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**A Regra de Bergmann: estudos de caso e suas implicações**

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Dissertação apresentada ao Programa de  
Programa de Pós-Graduação em  
Ciências Biológicas, da Universidade  
Federal do Estado do Rio de Janeiro  
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Mestre em Biodiversidade Neotropical.

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Rio de Janeiro, \_\_\_\_ de \_\_\_\_\_ de 2016

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## SUMÁRIO

<b>1. INTRODUÇÃO GERAL</b> .....	01
<b>2. CAPÍTULO I: The Application of Bergmann's Rule to <i>Carollia perspicillata</i> Linnaeus 1758 (Mammalia, Chiroptera)</b> .....	05
2.1. Abstract .....	05
2.2. Introduction .....	05
2.3. Material and Methods .....	06
2.4. Results .....	08
2.5. Discussion and Conclusion .....	09
2.6. Acknowledgements .....	12
2.7. References .....	12
<b>3. CAPÍTULO II: The application of Bergmann's Rule to the marine environment: a test with fishes</b> .....	14
3.1. Abstract .....	15
3.2. Introduction .....	16
3.3. Material and Methods .....	16
3.4. Results .....	18
3.5. Discussion and Conclusion .....	19
3.6. Acknowledgements .....	22
3.7. Tables and Figures .....	23
<b>4. CONSIDERAÇÕES FINAIS</b> .....	31
<b>5. REFERÊNCIAS BIBLIOGRÁFICAS</b> .....	32

## INTRODUÇÃO GERAL

Entre os atributos das espécies, o tamanho do corpo é considerado um dos mais importantes, sendo identificado como um fator crítico para a definição de padrões e processos ecológicos e evolutivos (Gillooly *et al.*, 2001; Brown *et al.*, 2004). De fato, o tamanho do corpo está relacionado a quase todos os aspectos de um organismo, sejam morfológicos, fisiológicos, ecológicos ou evolutivos (Stanley, 1973; Cardillo *et al.*, 2005; Olden *et al.*, 2007; Enquist *et al.* 2015). O estudo dos tamanhos de corpo pode revelar mecanismos e forças que estruturam a diversidade biológica (Grime, 2006; Stegen *et al.*, 2009), o que pode contribuir para a melhora na generalidade e na previsibilidade de modelos ecológicos (Diaz *et al.*, 2004). Tais estudos levaram à formação de várias regras ecogeográficas em ampla escala, com destaque para as regras de Foster, de Cope e de Bergmann, que tratam do tamanho do corpo e sua relação com inúmeros fatores bióticos e abióticos (Bergmann, 1847; Cope, 1887; Foster, 1964).

A Regra de Bergmann é um princípio ecogeográfico que afirma que, dentro de um clado taxonômico amplamente distribuído, populações e espécies de maior tamanho encontram-se em ambientes mais frios e espécies de menor tamanho são encontradas em regiões mais quentes. Ao longo dos anos, esta regra tem sido avaliada por diversos pesquisadores, em estudos aplicados a diversos grupos de organismos, o que deu origem a um extenso debate acerca de sua validade e definição. Parte deste debate deve-se ao fato de que o padrão foi originalmente descrito em alemão, de modo que a maioria dos pesquisadores nunca leu o artigo original e tomou como base traduções feitas por outros artigos. O padrão foi proposto em 1847 por Carl Bergmann, que, de acordo com a tradução direta realizada por Watt *et al.* (2010), afirma que:

*"for the amount of warmth, of which an animal can raise itself above its surrounding, the relation of its volume to its surface is of course of great importance; it is thus clear, that animals, have to create less warmth in relation to their size the larger they are, to gain a certain increase in temperature above the one of their surrounding. This law must be of great importance on the mode of life of warm-blooded animals"* and *"if there would*

*be genera, which species are distinguished as much as possible only by size, the smaller species would all need a warmer climate.”*

O conceito original proposto por Bergmann sugere que o mecanismo que determina o padrão seria a razão superfície/volume, que é menor em animais maiores, o que resultaria em uma vantagem energética em ambientes mais frios. O metabolismo é um importante fator para o entendimento do padrão, devendo ser enfatizado que a regra, como proposta originalmente, refere-se à endotermia, já que propõe que o tamanho corporal possui valor adaptativo e que animais grandes necessitam produzir proporcionalmente menos calor para aumentar a sua temperatura corporal acima das encontradas no ambiente.

De acordo com Watt *et al.* (2010), “*Bergmann’s original text leaves no room for interpretation; Bergmann clearly compared species within genera and proves the rule with empirical data. However, Bergmann did leave the door open for testing at other taxonomic levels because he himself tried to test the rule among races of domestic animals; thus, authors would be advised to cite the rule as an interspecific phenomenon, but recognize that testing at other taxonomic levels can be done...*”.

Embora o trabalho original evidencie que a Regra de Bergmann compara a diferença de tamanho corporal em espécies dentro de um mesmo gênero, persiste uma discussão entre os pesquisadores sobre o nível de organização em que a regra deve ser aplicada. Meiri (2011) argumenta que a Regra de Bergmann pode ser estudada considerando qualquer táxon e nível taxonômico, além de poder ser aplicada em uma abordagem de assembleia, utilizada em estudos do gradiente de tamanho corporal em grupos de homeotérmicos, vertebrados e invertebrados (*e.g.* Olalla- Tàrraga *et al.*, 2006; Diniz-Filho *et al.*, 2007).

Além disso, o padrão tem sido corroborado por diversos estudos, tanto com endotérmicos (*e.g.* Blackburn & Ruggiero, 2001; Storz *et al.*, 2001; Blackburn & Hawkins, 2004) quanto ectotérmicos (*e.g.* Belk & Houston, 2002; Arnett & Gotelli, 2003; Olalla-Tàrraga *et al.*, 2006; Wilson, 2009; Zamora-Camacho *et al.*, 2014; Penniket & Cree, 2015), sendo a hipótese de explicação original, por vezes, aplicada a animais ectotérmicos (Olalla-Tàrraga, 2011; Zamorra-Camacho *et al.*, 2014).

Shelomi (2012), em recente revisão da aplicação da Regra de Bergmann em insetos, verificou que em 34% dos estudos o padrão foi identificado, em 30% foi detectado em sua forma “Converse” e em 36% dos estudos não foi registrado, sendo esta inconsistência na

detecção do padrão muitas vezes associada ao design experimental empregado. O mesmo desacordo acerca da aplicação do padrão foi observado para outros táxons superiores ou grupos funcionais, como moluscos bivalves (Berke *et al.* 2013), répteis (Pincheira-Donoso & Meiri, 2013), peixes dulcícolas (Rypel, 2014) e animais ectotérmicos (Vinarski, 2014).

Devido a essa controvérsia, muitas hipóteses foram propostas ao longo dos anos para explicar o padrão; adotada por vários estudos com animais ectotérmicos, a hipótese da resistência à escassez de recursos postula que animais de grande porte poderiam tolerá-la mais, aumentando suas reservas energéticas de gordura, ao invés de aumentar suas taxas metabólicas (Arnett & Gotelli, 2003; Blackburn & Hawkins, 2004; Rodríguez *et al.*, 2006), de forma que haveria uma vantagem adaptativa nos ambientes sazonais das altas latitudes. Outra hipótese poderia ser a influência da temperatura nas taxas de crescimento, uma vez que animais ectotérmicos expostos a baixas temperaturas com frequência irão amadurecer mais tardiamente, porém com maior tamanho corporal (Regra da Temperatura/Tamanho), assim sendo, o tamanho máximo em adultos poderia ser determinado pelo tamanho atingido na maturidade, como observado por Penniket & Cree (2015).

O estudo de Medina e colaboradores (2007) com roedores subterrâneos mostrou que algumas estratégias de vida de alguns grupos animais podem afetar a observação deste padrão, tais como os roedores do gênero *Ctenomys* (tuco-tucos) que também apresentaram a Regra de Bergmann “Converse”. Como o hábito de vida subterrâneo pode isolar estes roedores das temperaturas externas, o gradiente de tamanho corporal observado provavelmente estará mais relacionado à sazonalidade, à energia disponível no ambiente, à produtividade primária e/ou à intensidade da predação, do que propriamente à exposição a temperaturas externas.

Atualmente se reconhece a influência que diversos aspectos da história de vida dos animais podem ter no estabelecimento deste padrão, como o hábito de vida (Medina *et al.*, 2007; Feldman & Meiri, 2014; Penniket & Cree, 2015), a estratégia reprodutiva (Wilson, 2009), o nicho trófico (Ho *et al.* 2010), além da associação com outros padrões ecogeográficos existentes para o mesmo gradiente (Boyer *et al.*, 2010; Slavenko & Meiri, 2015). Apesar de todas estas explicações propostas, e do mecanismo original de termoregulação ainda requerer mais testes para ser considerado um bom fator na determinação do tamanho corporal (Zamora-Camacho *et al.*, 2014; Penniket & Cree, 2015),



ainda persiste a necessidade de uma proposta unificadora para explicar a Regra de Bergmann (Olalla-Tárraga, 2011).

