP	0.34	−0.36	1		
NPP range	0.38	−0.14	0.78**	1	
Shelf area	−0.56**	0.64**	−0.61**	−0.48*	1
Depth range	−0.09	−0.45*	−0.08	−0.13	−0.32
Depth range (#)	−0.56**	−0.14	−0.35	−0.27	−0.05

model was 2. Thus, a multiple regression model with 2 independent variables and second order autoregressive errors is defined as follows:

$$y_l = \beta_0 + \beta_1\, x_{1l} + \beta_2\, x_{2l} + \varepsilon_l \tag{1}$$

$$\varepsilon_l = \rho_1\, \varepsilon_{l-1} + \rho_2\, \varepsilon_{l-2} + a_l \tag{2}$$

where y_l and x_{il} for $i = 1, 2$ are the observations of the response (size) and predictor variables (i.e. sea surface temperature, depth, etc.) respectively, at latitude l, ε_l is the error term in the model at latitude l, a_l is a normally and independently distributed $(0, \sigma_a^2)$ random variable, and ρ_i with $i = 1, 2$ is the autocorrelation parameter or order 1 and 2 respectively. This model can easily be converted to a simple regression model by making $\beta_2 = 0$ and to have an autoregressive error of order 1 by setting $\rho_2 = 0$. If no autocorrelation is present in the model, then $\rho_i = 0$ for $i = 1, 2$.

The AUTOREG procedure in SAS was used for the analyses, and the method of maximum likelihood was chosen over the Yule-Walker approach as the method of estimation because some of the data contained missing values (SAS 2008). Also, the estimates of standard errors calculated with the maximum likelihood method take into account the joint estimation of the regression parameters and AR components and may give more accurate standard errors than the Yule-Walker method. The goodness of fit statistics reported are the total-R^2 and the Akaike's information criterion (AIC):

$$R_{tot}^2 = 1 - [SSE/SSTotal] \tag{3}$$

where SSTotal is defined as the corrected sum of squares total for the response variable, and SSE is the final error sum of squares. AIC is defined as follows:

$$AIC = -2\ln(L) + 2k \tag{4}$$

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

RESULTS

Latitude and body size

The latitudinal distribution in mean body size of coastal cephalopod fauna in the western Atlantic (WA) and eastern Atlantic (EA) is shown in Fig. 2. The mean body size of squids (Order Teuthida) increased significantly towards the poles (Fig. 2C) in both the WA and EA (p < 0.05; Table 2). However, size-latitude relationships were more complex in the other cephalopod groups. While the mean body size of EA octopods followed a similar trend (p < 0.05; Fig. 2D, Table 2), the size of WA octopods increased from the Patagonian shelf (55° S) toward the equator but showed a steady increase toward the pole in the northern hemisphere. Sepiids, which became extinct in the WA, also revealed a clear trend of increasing size toward the pole in the northern hemisphere but not in the southern hemisphere (Fig. 2A). Sepiolids showed a marked difference in mean size from the Patagonian shelf to the other regions in the WA (Fig. 2B). In the EA, sepiolid body size was quite similar along the African coast until the Iberian/Mediterranean latitudes, where it decreased due to the occurrence of several small Mediterranean endemic species (see historical explanations by Rosa et al. 2008a). Sepiolids were the only group to show, on average, smaller sizes in the EA than in the WA, and this had an enormous influence on the overall spatial-size pattern observed for the Class Cephalopoda in the EA (Fig. 2F, Table 2). The relationship between latitude and body size completely changed from a negative linear to a positive quadratic association with the inclusion (black circles in Fig. 2F) or exclusion (grey circles in Fig. 2F) of EA sepiolids. In the WA, the mean body size of Cephalopoda increased poleward (p < 0.05; Fig. 2E, Table 2), which was also clearly associated with an increase in size disparity (Fig. 3). It is worth noting that, in contrast to our previous study regarding spatial gradients of
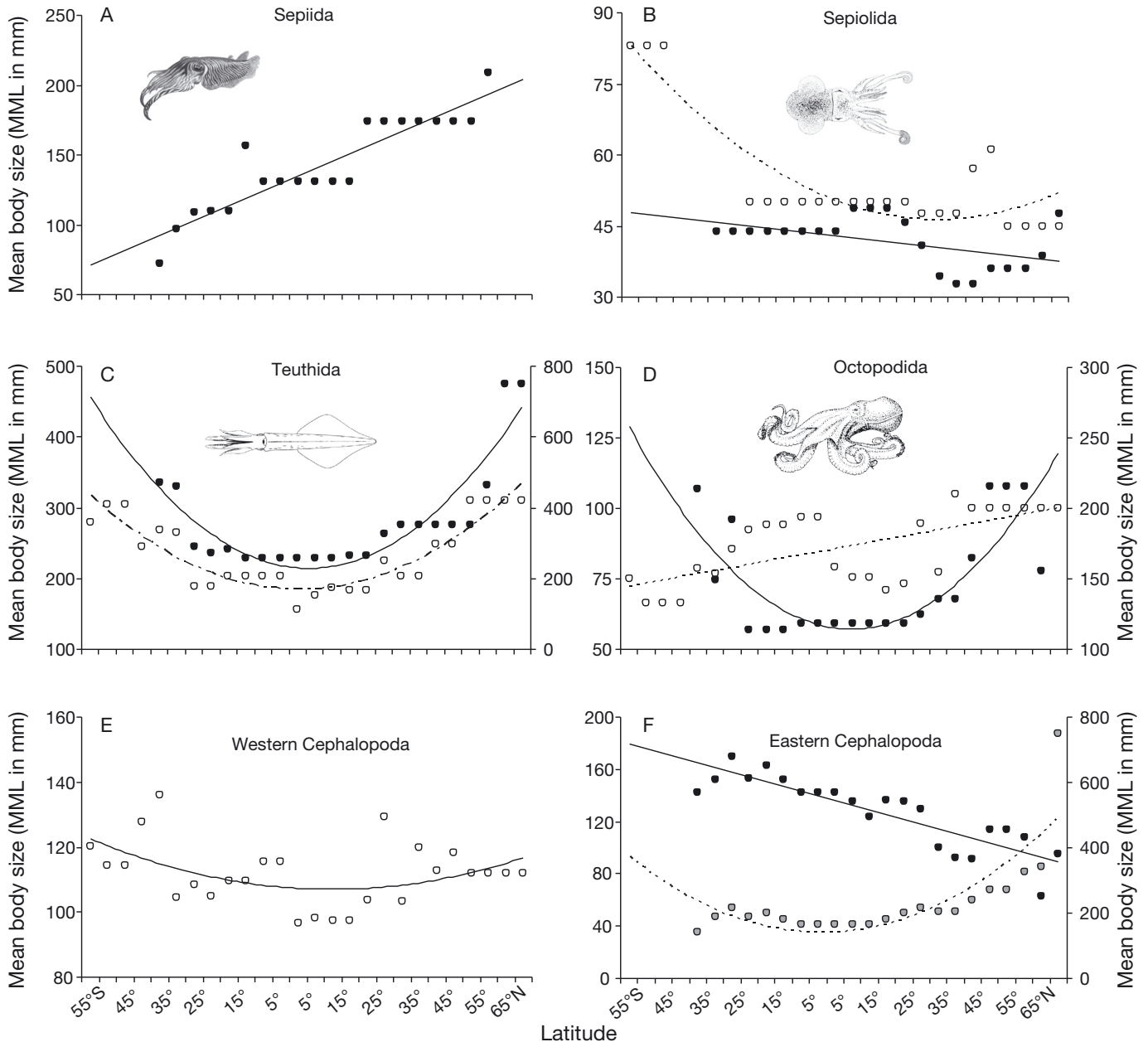
Fig. 2. Latitudinal variation in mean body size (maximum mantle length, MML in mm) of coastal cephalopods in the western (○, left *y*-axis in panels C, D) and eastern (●, right *y*-axis in panels C, D) Atlantic. Grey circles in panel F represent the latitudinal-size relationship of the Class Cephalopoda in the eastern Atlantic after excluding the Order Sepiolida (right *y*-axis scale). Results from regression analysis, accounting for spatial autocorrelation, are shown in Table 2

cephalopod diversity (Rosa et al. 2008a), we did not include data from the Southern Ocean due to a lack of information on the maximum body size (mantle length) of coastal cephalopod fauna (namely octopods) on the Antarctic shelves. This fact limited the identification of spatial size patterns toward the South Pole, especially in EA, where the continental shelves end at ~35° S (Figs. 2F & 3).

Depth range, environmental predictors, shelf area and body size

Depth range played an important role in the observed body size patterns. In the WA, greater depth ranges were significantly associated with greater sizes in all group orders and at the class level (Table 3, Model 1). In the EA, in contrast, the associations were
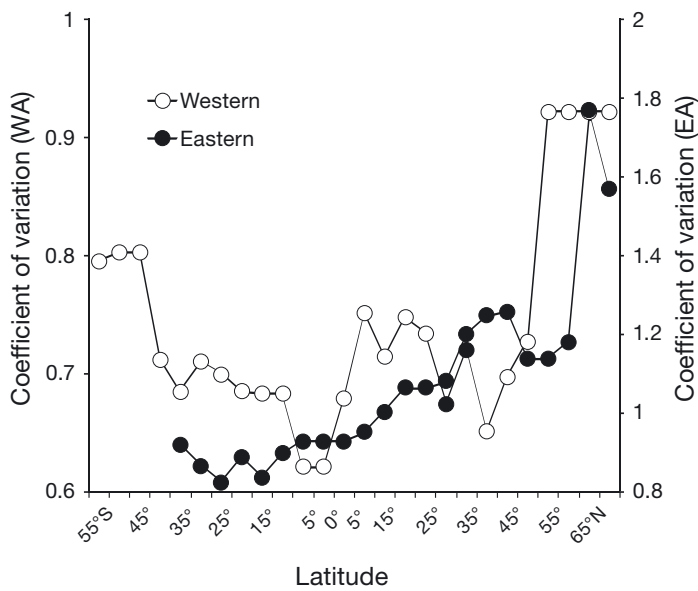
Fig. 3. Latitudinal trends in body size disparity (coefficients of variation) for Cephalopoda in the western (WA) and eastern (EA) Atlantic