Embora o número de estudos relacionados à Regra de Bergmann tenha aumentado bastante nas últimas décadas, existem claros vieses na literatura. É ilustrativo o fato de que 24% dos 390 artigos publicados sobre a Regra de Bergmann entre 1991 e 2013 tenham sido realizados com mamíferos. Além disto, dentre os 92 estudos com mamíferos, apenas dois foram realizados com morcegos, ainda que este grupo represente uma parcela significativa da diversidade de mamíferos. A existência de viés taxonômico também foi relatada por outros autores (Meiri *et al.*, 2004; Vinarski, 2014), mostrando a necessidade de se continuar a avaliar a aplicabilidade deste padrão para outros táxons. Cumpre destacar que existe também um viés ambiental, pois embora os oceanos cubram cerca de 70% da superfície do planeta, somente 10 a 15% dos estudos em biogeografia foram realizados neste ambiente.

Tendo em vista o cenário de controvérsias e vieses em torno da Regra de Bergmann, esta dissertação se propõe a testar a aplicabilidade da Regra sob óticas distintas, através de dois estudos de caso que abrangem situações contrastantes em termos de nível de organização (intraespecífico *vs.* assembleia), de fonte de energia (endotérmico *vs.* ectotérmico), de ambiente (terrestre *vs.* marinho) e de extensão geográfica (regional *vs.* global). No Capítulo I testamos até que ponto o padrão e o mecanismo descritos por Bergmann podem ser aplicados a populações brasileiras do morcego *Carollia perspicillata*, espécie de ampla distribuição na América do Sul, que representa um mamífero endotérmico com estilo de vida distinto (voador) e com uma peculiaridade na forma do corpo (asa desnuda). No Capítulo II iremos além do postulado original, testando a aplicabilidade da Regra de Bergmann a animais ectotérmicos, analisando a variação de tamanho corporal em assembleias de peixes ósseos e cartilagosos, ao longo das principais regiões oceânicas do mundo.

### The Application of Bergmann's Rule to *Carollia perspicillata* Linnaeus 1758 (Mammalia, Chiroptera)

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#### ARTICLE

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**Abstract.** Bergmann's Rule describes the association between body size of species and latitude. The proposed mechanism to explain the pattern would be the lowest surface/volume ratio found in large animals, which should result in an energy advantage in cold environments. The present study tested to what extent this pattern can be applied in bat populations of *Carollia perspicillata* (Linnaeus, 1758). We used secondary data, taken from the collection of Universidade Federal Rural do Rio de Janeiro (UFRRJ) and raw data provided by researchers, covering a latitude gradient ranging from 23°03' S to 0°10' N, at altitudes ranging from 10 to 1093m above sea level. Climatological data were obtained from the website of Instituto Nacional de Meteorologia (INMET). Body size analyses were based on mean and maximum length of forearm and body mass, and carried out through latitude, altitude and temperature gradients. A total of 488 adult specimens were analyzed, summarizing data for 23 localities. Body size variables showed a decrease toward higher latitudes and higher altitudes, and an increase in relation to increasing temperature. The results partially follow an inverse trend of the original proposal, called Bergmann's Rule "converse". Bats's wings are highly vascularized naked membranes, making their surface/volume ratio higher than that of other animals of similar size; thus a large body size would in fact result in bigger ratios and greater heat loss. The low values of all explicability indexes ( $R^2$ ) and linear coefficients ( $\beta$ ) suggest that geographical variation in a species' morphology cannot be only explained on the basis of latitudinal clines.

**Keywords:** Bergmann's Rule; Bats; Morphological variation; Brazil; Biogeography.

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#### Introduction

##### *Bergmann's Rule*

Bergmann's Rule describes the tendency for positive correlation between an animal's body size in higher monophyletic taxon and the latitude inhabited by these species (Blackburn et al. 1999). This new definition of Bergmann's Rule differs from the original. This version suggests that there is a relationship between two variables, body size and latitude, and that this pattern can be described distinctly from mechanism proposed originally to explain it. Although they suggest this definition independent of heat conservation hypothesis, this manuscript offers several mechanisms that could explain Bergmann's Rule (phylogenetic

hypotheses, migration ability hypothesis, starvation resistance hypothesis and resource availability hypothesis).

Bergmann's original concept was that the mechanism which controls the pattern would be the surface / volume ratio, which is small for large animals, giving them an energy advantage in cold environments. The Bergmann's Rule, as it was originally proposed, refers to endothermy, given the proposed theory that the body size has adaptive value and larger animals need to produce less heat in proportion to raise their body temperature above that of their the surroundings (Watt et al. 2010). The metabolism is an important factor in understanding the rule, and it should be emphasized that the terms endotherm and

homeothermy are not synonymous. Endotherm is defined as the body's ability to produce heat by metabolic activity, while homeothermy refers to the ability to conserve body heat to withstand temperature fluctuations in the environment (Ricklefs & Miller, 1999).

The problem with this hypothesis is that the decrease in cooling rate related to body size is small when compared to the effects of thermal insulation. Another way to understand this mechanism would be that the variation in body size responds to the demands of cooling, rather than keeping warm. Thus, animals that live in hot, dry environments take advantage of evapotranspiration as a mechanism to cool. Animals that live in warm and humid environments cannot make use of this mechanism, as an alternative strategy to increase the rate of heat loss through a large surface/volume ratio (Blackburn & Hawkins, 2004).

Another hypothesis is widely used in studies of ectothermic, the starvation resistance hypothesis. It states that larger animals can tolerate resource scarcity better, increasing fat reserves instead of increasing their metabolic rates (Arnett & Gotelli, 2003; Blackburn & Hawkins, 2004; Rodríguez et al., 2006). This may be a selective advantage in seasonal environments in higher latitudes. Although this hypothesis is supported by some taxa (birds and mammals), in other species (insects and insectivores) exceptions are noted, because these animals can take selective advantage of seasonal scarcity by adopting other strategies.

From a huge literature review, from 1991 until now, 390 manuscripts works with Bergmann's Rule, with 92 of them testing this pattern with mammals. Although Chiroptera represents about 40-50% of mammal species in many tropical regions (Timm, 1994), and considering that some studies of the rule in mammals either omit this taxon altogether (Rodríguez et al., 2008) or do not differentiate it from other mammals (Rodríguez et al. 2006), only two studies tested this rule (intraspecifically) with bats. Despite the huge data reviewed, there are few studies testing the rule for bats, and only McLellan (1984) supplies data on *Carollia perspicillata*, showing the species's compliance with the predictions of the rule.

The Phyllostomidae is the most diverse family in the Neotropical region, with 160 recognized species in 57 genera (Vaughan et al. 2000).

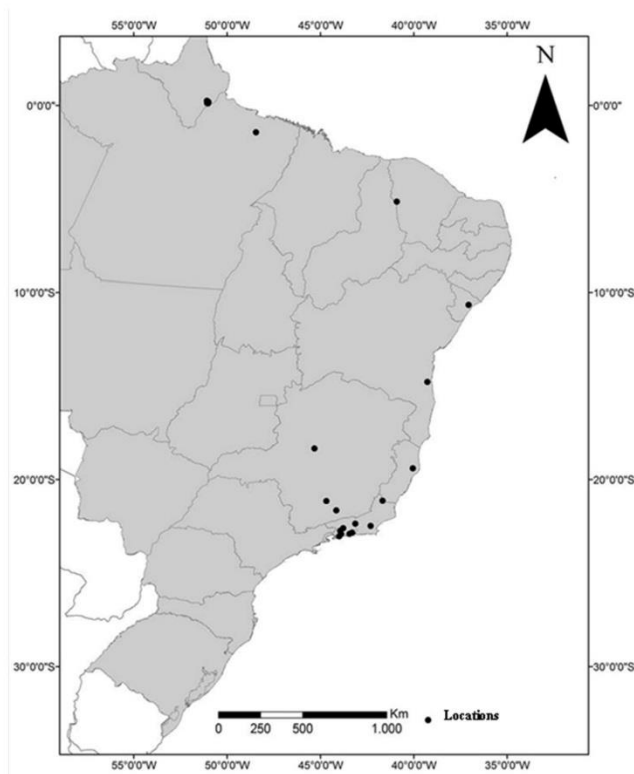
*Carollia perspicillata* (Linnaeus, 1758) is a robust bat, small to medium-sized (body mass around 18.5g; total length, 66-95mm). Their geographical distribution extends from Veracruz and Oaxaca (Mexico) to the south of Bolivia, Paraguay and Brazil, where it is one of the most captured bats (Cloutier & Thomas, 1992). Their diet consists mainly of various species of fruit and insects, and their preference is for fruits of the genus *Piper* (Altringham, 1996; Fleming, 1988; Mello et al. 2004) and is considered an important agent of seed dispersal, especially for the *Piperaceae* family (Fleming & Heithaus, 1981; Bizerril & Raw, 1998).

The present study aims to test the extent to which the pattern described by Bergmann's Rule can be applied to Brazilian populations of *Carollia perspicillata*, regarding the proposed mechanism in Bergmann's original concept.

## Material and Methods

This study used secondary data provided by various researchers and obtained from log books from Adriano Lucio Peracchi Zoological collection (ALP), located at the Universidade Federal Rural do Rio de Janeiro (UFRRJ). These data are from various collects that were taken between the 1970s and 2011, carried out in eight Brazilian states (Rio de Janeiro, Minas Gerais, Espírito Santo, Bahia, Sergipe, Ceará, Pará and Amapá), covering a latitude gradient ranging from 23°03' S (Marambaia / RJ) to 0°10' N (Macapá / AP), at altitudes ranging from 10 to 1093m above sea level (Figure 1).

Climatological data – maximum, mean and minimum temperatures – were obtained from the Instituto Nacional de Meteorologia (INMET) website (Table 1). Due to the time span of the used data (40 years of collection, approximately), they were based on Brazilian climatological normals, reference points used by climatologists to compare current climatological trends to that of the past or what is considered “normal”. A Normal is defined as the arithmetic average of a climate element (e.g. temperature) over a 30-year period, as it is long enough to filter out any interannual variation or anomalies, but also short enough to be able to show longer climatic trends. The current climate normal period is calculated from 1 January 1961 to 31 December 1990 (WMO, 2013).



**Figure 1.** Map with the locations where *C. perspicillata* was sampled. Name of location, number of collection points evaluated, geographical coordinates and altitude: 1 - Amapá 6 (0°06' - 0°10'N 50°59' - 51°04'O, 10-20 m); 2 - Pará 1 (1°26'S 48°27'O, 20 m); 3 - Ceará 1 (5°08'S 40°54'O, 680 m); 4 - Sergipe 1 (10°55'S 37°04'O, 10 m); 5 - Bahia 1 (14°46'S 39°16'O, 60 m); 6 - Pirapitinga 1 (18°22'S 45°19'O, 600 m); 7 - Linhares 1 (19°23'S 40°03'O, 27 m); 8 - Bom Jesus 1 (21°07'S 41°40'O, 100 m); 9 - Minas Gerais 2 (21°08' - 21°40'N 44°08' - 44°40'O, 885-1093m); 10 - Silva Jardim 1 (22°30'S 42°18'O, 70 m); 11 - Itaipava 1 (22°23'S 43°07'O, 700 m); 12 - Paracambi 1 (22°37'S 43°47'O, 300 m), Serra da Tiririca 1 (22°52'S 43°17'O, 70 m), Pedra Branca 1 (22°55'S 43°26'O, 140 m), Marambaia 1 (23°03'S 43°59'O, 10 m), Pirai 1 (22°46'S 43°56'O, 450 m); Ilha de Itacuruçá 1 (22°56'S 43°53'O, 10m).

Although Bergmann's Rule has been originally formulated for body size of endotherms, according to the translation provided by Watt et al. (2010), it doesn't specify which morphological characters surrogate for body size. Therefore some studies used linear measurements, body mass, dental measurements or a combination of characters for size parameter (Meiri & Dayan, 2003). In order to analyze body size of the individuals we used mean and maximum values (Fisher et al. 2010; Berke et al. 2012) of forearm length (in mm) and body mass (in grams), measures commonly recorded in captures of bats (Teixeira et al. 2013) and more easily obtained from secondary data. Besides, for bats, length of forearm is a common estimate of body size (Bornholdt et al. 2008). The measures are from adults, with males and females being treated separately because of sexual dimorphism

(Pine, 1972; Cloutier & Thomas, 1992). To avoid the influence of seasonal and inter-annual variation in reproductive condition and nutrient reserves, analysis of the body mass data was restricted to males and non-pregnant and non-lactating females (Storz et al. 2001).

For the pattern analysis, linear regression analyses (OLS), were plotted body size of the data summarized for all 23 sampled populations (Y axis) along the latitudinal and altitudinal gradients at which the species occurs (X axis). As the Rule's mechanism involves heat conservation, we saw fit to also test body size along the thermal gradient (maximum, mean and minimum temperatures). The relationship of the pattern was evaluated using the index explicability ( $R^2$ ), with the significance limit of 0.0127 for the Šidák method and 0.0125 for the Bonferroni method. We measured the degree of spatial autocorrelation in model residuals for all tests of Bergmann's Rule by computing the Moran's I statistic for neighborhood sizes of 27, 112, 253, 457, 1059, 1673, 2192, 2497, 2619 and 2684 km (Diniz-Filho et al. 2002; Hawkins et al. 2007). To control the spatial autocorrelation was performed simultaneous autoregressive (SAR) models (Hawkins et al. 2007).

We used multiple regression models to test factors that might explain the Bergmann's Rule based on heat conservation hypothesis, including maximum, mean and minimum temperatures (Diniz-Filho et al. 2008). In order to account the possible strong collinearity among these variables in our data set, we used the Akaike information criterion (AIC) which provides a parsimonious balance between model predictive power and complexity. The best models are those with the lowest AIC values, but the common approach is to use the  $\Delta AIC$  (difference between AIC of the model and the minimum AIC), whereas values less than 2 indicate models that have good fit and the  $w_i$  (Akaike weight), which show the explanatory power (probability) of the models (Diniz-Filho et al. 2008).

We used the software package PAST 3 (Hammer et al. 2001) to analyses data normality by the normality Kolmogorov-Smirnov test and data homoscedasticity by Breusch-Pagan test and

**Table 1.** Environmental variables from localities considered in this study. Mx Temp – maximum temperature; M Temp – mean temperature; Mi Temp – minimum temperature.

Locality	Altitude (m)	Latitude	Longitude	Mx Temp (°C)	M Temp (°C)	Mi Temp (°C)
Amapá 01	10	0.2469	-51.0784	30	27	23
Amapá 02	10	0.2151	-51.0266	30	27	23
Amapá 03	11	0.1813	-50.9946	30	27	23
Amapá 04	14	0.1416	-51.0089	30	27	23
Amapá 05	10	0.1233	-51.0669	30	27	23
Amapá 06	20	0.1180	-51.0130	30	27	23
Pará	20	-1.4351	-48.4504	32	27	23
Ceará	680	-5.1422	-40.9131	34	27	21
Sergipe	10	-10.6667	-37.4167	30	25	23
Bahia	60	-14.7818	-39.2674	28	25	21
Pirapitinga	600	-18.3667	-45.3167	30	23	17
Linhares	27	-19.3967	-40.0520	30	23	21
Bom Jesus	100	-21.1331	-41.6696	30	23	21
Minas Gerais 01	885	-21.1468	-44.6757	26	19	15
Minas Gerais 02	1093	-21.6773	-44.1464	26	19	15
Itaipava	700	-22.3871	-43.1326	28	21	17
Silva Jardim	70	-22.5093	-42.3087	28	21	19
Paracambi	300	-22.6282	-43.7845	28	21	17
Pirai	450	-22.7672	-43.9419	28	23	17
Serra da Tiririca	70	-22.8667	-43.3000	28	23	19
Pedra branca	140	-22.9307	-43.4806	28	23	19
Ilha de Itacuruçá	10	-22.9433	-43.8928	28	23	17
Marambaia	10	-23.0578	-43.9903	28	23	19

**Table 2.** Descriptive statistics of data used in the analyses, relating to length of forearm.

Locality	Males					Females				
	Mean (mm)	Standard Deviation	Range	Variance	n	Mean (mm)	Standard Deviation	Range	Variance	n
Amapá 01	40.6	0.85	40.00 - 41.20	0.72	2	40.54	1.01	39.60 - 41.60	1.02	5
Amapá 02	39.23	0.35	38.90 - 39.60	0.12	3	39.38	0.7	38.80 - 40.40	0.5	4
Amapá 03	40.06	0.59	39.20 - 41.30	0.35	13	40.39	1.65	38.30 - 45.80	2.72	27
Amapá 04	40.81	1.63	38.10 - 43.30	2.65	14	40.8	1.38	38.30 - 43.60	1.9	12
Amapá 05	39.65	0.6	39.00 - 40.30	0.36	4	39.27	0.64	37.90 - 40.30	0.41	11
Amapá 06	40.18	1.17	38.20 - 42.30	1.37	29	40.42	0.81	38.50 - 41.40	0.66	17
Pará	40.65	3.44	35.25 - 43.80	11.81	5	40.76	3.55	35.50 - 43.30	12.63	4
Ceará	39.6	1.51	38.00 - 41.00	2.28	3	41.3	-	41.3	-	1
Sergipe	41.32	1.45	38.30 - 44.70	2.09	25	41.63	1.04	40.00 - 43.30	1.08	18
Bahia	40.1	-	40.1	-	1	41.08	1.38	39.35 - 43.70	1.9	10
Pirapitinga	41.45	1.41	39.88 - 42.62	2	3	41.27	0.74	40.38 - 42.46	0.55	7
Linhares	38.7	2.01	34.10 - 41.40	4.02	10	39.44	0.94	38.20 - 40.50	0.89	4
Bom Jesus	38.74	1.05	36.67 - 40.60	1.1	16	38.96	1.15	37.23 - 41.25	1.33	18
Minas Gerais 01	38.83	0.55	38.30 - 39.40	0.3	3	37.3	2.25	35.00 - 39.50	5.07	3
Minas Gerais 02	39.63	1.74	38.30 - 41.60	3.02	3	38	1.41	37.00 - 39.00	2	2
Itaipava	39.25	1.38	37.62 - 40.92	1.91	4	40.01	0.99	38.70 - 41.70	0.99	6
Silva Jardim	39.35	1.55	36.00 - 43.86	2.4	55	40.43	1.48	37.00 - 43.50	2.18	57
Paracambi	38.98	1.65	36.30 - 42.00	2.74	13	39.77	1.49	37.50 - 42.00	2.22	7
Pirai	39.32	0.8	38.00 - 40.40	0.64	10	39.58	1.54	37.70 - 42.80	2.36	9
Serra da Tiririca	39.17	2.46	36.60 - 41.50	6.04	3	38.38	1.13	37.00 - 39.70	1.28	4
Pedra Branca	39.28	1.84	35.70 - 41.60	3.39	9	41	2.97	38.40 - 45.60	8.8	5
Ilha de Itacuruçá	38.88	0.78	38.00 - 40.30	0.61	6	39.27	1.31	38.00 - 41.00	1.71	6
Marambaia	39.83	0.38	39.40 - 40.10	0.14	3	-	-	-	-	0
<b>Total</b>	<b>39.75</b>	<b>1.62</b>	<b>34.10 - 44.70</b>	<b>2.61</b>	<b>237</b>	<b>40.22</b>	<b>1.6</b>	<b>35.00 - 45.80</b>	<b>2.55</b>	<b>237</b>

the software package SAM (Rangel et al. 2010) to model selection and all regression analyses.