generally negative (Table 4, Model 1), with the exception of the Teuthida (squids), which showed a significant positive relationship (p < 0.01). In both Atlantic margins, the depth range of Cephalopoda was significantly and negatively associated with SST (Table 1).

SST ranged from 6°C at the polar latitudes to >25°C at equatorial latitudes (Fig. 4A). For the WA, the temperature followed a near Gaussian distribution from polar to tropical latitudes. However, the patterns in the east were not nearly as continuous with latitude because of upwelling of cold water along the EA (e.g. the Benguela current off South Africa). Temperature was negatively associated with body size for almost all cephalopod orders and at the class level in both the WA and EA (Model 2 in Tables 3 & 4). The strongest negative associations between size and temperature were observed in squids (WA p < 0.05, EA p < 0.01).

Mean NPP ranged from <500 mg C m^{-2} d^{-1} in the WA to >4000 mg C m^{-2} d^{-1} in the upwelling regions of the EA (Fig. 4B). The mean (±SD) NPP was 784 ± 317 mg C m^{-2} d^{-1} for the WA and twice as high at

Table 2. Relationships between mean body size and latitude in the western and eastern Atlantic Ocean. Autocorrelation is taken into account in the estimates. Restricted maximum likelihood was used to estimate the parameters of each of the autoregressive models (AR). AIC: Akaike information criterion; +: not present in the western Atlantic; #: excluding eastern Atlantic Sepiolida; –: no output

| | Western Atlantic | | | | | Eastern Atlantic | | | |
	Coefficient	t-ratio	p	Total R^2	AIC	Coefficient	t-ratio	p	Total R^2
Sepiida									
Latitude	+	+	+	+	+	1.07	9.54	<0.0001	0.84
Latitude^2	+	+	+			–	–	–	
AR(1)	+	+	+			–	–	–	
Sepiolida									
Latitude	−0.33	−5.11	<0.0001	0.86	136.92	−0.02	−0.21	0.8354	0.80
Latitude^2	0.00	2.51	0.0219			–	–	–	
AR(1)	0.63	3.04	0.0071			1.44	5.72	<0.0001	
AR(2)	–	–	–			−0.71	−2.87	0.0107	
Theutida									
Latitude	−0.88	−6.95	<0.0001	0.82	193.82	−2.16	−2.28	0.0348	0.86
Latitude^2	0.02	4.95	<0.0001			0.13	6.06	<0.0001	
AR(1)	–	–	–			−0.41	−1.85	0.0804	
Octopodida									
Latitude	0.25	2.49	0.0206	0.47	209.05	−0.66	−2.39	0.0278	0.62
Latitude^2	–	–	–			0.03	5.01	<0.0001	
AR(1)	0.39	2.05	0.0516			–	–	–	
All									
Latitude	−0.09	−1.78	0.0877	0.20	192.12	−0.73	−7.88	<0.0001	0.76
Latitude^2	0.00	2.20	0.0381			–	–	–	
AR(1)	–	–	–			–	–	–	
All (#)									
Latitude	–	–	–	–	–	−0.17	−0.21	0.8385	0.67
Latitude^2	–	–	–			0.07	4.06	0.0007	
AR(1)	–	–	–			–	–	–	

Table 3. Models assessing the importance of depth range, sea surface temperature (SST), net primary productivity (NPP), SST and NPP range and shelf area in predicting cephalopod body size variation in western Atlantic margins. For each variable, the *t*-ratios are included. Restricted maximum likelihood was used to estimate the parameters of each of the models. Models 1 to 5 evaluated the following: 1: size-depth clines; 2: the 'temperature-size rule'; 3: the 'resource availability' hypothesis; 4: the 'seasonality hypothesis'; 5: habitat availability as a surrogate for competition. *p < 0.05, **p < 0.01, [a]marginally significant (p = 0.05). AR: autoregressive

Order	Model	Depth range	SST	NPP	SST range	NPP range	Shelf area	AR order	Total R²
Sepiolida	1	5.98**						1	0.92
	2		−1.45					1	0.83
	3			−0.06				1	0.81
	4				−0.06	1.27		1	0.83
	5						−0.39	1	0.80
Theutida	1	2.01[a]						1	0.69
	2		−2.35*					1	0.70
	3			−0.03				1	0.62
	4				−0.36	0.76		1	0.63
	5						0.65	1	0.63
Octopodida	1	2.72*						1	0.53
	2		−1.14					1	0.41
	3			−0.50				1	0.38
	4				1.49	−0.92		1	0.42
	5						2.19*	1	0.48
All	1	2.05[a]						–	0.15
	2		−2.20*					–	0.17
	3			0.58				–	0.01
	4				1.70	2.67*		–	0.41
	5						−0.03	–	0.00

1795 ± 864 mg C m⁻² d⁻¹ for the EA. No significant relationships were found between NPP and body size in either margin (p > 0.05, Model 3 in Tables 3 & 4). With the exception of EA sepiolids, no significant relationships between size and seasonal variability (SST and NPP ranges) were also observed (p > 0.05, Model 4 in Tables 3 & 4).

The continental shelf area was generally larger in the northern hemisphere than in southern hemisphere and increased towards the poles (Fig. 4C). The latitudinal variation of shelf area, here used as a proxy for habitat availability, was not relevant for the spatial size trends of all groups, except for octopods (WA p < 0.05, EA p = 0.05; Model 5 in Tables 3 & 4). The partly endemic EA sepiolids once again changed the relationship at the class level. With their exclusion, the association between shelf area and size of EA Cephalopoda turned from strongly significant (p < 0.0001) to non-significant (p > 0.05; Model 5 in Table 4).
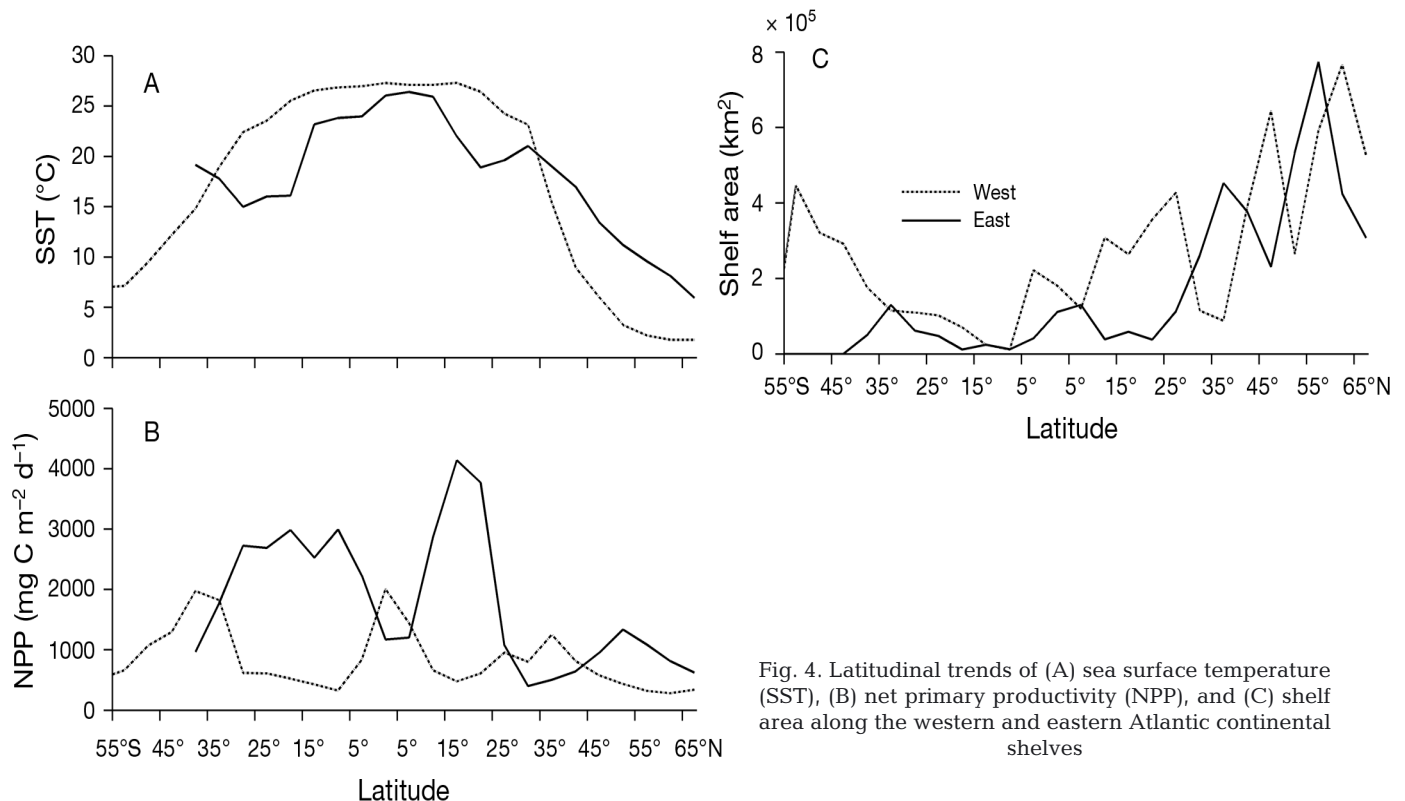