## Results

We analyzed 488 adult specimens of *C. perspicillata*, summarizing data for 23 localities. Due to the availability of morphological data, the

regression analyzes for the forearm length were performed on a sample of 474 specimens (Table 2) while the body mass was examined in 461 specimens (Table 3).

All dependent variables (mean and maximum length of forearm and body mass) showed data normality and homoscedasticity. Analysis of

geographic variation in body size based on mean and maximum length of forearm and body mass, in both genders, showed a decrease toward higher latitudes (Figures 2 and 3). The linear regression analysis found that latitude has a significant positive correlation only with mean body mass ( $R^2 = 0.306$ ,  $\beta = 0.036$ ,  $p = 0.006$ ) for males and with mean forearm length ( $R^2 = 0.256$ ,  $\beta = 0.036$ ,  $p = 0.014$ ) of males without considering the Bonferroni correction of significance. It is important to note that this positive correlation ( $\beta > 0$ ), however, demonstrates an inverse relationship between these two variables, as the latitudes of the southern hemisphere are expressed in decimal degrees, and thus have negative values (Figures 2 and 3). When observing the altitudinal pattern, none of them showed a significant relationship.

The analyses based on mean and maximum values of the forearm length and body mass, in both sexes, showed an increase in relation to the maximum, mean and minimum location temperatures (Table 4).

Analyzing the model selection, we found that only three models have significant relationships. The mean forearm length ( $R^2 = 0.301$ ,  $\beta = 0.370$ ,  $p = 0.01$ ) of females and mean body mass ( $R^2 = 0.403$ ,  $\beta = 0.279$ ,  $p = 0.001$ ) of males showed a significant positive relationship with mean temperature. The mean forearm length of females ( $R^2 = 0.350$ ,  $\beta = 0.370$ ,  $p = 0.004$ ) showed a significant positive relationship with maximum temperature. Without considering the Bonferroni correction of significance, others seven models show positive relationship with the independent variables analysed (Table 4).

### Discussion and Conclusion

Bergmann's Rule has been used to explain the increase in body size, with animals of colder environments exhibiting larger bodies and a smaller relative surface area, which allows them to obtain an adaptive advantage in a greater efficiency on heat retention. According to this explanation, one would expect to see an increase in body size with increasing distance from the equator (McLellan, 1984). In this study, we detected partially variation in body size of *Carollia perspicillata* (Figures 2 and 3), indicated by a decrease in forearm length and body mass in relation to an increasing latitude and thus with decreasing temperature. Hence, variation in body size follows a reverse trend, called Bergmann's Rule "converse", in which larger individuals inhabit the warmer areas and smaller inhabit cooler areas. According to the translation of Bergmann's Rule provided by Watt et al. (2010), the mechanism that guides this would be the surface/volume ratio, which decreases with increasing body size, reducing exposure to the environment and giving individuals a greater

energy advantage in cold environments. However, it can be expected that bats differ from the typical pattern of other homeothermic animals due to biophysical issues. Their wings are highly vascularized and naked, which causes the surface/volume ratio, and hence their exposure, to be higher than birds and other non-flying mammals of similar body mass (Storz et al. 2001). Following this reasoning, the decrease in body size (not the increase) could give adaptive advantage from more efficient heat retention.

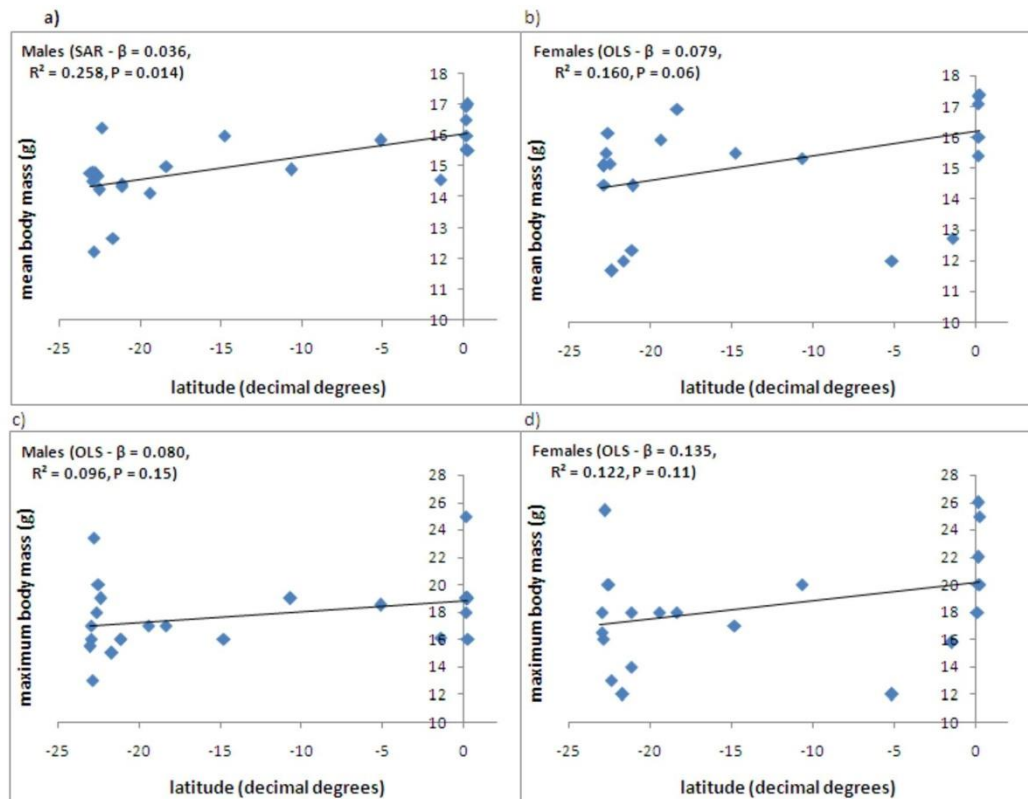
When looking at the thermal gradient, considering the significance established by corrected and uncorrected  $p$ , the number of non-significant models was higher in those that use maximum temperature as independent variable (Table 4).

This result may be due to behavioral factors of species. *C. perspicillata* commonly inhabits caves, hollow trees, culverts and tunnels, and its diurnal activity is occupied (98% of the time) by non-aggressive activities such as rest, scanning, vocalization and crawling (Porter, 1979 cited by Cloutier & Thomas, 1992). According to Medina et al. (2007), isolation from the external environment could cause body size to be less affected by abiotic factors, such as temperature, suggesting that variations in body size respond to other factors.