Fig. 4. Latitudinal trends of (A) sea surface temperature (SST), (B) net primary productivity (NPP), and (C) shelf area along the western and eastern Atlantic continental shelves

Table 4. Models assessing the importance of depth range, sea surface temperature (SST), net primary productivity (NPP), SST and NPP range and shelf area in predicting cephalopod body size variation in eastern Atlantic margins. For each variable, the t-ratios are included. Restricted maximum likelihood was used to estimate the parameters of each of the models. For the purposes of Models 1 to 5, see Table 3. #: excluding Sepiolida, *p < 0.05, **p < 0.01, [a] marginally significant (p = 0.05). AR: autoregressive

Order	Model	Depth range	SST	NPP	SST range	NPP range	Shelf area	AR order	Total R^2
Sepiida	1	−2.66[a]						1	0.69
	2		0.01					1	0.69
	3			−0.29				1	0.11
	4				−0.32	0.30		1	0.69
	5						−0.84	1	0.71
Sepiolida	1	−0.13						2	0.80
	2		−1.16					2	0.82
	3			0.24				2	0.80
	4				−5.48 **	3.06**		–	0.72
	5						−0.74	2	0.87
Theutida	1	7.69**						2	0.94
	2		−5.97**					2	0.83
	3			−1.44				1	0.73
	4				−0.41	−0.48		1	0.71
	5						−0.33	2	0.65
Octopodida	1	−0.45						1	0.45
	2		−2.07[a]					1	0.50
	3			−0.54				1	0.45
	4				0.48	−0.46		1	0.45
	5						2.03[a]	1	0.52
All	1	−0.76						1	0.63
	2		−0.74					1	0.63
	3			1.35				1	0.64
	4				−1.15	0.66		1	0.64
	5						−7.34**	2	0.71
All (#)	1	−5.37**						1	0.74
	2		−4.94**					–	0.55
	3			−0.17				1	0.46
	4				−0.49	−0.13		1	0.47
	5						−0.97	1	0.82

DISCUSSION

Effect of latitude and depth on body size

Previous studies have found a strong positive link between latitude and body size in shallow-living gastropods (Frank 1975), amphipods (Poulin & Hamilton 1995) and fish (Macpherson & Duarte 1994). However, latitude explained very little of the variance of body size in deep-sea gastropods (Olabarria & Thurston 2003) or shallow-living bivalves (Roy & Martien 2001). Here, we show that latitude has a significant effect on the mean body size of coastal cephalopods (Fig. 2, Table 2). A size increase toward the poles was supported at the class level (Cephalo-

poda). At the order level, however, the increase in body size toward the poles was more robust in some groups (e.g. squids) than in others (e.g. sepiolids), and was inconsistent between hemispheres (e.g. for sepiids) and Atlantic margins (e.g. for octopods). These differences illustrate the greater complexity of patterns shown by ectotherms, as already seen in terrestrial systems (Hawkins & Lawton 1995, Ashton & Feldman 2003, Olalla-Tarraga & Rodriguez 2007). Nonetheless, size increase toward the poles was supported at a higher taxonomic (class) level.

Depth range was significantly associated with body size in neritic cephalopods, underscoring the importance of accounting for this variable even in surveys restricted to coastal waters. However, opposite significant associations in the WA (positive) and EA (negative) were obtained (Tables 3 & 4). Curiously, in addition to increasing their size, the members of the western neritic cephalopod fauna also increased their depth range with increasing latitude (Rosa et al. 2008a). Because the depth-size associations along Atlantic margins found here have opposite signs, no single hypothesis can be supported.

Though the present study only included coastal habitats, the majority of the neritic cephalopods are not strictly limited to the continental shelves. Some undertake seasonal migration toward the shelf break or to the upper slope (up to 500 to 700 m) after breeding in more favorable onshore waters (e.g. coastal myopsid squids and incirrate octopuses *Octopus* and *Eledone*; Rosa & Sousa Reis 2004). Additionally, the strong positive depth-size relationships (and latitudinal size clines) in squids in both margins also derives, in part, from the contribution of a larger-sized group (Suborder Oegopsina) that is periodically abundant in coastal habitats (e.g. genera *Illex*, *Todaropsis* and *Todarodes*; Boyle & Rodhouse 2005). These squids are highly mobile predators with large bathymetric ranges that are well adapted to the seasonality of food resources and particularly abundant in highly productive regions at

central (temperate) latitudes (Rosa et al. 2008b). Therefore, in addition to environmental forcing and physiological constraints (discussed below), the size-depth-latitude relationships also reflect fundamental aspects of cephalopod feeding ecologies and life histories.

Relating thermal energy and resource and habitat availability with body size

Although the climate-based heat conservation hypothesis (see 'Introduction') may be plausible for endotherms (thermoregulators), it does not explain latitudinal-size relationships in marine ectotherms (thermoconformers), such as cephalopods. The prevalence of negative associations between temperature and body size in cephalopods (Tables 3 & 4) seems to support the concept of the 'temperature-size rule' (Atkinson 1994), i.e. at lower temperatures, cephalopods exhibit lower growth rates and delayed maturation but also grow to a larger body size. For instance, the giant octopus *Enteroctopus dofleini* lives at average temperatures of 10°C in the NE Pacific Ocean, achieves maturity at 10 to 15 kg (~1020 d of age), grows to more than 5 m length (>50 kg) and has a life span of 4 to 5 yr (Hartwick 1983). In contrast, the pigmy octopus *Octopus joubini* from WA tropical shallow waters (average lifetime temperatures of 25°C) matures in 182 d (to a final weight of 30 g) and attains a maximum total length of 15 cm (Hanlon 1983). Outside the neritic province, the 2 most striking examples of cold-associated gigantism are the 2 largest invertebrates of the oceans, namely the colossal *Mesonychoteuthis hamiltoni* and giant squids *Architeuthis* sp. Knowledge of the biology and ecology of those organisms is scarce (Pereira et al. 2005, Rosa & Seibel 2010a). The first is known to be a reclusive inhabitant of the circumpolar Antarctic region that can weigh >500 kg (Rosa & Seibel 2010a), while the second is a widespread large oceanic predator (up to 16 m of total length) that, presumably, lives at mesopelagic depths (in temperatures of~10 to 13°C) and has a life span of several years (Landman et al. 2004). Although many small-sized counterexamples in polar/deep-sea habitats can be identified (e.g. small octopus *Bathypolypus arcticus* in North WA), the greater disparity of sizes in these cold environments seems unequivocal. This evidence is also supported by the general increase in size disparity (coefficients of variation) toward the poles shown in the present survey (Fig. 3). Other inter-specific studies also point out that larger

size at maturity in cephalopods is a result of longer life spans (Van Heukelem 1976, Forsythe 1984, Wood & O'Dor 2000) rather than faster growth rates (Calow 1987).

The 'temperature-size rule' was only tested in single populations of a single species (in a controlled environment), and therefore it assumes that all populations of a single species have the same reaction norm (i.e. no genetic differences between size at maturity and rearing temperature; see Belk & Houston 2002, p. 807). Genetic divergence has been associated with latitudinal clines in body size (Partridge & Coyne,1997, Gockel et al. 2001, de Jong & Bochdanovits 2003); however, phenotypic plasticity seems to be a major contributor. Plasticity may be associated with thermal effects on growth and differentiation, namely on the size of cells (Partridge et al. 1994, Van Voorhies 1996), number of cells (James et al. 1997, Noach et al. 1997) or both (Zwaan et al. 2000) and at supra-cellular levels (e.g. organs; Nijhout 2003). These temperature-induced size changes can be interpreted as an integrated adaptive suite of acclimatory responses at all levels of organization to maintain aerobic scope and regulate oxygen supply (Pörtner 2002) as well as adjustments (Hochachka & Somero 2002).

Some advocate that size decrease at lower (tropical) latitudes may be a strategy to mitigate oxygen limitation (i.e. small size may reduce maintenance costs that are otherwise elevated by temperature), which may also be exacerbated by the reduction in oxygen solubility with increasing temperature (Chapelle & Peck 1999, Woods 1999). Although growth is initially faster at higher temperatures, it may slow down at a smaller size due to insufficient resource (oxygen) acquisition (Atkinson & Sibly 1997). Reduced adult size at increased temperature and lower oxygen levels has also been observed in terrestrial ectotherms (Frazier et al. 2001). However, there is no evidence that the generally smaller size of tropical cephalopods is related to oxygen limitation. In fact, shallow-living cephalopods are not generally oxygen limited (especially octopuses and cuttlefish, but even squids) because they can regulate their oxygen consumption rate to ~50% saturation. A good example is the jumbo squid *Dosidicus gigas*, a large jet-propelled predator (up to 50 kg of total weight) that lives in the eastern tropical Pacific, where temperature and oxygen are already found near the extremes in the oceans. It displays metabolic rates among the highest found in the oceans (Rosa & Seibel 2008) and undergoes diel vertical migrations into the mesopelagic oxygen minimum zones. Inter-

estingly, *D. gigas* circumvents oxygen limitation in the deep and hypoxic water (during the daytime) via metabolic suppression (Rosa & Seibel 2010b).

Increased primary productivity has also been shown to have a positive effect on body size (Aava 2001) and is considered as a potential explanation of Bergmann's rule in terrestrial habitats (Rosenzweig 1968). At a given temperature, growth rates and size at maturity increase as food or resource availability increases (Atkinson & Sibly 1997). In the present study, the differences in resource availability (as NPP) did not explain much of the variation of mean body size (Tables 3 & 4). Seasonality (or fasting endurance) has also been advocated to explain latitudinal size clines (see 'Introduction'), but we did not find any evidence to support this hypothesis because environmental seasonality (as indicated by the range in SST and NPP) did not explain much of the variance of cephalopod size.