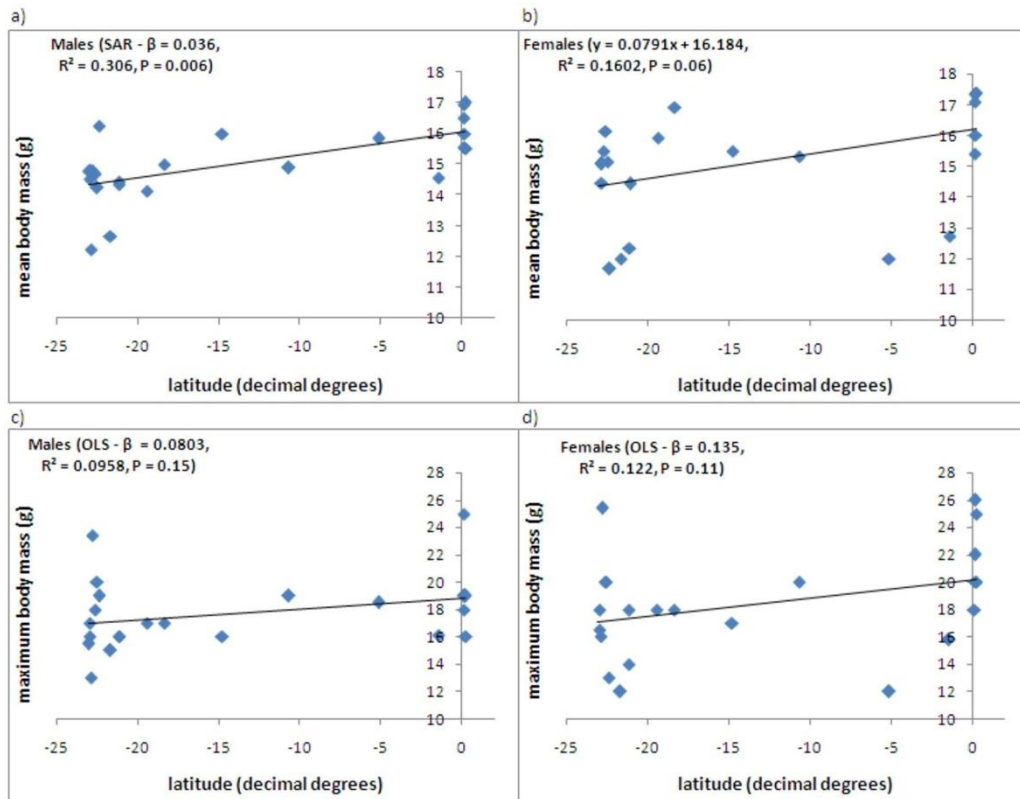
Local humidity levels can be a factor that influences body size if we consider the exposure to the environment due to wing size. Hot dry conditions would allow animals to take advantage of evapotranspiration as a mechanism to cool off, but at the same time make them susceptible to drying out in arid environments. Hot and humid environments affect heat dissipation in body (Storz et al. 2001), which could reduce heat loss into the environment. However it should be noted that, in this study, this influence could not be measured accurately due to the time span of the data used (40 years of collection, approximately), and to changes in the composition of the collection sites. With increasing urbanization, cover has been removed or altered in many cases, altering the microclimate site along with it. The results observed to date partially indicate that geographic variation has an influence on body size in *C. perspicillata*, as proposed by Bergmann's Rule, through the surface / volume ratio. However, a more accurate assessment of this mechanism requires the measurement of other components of the wing in addition to the length of the forearm Storz et al. (2001) and Stockwell (2001). The low values of all explicability indexes ( $R^2$ ) and linear coefficients ( $\beta$ ) suggest that geographical variation in a species' morphology cannot be only explained on the basis of latitudinal clines (Meiri et al. 2007). Other species (phylogeny, diet and spatial

**Table 3.** Descriptive statistics of data used in the analyses, relating to body mass.

Locality	Males					Females				
	Mean (g)	Standard Deviation	Range	Variance	n	Mean (g)	Standard Deviation	Range	Variance	n
Amapá 01	15.5	0.71	15.00 - 15.50	0.5	2	17.4	3.21	13.00 - 20.00	10.3	5
Amapá 02	17	1.73	16.00 - 19.00	3	3	19.5	3.7	17.00 - 25.00	13.67	4
Amapá 03	16	1.73	12.00 - 19.00	3	13	16	2.02	12.00 - 20.00	4.08	27
Amapá 04	16.93	3.5	14.00 - 25.00	12.23	14	17.33	3.47	14.00 - 26.00	12.06	12
Amapá 05	16.5	1.91	14.00 - 18.00	3.67	4	17.09	3.08	14.00 - 22.00	9.49	11
Amapá 06	15.55	2.1	11.00 - 19.00	4.4	29	15.41	1.46	13.00 - 18.00	2.13	17
Pará	14.56	2.09	11.25 - 16.10	4.37	6	12.72	2.08	10.00 - 15.80	4.32	8
Ceará	15.83	2.31	14.50 - 18.50	5.33	3	12	-	12	-	1
Sergipe	14.88	1.39	12.00 - 19.00	1.94	25	15.33	2.81	10.00 - 20.00	7.88	18
Bahia	16	-	16	-	1	15.5	0.97	14.00 - 17.00	0.94	10
Pirapitinga	15	2	13.00 - 17.00	4	3	16.93	1.27	14.50 - 18.00	1.62	7
Linhares	14.13	2.15	10.00 - 17.00	4.64	10	15.93	1.79	14.80 - 18.00	3.21	3
Bom Jesus	14.44	1.21	12.00 - 16.00	1.46	16	14.43	1.4	13.00 - 18.00	1.96	14
Minas Gerais 01	14.33	2.08	12.00 - 16.00	4.33	3	12.33	2.08	10.00 - 14.00	4.33	3
Minas Gerais 02	12.67	2.08	11.00 - 15.00	4.33	3	12	-	12	-	1
Itaipava	16.25	2.63	14.00 - 19.00	6.92	4	11.67	1.21	10.00 - 13.00	1.47	6
Silva Jardim	14.24	2.77	10.00 - 20.00	7.66	58	15.14	2.7	10.00 - 20.00	7.27	43
Paracambi	14.69	1.84	12.00 - 18.00	3.4	13	16.14	2.19	13.00 - 20.00	4.81	7
Pirai	14.76	3.2	12.40 - 23.40	10.24	10	15.49	4.13	12.80 - 25.40	17.06	9
Serra da Tiririca	12.23	1.08	11.00 - 13.00	1.16	3	14.47	1.36	13.40 - 16.00	1.85	3
Pedra Branca	14.52	0.79	13.50 - 16.00	0.63	9	15.08	1.45	13.50 - 16.50	2.09	5
Ilha de Itacuruçá	14.83	1.17	14.00 - 17.00	1.37	6	15.08	1.74	13.00 - 18.00	3.04	6
Marambaia	14.77	0.75	14.00 - 15.50	0.56	3	-	-	-	-	0
<b>Total</b>	<b>14.92</b>	<b>2.33</b>	<b>10.00 - 25.00</b>	<b>5.44</b>	<b>241</b>	<b>15.45</b>	<b>2.69</b>	<b>10.00 - 26.00</b>	<b>7.23</b>	<b>220</b>



**Figure 2.** Plots of length of forearm (mm) vs. latitude (decimal degrees). Mean length of forearm for males (a) and females (b). Maximum length of forearm for males (c) and females (d).



**Figure 3.** Plots of body mass (g) vs. latitude (decimal degrees). Mean body mass for males (a) and females (b). Maximum body mass for males (c) and females (d).

**Table 4.** Descriptive statistics of data used on models selection. This table show only models that have significance with Bonferroni correction\* and without Bonferroni correction\*\*. Mx Temp – maximum temperature; M Temp – mean temperature; Mi Temp – minimum temperature.

Sex	Body Size	Variables Selected	Model Selection					Regression Analysis				
			Models	R <sup>2</sup>	AICc	ΔAICc	W <sub>AIC</sub>	Tipo	R <sup>2</sup>	β	p	
Male	Mean length of forearm	M T	1	0.236	55.3	0	0.44	OLS	0.236	0.145	0.020**	
		Mi T	2	0.173	57.1	1.8	0.17	OLS	0.173	0.119	0.050**	
Female	Mean body mass	M T	1	0.403	67.3	0	0.56	OLS	0.403	0.279	0.001*	
		Mx T	1	0.046	168.4	0	0.32	OLS	0.35	0.37	0.004*	
	Mean length of forearm	M T	2	0.022	168.9	0.6	0.24	OLS	0.301	0.23	0.010*	
		Mi T	3	0.019	169	0.6	0.23	OLS	0.25	0.198	0.020**	
	Mean body mass	M T	1	0.101	129.5	0	0.31	OLS	0.227	0.35	0.030**	
		Mi T	2	0.099	129.6	0.1	0.3	OLS	0.227	0.333	0.030**	
Maximum body mass	M T	1	0.122	146.4	0	0.31	OLS	0.174	0.598	0.050**		
	Mi T	2	0.121	146.4	0	0.31	OLS	0.176	0.573	0.050**		

distribution) and environmental (resource availability and interspecific competition) attributes can be key factors accounting for variation in body size (Meiri et al. 2007). Besides, for bats, this geographic variation in body size may reflect the influence of competition in areas where ecologically similar species compete for the

same resources (Storz et al. 2001), food availability (months of flowering and fruiting) and other physical location parameters (relative humidity, annual precipitation).

The tests done by multiple studies of ecogeographical rules, as the Bergmann's Rule, can help us to understand the mechanisms which explain them. Besides the experimental studies,



another way to test these biogeographical patterns is comparing their behavior on studies which work with different taxa and/or on different regions. Accumulating evidences of different applications of these patterns can lead us to improve their understanding. One example of this is the study that suggests the absence of Bergmann's Rule in *Ctenomys* due to its subterranean lifestyle which probably insulates these rodents from the external temperature (Medina et al. 2007). These results suggest that other mechanism, instead of heat conservation hypothesis, can explain this pattern better. The present study can join in this group of studies that suggest additional aspects on the mechanism which explains Bergmann's Rule, by adding an aspect that helps on understanding of its mechanism related to anatomical features, such as presence and anatomy of the wings of bats.