Because the feeding, behavior and reproduction of neritic cuttlefish, octopuses and squids are closely associated with seabed characteristics, larger continental shelves (greater habitat availability) could also explain body size variation by reducing competition. Reduced competition near the poles, where the continental shelves are wider, may also permit greater body sizes. This hypothesis seems to find some support among the order Octopodida, which curiously is the group more closely associated with the seabed. However, there is no direct evidence that competition for resources is a major driver of the growth and population dynamics of cephalopods.

Cephalopods are voracious carnivores with many different feeding strategies (including cannibalism) that enable them to feed opportunistically on a wide range of prey (e.g. Table 1 in Rosa et al. 2004), and, as already pointed out, many cephalopods also evolved migratory behaviors to exploit the seasonality of food resources. Thus, the growth of cephalopods in the wild seems to be primarily limited by predation rather than food shortages (Wood & O'Dor 2000). Predation is more likely to limit the growth of cephalopods because consumption by marine mammals, sea birds and fish is widespread, with some feeding exclusively on cephalopods (e.g. some elasmobranchs; Boyle & Rodhouse 2005). Yet, for the predation hypothesis to explain the present latitudinal size trends, the predation intensity for most cephalopod species must be positively correlated with latitude, which cannot be tested because relevant data are not available.

In conclusion, temperature seemed to play the most important role in structuring the distribution of cephalopod body size along the continental shelves of the Atlantic Ocean. Our findings show only a limited role of resource availability, seasonality or competition in determining latitudinal body size patterns.

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Appendix 1. Diversity (Fig. A1) and body size (maximum mantle length, MML, Tables A1 & A2) in coastal cephalopods of the Atlantic Ocean
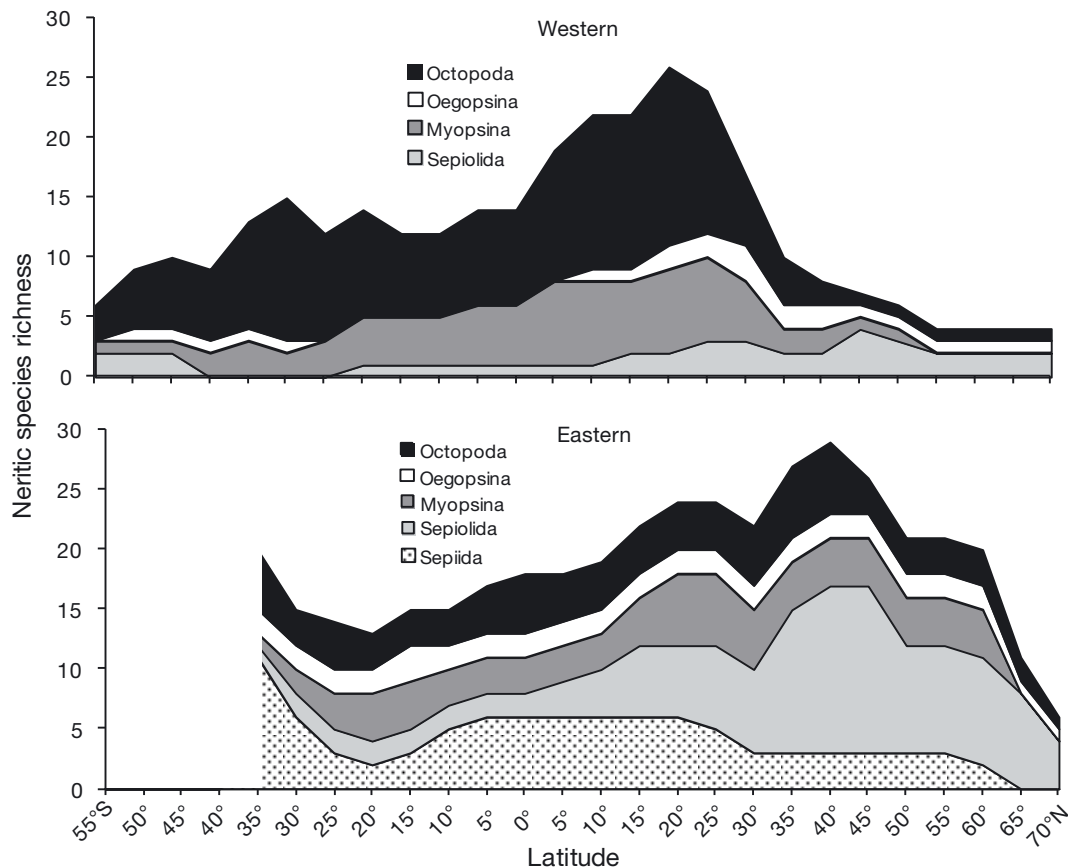

Fig. A1. Number of species per bin in both Atlantic margins (Western: from 55° S to 70° N, Eastern: from 35° S to 70° N). These diversity data were first presented and discussed by Rosa et al. (2008a)

Table A1. Cephalopod sizes in the western Atlantic

Species	Maximum mantle length (mm)
Rossia palpebrosa	45
Semirossia tenera	50
Neorossia caroli	83
Loligo gahi	280
Loligo ocula	130
Loligo pealeii	200
Loligo plei	350
Loligo roperi	70
Loligo sanpaulensis	160
Loligo surinamensis	120
Lolliguncula (*Lolliguncula*) *brevis*	120
Sepioteuthis sepioidea	200
Illex coindetti	370
Illex illecebrosus	310
Illex argentines	330
Illex oxygonius	230
Enteroctopus megalocyathus	75
Euxaoctopus pillsburyae	24
Octopus (*Octopus*) *vulgaris*	300
Octopus (*Octopus*) *briareus*	120
Octopus (*Octopus*) *burryi*	70
Octopus (*Octopus*) *carolinensis*	200
Octopus (*Octopus*) *defilippi*	55
Octopus (*Octopus*) *filosus*	72
Octopus (*Octopus*) *joubini*	45
Octopus (*Octopus*) *lobensis*	37
Octopus (*Octopus*) *macropus*	155
Octopus (*Octopus*) *maya*	119
Octopus (*Octopus*) *mercatoris*	20
Octopus (*Octopus*) *tehuelchus*	105
Octopus (*Octopus*) *verrucosus*	80
Octopus (*Octopus*) *zonatus*	30
Pteroctopus tetracirrhus	130
Pteroctopus schmidti	57
Scaeurgus unicirrhus	90
Eledone massyae	75

Species not included (no available information): *Rossia moelleri, Rossia brachyura, Rossia bullisi, Semirossia patagonica, Pickfordiateuthis pulchella, Octopus* (*Octopus*) *alecto, Octopus* (*Octopus*) *pentherinus, Octopus* (*Octopus*) *sanctaehelenae, Eledone gaucha, Vosseledone charrua*

Table A2. Cephalopod sizes in the eastern Atlantic

Species	Maximum mantle length (mm)
Sepia (*Sepia*) *officinalis*	490
Sepia (*Sepia*) *bertheloti*	175
Sepia (*Sepia*) *elobyana*	53
Sepia (*Sepia*) *hierredda*	500
Sepia (*Sepia*) *insignis*	60
Sepia (*Sepia*) *papillata*	140
Sepia (*Sepia*) *tuberculata*	82
Sepia (*Sepia*) *vermiculata*	287
Sepia (*Anomalosepia*) *australis*	85
Sepia (*Hemisepius*) *typica*	26
Sepia (*Hemisepius*) *pulchra*	22
Sepia (*Rhombosepion*) *elegans*	89
Sepia (*Rhombosepion*) *orbignyana*	120
Sepiella ornata	100
Sepiola rondeleti	60
Sepiola affinis	25
Sepiola atlantica	21
Sepiola aurantiaca	20
Sepiola intermedia	28
Sepiola knudseni	18
Sepiola ligulata	25
Sepiola robusta	28
Sepiola steenstrupiana	30
Sepiola pfefferi	13
Rondeletiola minor	23
Sepietta obscura	30
Sepietta oweniana	40
Sepietta neglecta	33
Rossia macrossoma	60
Rossia palpebrosa	45
Neorossia caroli	83
Loligo (*Loligo*) *vulgaris vulgaris*	420
Loligo (*Loligo*) *vulgaris reynaudi*	400
Loligo (*Alloteuthis*) *media*	120
Loligo (*Alloteuthis*) *subulata*	200
Loligo (*Alloteuthis*) *africana*	190
Loligo forbesii	900
Lolliguncula (*Lolliguncula*) *mercatoris*	50
Illex coindetti	370
Todarodes sagittatus	750
Todarodes angolensis	350
Todaropsis eblanae	270
Octopus (*Octopus*) *vulgaris*	300
Octopus (*Octopus*) *burryi*	70
Octopus (*Octopus*) *defilippi*	55
Octopus (*Octopus*) *macropus*	155
Octopus (*Octopus*) *salutii*	130
Pteroctopus tetracirrhus	130
Scaeurgus unicirrhus	90
Eledone cirrhosa	155
Eledone moschata	188

Species not included (no available information): *Sepia* (*Sepia*) *angulata, Sepia* (*Hemisepius*) *dubia, Sepia* (*Hemisepius*) *robsoni, Sepia* (*Rhombosepion*) *hieronis, Inioteuthis capensis, Aphrodoctopus schultzei, Enteroctopus magnificus, Octopus* (*Octopus*) *sanctaehelenae, Eledone nigra, Eledone thysanophora*