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**CAPÍTULO II: The application of Bergmann's Rule to the marine environment: a test with fishes.**

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## **Abstract**

Bergmann's Rule describes the association between body size of species and latitude. The proposed mechanism to explain the pattern would be the lowest surface/volume ratio found in large animals, which should result in an energy advantage in cold environments. Other hypotheses have been proposed to explain this pattern: phylogenetic hypotheses, migration ability, starvation resistance (widely used on studies of ectothermics) and resource availability. Using a world fish database (Froese & Pauly, 2015), we compiled geographical distribution, latitudinal range and body size data for 8040 bony fish species and 480 cartilaginous fish species that inhabit continental shelf waters from Pacific, Atlantic and Indian Oceans, at depths of less than 200 meters; due to their distinctive traits, we analyzed bony and cartilaginous fish separately. We evaluated the pattern at assemblage level, plotting the assemblage's body size as dependent variable (axis Y) and latitude as independent variable (axis X). We also conducted the same analyses to test body size variation along thermal gradients, using annual, summer and winter temperatures of global surface water, separately, as an independent variable. Mean body size considering all species constituting the assemblage in each 5° latitudinal band was modeled as a univariate linear function of latitude, conducting separate analyses for each of the 12 ocean regions. Overall, significant size–latitude and size–temperature trends occur on assemblages of bony and cartilaginous fish species for most ocean regions analyzed. Our results partially support Bergmann's Rule, as bony and cartilaginous fishes show an increase in body size with increasing latitude and decreasing temperatures. When we evaluated our results it becomes clear that the applicability of Bergmann's Rule presents a relationship with several aspects, both environmental and related to the taxa under analysis. Although some geographical features and biotic strategies of some of them biased or weakened the detection of this pattern, our results make clear this was not sufficient to disprove its existence. More detailed analyses is necessary to clarify which oceanographic features are responsible for the differences in the pattern observed amongst the oceans.

**Keywords:** Bergmann's Rule, fishes, marine, biogeography, body size

## **Introduction**

### Bony and cartilaginous fishes

Bony and cartilaginous fish are groups with distinct morphological and physiological traits: the former are usually bilaterally flattened, and many species present external fertilization without an egg case, their offspring composed by a large number of small eggs with little yolk; on the other hand, cartilaginous fishes are usually dorso-ventrally flattened, have internal fertilization, can be oviparous/ovoviviparous and viviparous, and their offspring usually presenting external development without an egg case.

Despite being all ectotherms, such differences are expected to reflect on their response to the environment and its constraints. In order to avoid some unpredicted responses, we focused in coastal and shelf waters, as they have greater species numbers, higher productivity, and they are also biogeographically distinct from the adjacent high seas and deep benthic environments (Briggs, 1974; Spalding *et al.*, 2007).

In addition, from 1991 to 2013 about 24% of 390 studies applied Bergmann's Rule to mammals (Barros *et al.*, 2014), a taxa selection bias also noted by other authors (Meiri *et al.*, 2004; Vinarski, 2014), and only 10 to 15% of biogeographic studies were conducted on the marine environment. Considering this scenario, the present study aims to evaluate the applicability of Bergmann's Rule to marine fishes.

## **Materials and Methods**

Using a world fish database (Froese & Pauly, 2015), we compiled geographical distribution, latitudinal range and body size data for 8040 bony fish species and 480 cartilaginous fish species that inhabit continental shelf waters at depths of less than 200 meters. Although other studies considered the wide bathymetric range species (Fisher *et al.* 2010; Fortes & Absalão, 2010), we focused in coastal and shelf waters. Besides, as Bergman's Rule relates body size with environment temperature, we believe that this approach can improve the detection of the pattern, by avoiding the use of oceanic species that make diurnal vertical migration and tolerate wide thermic variations.

To determine the latitudinal distribution for each focal species, we used distribution

data (maximum latitude and latitudinal range) reported at the FishBase ([www.fishbase.org](http://www.fishbase.org)) or IUCN Red List ([www.iucnredlist.org](http://www.iucnredlist.org)) online databases. For each species, we extracted the maximum total length (in centimeters) from FishBase. This maximum total length correlates well with overall body size (Kosnik *et al.*, 2006), and is the only size metric available for all species. Hereafter, we will refer to this maximum total length simply as ‘body size’.

Our compiled database encompasses fish species living at shelf depths worldwide, in the Pacific, Atlantic and Indian Oceans (Figure 1). Due to the distinct dynamics of the oceanic currents and their relationship with coastal zones, we treated East and West coasts separately. To account for the fact that latitude is a bidirectional gradient and some groups show broadly symmetrical size patterns across the equator (Berke *et al.*, 2013), we also conducted separate analyses for each of the major north–south coastlines. Consequently, we conducted analyses for 12 regions, 4 for each ocean: North-West Pacific, South-West Pacific, North-East Pacific and South-East Pacific; North-West Atlantic, South-West Atlantic, North-East Atlantic and South-East Atlantic; North-West Indian, South-West Indian, North-East Indian and South-East Indian. The Arctic and Antarctic Oceans were excluded from our analyses because these regions presented a very low number of species with complete data and lack sufficient thermal variability.

Each of those 12 regions was divided into assemblages, constituted by all species that occur in each 5° latitudinal band spanning each coastline, starting from Equator. This seems a reasonable approach, since the Bergman's Rule relates body size variation with temperature variation, which is often associated to latitudinal variation (Watt *et al.*, 2010). Therefore, Atlantic and Pacific Oceans regions range from 0° to 60° in both hemispheres, as well as the southern regions of the Indian Ocean, whereas the northern regions range only from 0° to 30°N, due to limitations imposed by the Asian continent (Figure 1c).

We evaluated the applicability of Bergmann's Rule to marine fishes at assemblage level using ordinary least square regressions (OLS); due to their distinctive traits, we analyzed bony and cartilaginous fish assemblages separately. First, we plotted the assemblage's body size as dependent variable (axis Y) and latitude as independent variable (axis X). Mean body size considering all species constituting the assemblage in each 5° latitudinal band was modeled as a univariate linear function of latitude, conducting separate analyses for each of the 12 ocean regions. Considering the potential bearing of the

temperature on the mechanisms suggested to explain Bergmann's rule, we also conducted the same analyses to test body size variation along thermal gradients, using annual, summer and winter temperatures of global surface water, separately, as an independent variable. These climatic data were obtained from the U.S. Government National Oceanographic Data Center website ([www.nodc.noaa.gov](http://www.nodc.noaa.gov)). The relationships between body size and latitudinal/thermal gradient were evaluated using the explicability index ( $R^2$ ), with the significance threshold set at 95% for the Pearson's linear regression.

Some authors (Blackburn & Ruggiero, 2001; Diniz-Filho & Tôrres, 2002; Diniz-Filho *et al.*, 2005; Harcourt, 2006) used complementary analyses to avoid describing macroecological relationships and interpreting them without previous control of non-independence in data caused by phylogenetic patterns. However, the paucity of phylogenetic analyses for some taxa often precludes the use of procedures to account for the effect of phylogenetic structure on species traits (Brehm & Fiedler, 2004). That is the case of our target group, for which there is no phylogenetic tree encompassing all the species studied, even at family level.

## **Results**

### Latitudinal variation in body size

Overall, significant size–latitude trends occur on assemblages of bony and cartilaginous fish species for most ocean regions analyzed, 58.33% of them following Bergmann's Rule and showing an increase in body size towards increasing latitude ( $\beta > 0$ ). For the bony fishes this represents 77.77% of the statistically significant ones, and 70% for the cartilaginous fish analyses ( $p < 0.05$ ).

The analyses of bony fish species indicate that Bergmann's Rule is valid for 7 of the 12 regions (Table 1, Figure 2). However, in two of them (North-West Indian and South-East Indian) we found the opposite trend called Bergmann's Rule "Converse", wherein body size varies inversely ( $\beta < 0$ ) to the latitudinal variation (Table 1).

Analyses of cartilaginous fish assemblages had similar results, showing that the pattern is valid for 7 of the 12 regions as well (Table 2, Figure 3). It was also noted the Converse trend ( $\beta < 0$ ) in 3 of them: South-West Atlantic, North-East Atlantic and South-

East Atlantic (Table 2).

#### Thermal variation in body size

Models for the thermal gradient presented similar overall results, most of them corroborating Bergmann's Rule and showing an increase of body size to decreasing temperature ( $\beta < 0$ ). For the bony fish assemblages this represents 55.55% of the gross analyses, and 80% of the statistically significant ones; as for the cartilaginous fish assemblages, also 55.55% of the gross and 68.96% of the significant analyses ( $p < 0.05$ ).

The Rule was corroborated ( $\beta < 0$ ) by 20 of 36 analyses of bony fish assemblages, while 5 of them followed the Converse trend, with body size variation showing positive relationship ( $\beta > 0$ ) with temperature variation (Table 3). The observed trends, both regular and converse, were detected for all three temperatures (annual, summer and winter temperature) in most regions but the Indian Ocean, for winter temperature.

Regarding the cartilaginous fishes, 20 of 36 models corroborated the Rule ( $\beta < 0$ ) and 9 of them the opposite trend ( $\beta > 0$ ). Once again, the observed trends were detected for all three temperatures (annual, summer and winter temperature) in every region, except for winter temperature at the North-West Indian (Table 4).

### **Discussion and Conclusion**

Our results partially support Bergmann's Rule, since 56.25% of 48 tests done for each group, bony and cartilaginous fishes show an increase in body size with increasing latitude and decreasing temperatures; among the statistically significant ones, this represents 79.41% of bony fish and 69.23% of cartilaginous fish analyses. As seen in other studies evaluating Bergmann (e.g. Shelomi, 2012; Berke et al 2013; Pincheira-Donoso & Meiri, 2013; Rypel, 2014; Vinarski, 2014), our results showed both Bergmann's Rule and the Converse trend.

The decision to limit our analyses to species inhabiting depths up to 200 meters, excluding species with wide bathymetric range, able to make vertical migrations, improved our results considerably. Such improvement was more noticeable for the cartilaginous fishes (Fortes, 2007), increasing from 3 to 10 the number of statistically significant analyses (Table



5). Many species of cartilaginous fishes occupy higher trophic levels, with diurnal vertical migrations as part of their foraging behavior, increasing their foraging area and consequently enhancing their capacity to acquire the required amount of energy for their survival (Villegas-Amtmann *et al.*, 2011; Gutowsky *et al.* 2013). In doing so they're also subjected to greater thermal variations than species restricted to shallower waters.

Fisher *et al.* (2010) also observed a positive correlation between fishes' body length and latitude. Their work used the assemblage approach as well, but using each LMEs (Large Marine Ecosystems) midpoint as the latitudinal gradient, which is quite different from our 5° latitudinal bands; despite the differences, there are some similarities between the results, like the anomalies in the North Atlantic. Here the cartilaginous fish assemblages present non-significant relationship or display the converse trend, while the bony fish assemblages show significant relationship only in the West side (Table 6). Fisher *et al.* (2010), testing the temporal difference in body size in this region, observed that the absence of a cline may be the result of overfishing and environmental change, both of which negatively affect average body size and ecosystem functioning; in response, many of the LMEs at this region experienced the collapse of their large-body top predators in early 1990.

Other studies also detected Bergmann's Rule, for a worldwide fish database (Blanchet *et al.*, 2010) and North American database (Rypel, 2014). The latter tested it intraspecifically and, as in our study, detected both patterns: fish inhabiting cold waters conformed to Bergmann's Rule, and those inhabiting warm waters conformed to the Converse trend. Rypel (2014) and Blanckenhorn & Demont (2004) suggest that the detection of both trends could be related to the length of growth period, and how the species' growth responds to the environmental constraints. A faster growth on species inhabiting environments at higher latitudes would lead to the normal trend, and a slow growth would result in the Converse trend; the conformance of Bergmann's Rule trends would depend on how the species of each assemblage relates to their environment and how they are limited by their ecological features. Unfortunately, our database didn't allow us to test this hypothesis, but the fact that we observed the two trends of Bergmann's Rule and have tested the pattern at different oceans with two distinct groups, highlights the role that different ecological features and life traits might have in determining the pattern.

As Bergmann's original work mentions that "smaller species would all need a warmer climate." (Watt *et al.* 2010), we also tested the pattern in a thermal gradient: our

results were consistent, as altering the independent variable did not change the pattern detected for a region, or the lack of a pattern (Table 6). Although these results reinforce the important role that climatic conditions (temperature) have on the establishment of a latitudinal gradient of body size, the slight slopes ( $\beta$ ) of the regression analyzes, could indicate that other environmental features which are related to the latitudinal gradient can influence it, differently in each part of the world, as energy and resource availability vary (Ho *et al.* 2010; Huston & Wolverson, 2011; Sepúlveda *et al.*, 2013; Vinarski, 2014).

The Bergmann's Rule "Converse" was observed two times in analyses of bony fishes and three times in analyses of cartilaginous fishes (Table 6). It was restricted to one ocean for each group, Indian Ocean for bony fishes and Atlantic Ocean for cartilaginous fishes. It is not clear if this trend is related to a historical perspective about the evolution of the taxa inhabiting these oceans, or a response to environmental features of them. In these waters, the pronounced seasonality of resource availability may not favor large-bodied species, because of the smaller energy supply for their populations (Smith & Brown, 2002; McClain, 2004). Although larger species could improve their capacity to tolerate resource scarcity by storing energy, the constraints on environmental energy would limit this gain. For these species, the adoption of other behavioral and / or physiological mechanisms could be a better solution for this constraint (Smith & Brown, 2002; Blanckenhorn & Demont, 2004; Fortes & Absalão, 2010).

Another important feature of cartilaginous fishes must be determinant for the validation of Bergmann's Rule "Converse": the reproductive strategy (Smith & Brown, 2002). The evolution of internal fertilization led to the production of large-bodies, less-abundant offspring, sustained inside the female's body during the gestation period. This strategy requires a significant energy investment by the females. The existence of a temporal concentration in environmental resources at the higher latitudes leads to an increase in the costs of energy allocated to reproduction. As a result, natural selection may favor the smaller-bodied cartilaginous fishes in these regions. In our linear regression analyzes for this group that shows the Bergmann's Rule "Converse", we observed the smaller species at higher latitudes, which corroborated this hypothesis. In these analyzes, the decrease on mean body size at higher latitude is lighter and begins at lower latitudes, suggesting that for this group with high energetic constraints, the influence of cold waters on the decrease in body size is stronger. In future studies, the evaluation of these reproductive strategies adopted by

these different assemblages can help the understanding of this hypothesis.

In summary, when we evaluated our results it becomes clear that the applicability of Bergmann's Rule presents a relationship with several aspects, both environmental and related to the taxa under analysis. Although some geographical features and bionomic strategies of some of them biased or weakened the detection of this pattern, our results make clear this was not sufficient to disprove its existence. More detailed analyses are necessary to clarify which oceanographic features are responsible for the differences in the pattern observed amongst the oceans. The simple idea of investigating the pattern at an appropriate geographic scale, and in a group with different life traits, has allowed us to assess some possible explanations for apparent invalidities.

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## Tables and Figures

Table 1: The results of Bergmann's Rule analyses of bony fish assemblages for the latitudinal gradient.  $\beta$  = regression slope;  $R^2$  = coefficient of determination. Dark-grey (Bergmann's Rule); Grey (Converse); White (no significance).

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Oceans	$R^2$	$\beta$
North-West Pacific	0,59	0,12
South-West Pacific	0,84	0,29
North-East Pacific	0,08	0,06
South-East Pacific	0,82	0,41
North-West Atlantic	0,80	1,06
South-West Atlantic	0,83	0,69
North-East Atlantic	0,04	0,02
South-East Atlantic	0,82	0,62
North-West Indian	0,88	-0,04
South-West Indian	0,02	0,02
North-East Indian	0,82	0,06
South-East Indian	0,38	-0,10

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Table 2: The results of Bergmann's Rule analyses of cartilaginous fish assemblages for the latitudinal gradient.  $\beta$  = regression slope;  $R^2$  = coefficient of determination. Dark-grey (Bergmann's Rule); Grey (Converse); White (no significance).

Oceans	$R^2$	$\beta$
North-West Pacific	0,15	0,66
South-West Pacific	0,73	1,15
North-East Pacific	0,47	1,18
South-East Pacific	0,86	1,31
North-West Atlantic	0,05	0,30
South-West Atlantic	0,87	-2,00
North-East Atlantic	0,46	-0,93
South-East Atlantic	0,51	-1,17
North-West Indian	0,89	0,65
South-West Indian	0,74	3,77
North-East Indian	0,98	0,60
South-East Indian	0,49	3,55

Table 3. The results of Bergmann's Rule analyses of bony fish assemblages for the thermal gradient.  $\beta$  = regression slope. Dark-grey (Bergmann's Rule); Grey (Converse); White (no significance).

Oceans	Annual Temperature		Summer Temperature		Winter Temperature	
	R <sup>2</sup>	$\beta$	R <sup>2</sup>	$\beta$	R <sup>2</sup>	$\beta$
North-West Pacific	0,46	-0,19	0,54	-0,20	0,34	-0,20
South-West Pacific	0,83	-0,60	0,81	-0,61	0,90	-0,57
North-East Pacific	0,06	-0,13	0,08	-0,14	0,05	-0,16
South-East Pacific	0,84	-0,98	0,78	-0,99	0,85	-0,97
North-West Atlantic	0,95	-2,45	0,96	-2,36	0,89	-2,52
South-West Atlantic	0,88	-1,34	0,88	-1,41	0,87	-1,33
North-East Atlantic	0,12	-0,09	0,06	-0,05	0,19	-0,13
South-East Atlantic	0,68	-1,09	0,69	-1,07	0,68	-1,13
North-West Indian	0,70	0,42	0,93	0,31	0,23	0,47
South-West Indian	0,00	0,01	0,01	0,02	0,00	0,00
North-East Indian	0,86	-0,62	0,77	-0,39	0,63	-1,89
South-East Indian	0,53	0,21	0,58	0,23	0,44	0,18

Table 4. The results of Bergmann's Rule analyses of cartilaginous fish assemblages for the thermal gradient.  $\beta$  = regression slope. Dark-grey (Bergmann's Rule); Grey (Converse); White (no significance).

Oceans	Annual Temperature		Summer Temperature		Winter Temperature	
	R <sup>2</sup>	$\beta$	R <sup>2</sup>	$\beta$	R <sup>2</sup>	$\beta$
North-West Pacific	0,19	-1,32	0,13	-1,01	0,22	-1,76
South-West Pacific	0,82	-2,69	0,86	-2,92	0,80	-2,30
North-East Pacific	0,56	-2,90	0,53	-2,58	0,53	-3,68
South-East Pacific	0,81	-3,07	0,79	-3,27	0,82	-3,02
North-West Atlantic	0,04	-0,58	0,04	-0,52	0,02	-0,41
South-West Atlantic	0,89	3,91	0,87	4,28	0,91	3,96
North-East Atlantic	0,61	3,22	0,55	2,73	0,68	4,13
South-East Atlantic	0,61	2,59	0,62	2,49	0,62	2,68
North-West Indian	0,81	-7,01	0,71	-4,22	0,09	-4,62
South-West Indian	0,95	-7,49	0,96	-7,75	0,94	-7,54
North-East Indian	0,94	-5,98	0,88	-3,85	0,74	-18,85
South-East Indian	0,67	-7,80	0,75	-8,74	0,63	-6,97

Table 5. The results of Bergmann's Rule analyses, comparing wide bathymetric range and continental shelf assemblages for (a) bony fish assemblages and (b) cartilaginous fish assemblages.  $\beta$  = regression slope;  $R^2$  = coefficient of determination. Dark-grey (Bergmann's Rule); Grey (Converse); White (no significance). Wide bathymetric range data from Fortes 2007 (unpublished results).

a)

	<b>wide bathymetric range</b>		<b>continental shelf</b>	
Oceans	$R^2$	$\beta$	$R^2$	$\beta$
North-West Pacific	0,94	0,16	0,59	0,12
South-West Pacific	0,76	0,18	0,84	0,29
North-East Pacific	0,28	0,06	0,08	0,06
South-East Pacific	0,69	0,10	0,82	0,41
North-West Atlantic	0,76	0,34	0,80	1,06
South-West Atlantic	0,34	0,06	0,83	0,69
North-East Atlantic	0,87	0,09	0,04	0,02
South-East Atlantic	0,06	-0,03	0,82	0,62
North-West Indian	0,05	0,01	0,88	-0,04
South-West Indian	0,55	0,12	0,02	0,02
North-East Indian	0,69	0,08	0,82	0,06
South-East Indian	0,60	0,13	0,38	-0,10

b)

	<b>wide bathymetric range</b>		<b>continental shelf</b>	
Oceans	$R^2$	$\beta$	$R^2$	$\beta$
North-West Pacific	0,19	0,48	0,15	0,66
South-West Pacific	0,15	1,03	0,73	1,15
North-East Pacific	0,51	1,19	0,47	1,18
South-East Pacific	0,40	-1,42	0,86	1,31
North-West Atlantic	0,55	1,22	0,05	0,30
South-West Atlantic	0,26	-1,14	0,87	-2,00
North-East Atlantic	0,00	-0,02	0,46	-0,93
South-East Atlantic	0,09	0,84	0,51	-1,17
North-West Indian	0,24	0,45	0,89	0,65
South-West Indian	0,21	1,35	0,74	3,77
North-East Indian	0,39	0,51	0,98	0,60
South-East Indian	0,23	1,71	0,49	3,55

Table 6. The results of Bergmann's Rule analyses, of (a) bony fish assemblages and (b) cartilaginous fish assemblages, for latitudinal and thermal gradients.  $\beta$  = regression slope. Dark-grey (Bergmann's Rule); Grey (Converse); White (no significance).

a)

Oceans	Latitude	Annual Temperature	Summer Temperature	Winter Temperature
	$\beta$	$\beta$	$\beta$	$\beta$
North-West Pacific	0,12	-0,19	-0,20	-0,20
South-West Pacific	0,29	-0,60	-0,61	-0,57
North-East Pacific	0,06	-0,13	-0,14	-0,16
South-East Pacific	0,41	-0,98	-0,99	-0,97
North-West Atlantic	1,06	-2,45	-2,36	-2,52
South-West Atlantic	0,69	-1,34	-1,41	-1,33
North-East Atlantic	0,02	-0,09	-0,05	-0,13
South-East Atlantic	0,62	-1,09	-1,07	-1,13
North-West Indian	-0,04	0,42	0,31	0,47
South-West Indian	0,02	0,01	0,02	0,00
North-East Indian	0,06	-0,62	-0,39	-1,89
South-East Indian	-0,10	0,21	0,23	0,18

b)

Oceans	Latitude	Annual Temperature	Summer Temperature	Winter Temperature
	$\beta$	$\beta$	$\beta$	$\beta$
North-West Pacific	0,66	-1,32	-1,01	-1,76
South-West Pacific	1,15	-2,69	-2,92	-2,30
North-East Pacific	1,18	-2,90	-2,58	-3,68
South-East Pacific	1,31	-3,07	-3,27	-3,02
North-West Atlantic	0,30	-0,58	-0,52	-0,41
South-West Atlantic	-2,00	3,91	4,28	3,96
North-East Atlantic	-0,93	3,22	2,73	4,13
South-East Atlantic	-1,17	2,59	2,49	2,68
North-West Indian	0,65	-7,01	-4,22	-4,62
South-West Indian	3,77	-7,49	-7,75	-7,54
North-East Indian	0,60	-5,98	-3,85	-18,85
South-East Indian	3,55	-7,80	-8,74	-6,97





Figure 2: Linear regression graphics of Bergmann's rule analyses of bony fish assemblages for the latitudinal gradient. Graphs: X-axis, latitudinal gradient (5° bands); Y-axis, mean body size (cm). Graphical edge: black, significant ( $p < 0.05$ ); white, non-significant ( $p > 0.05$ ). Map source: U.S. Government.

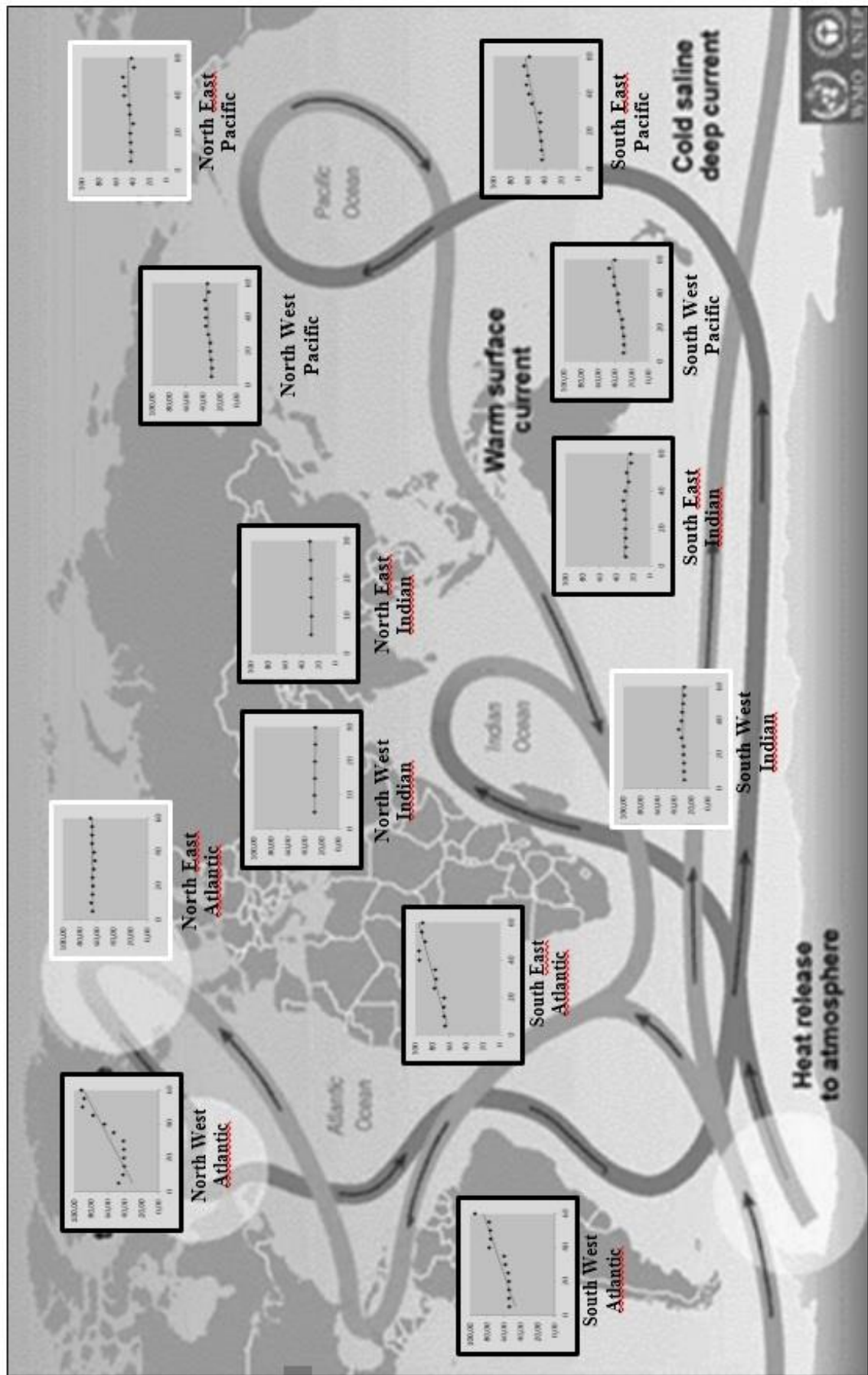
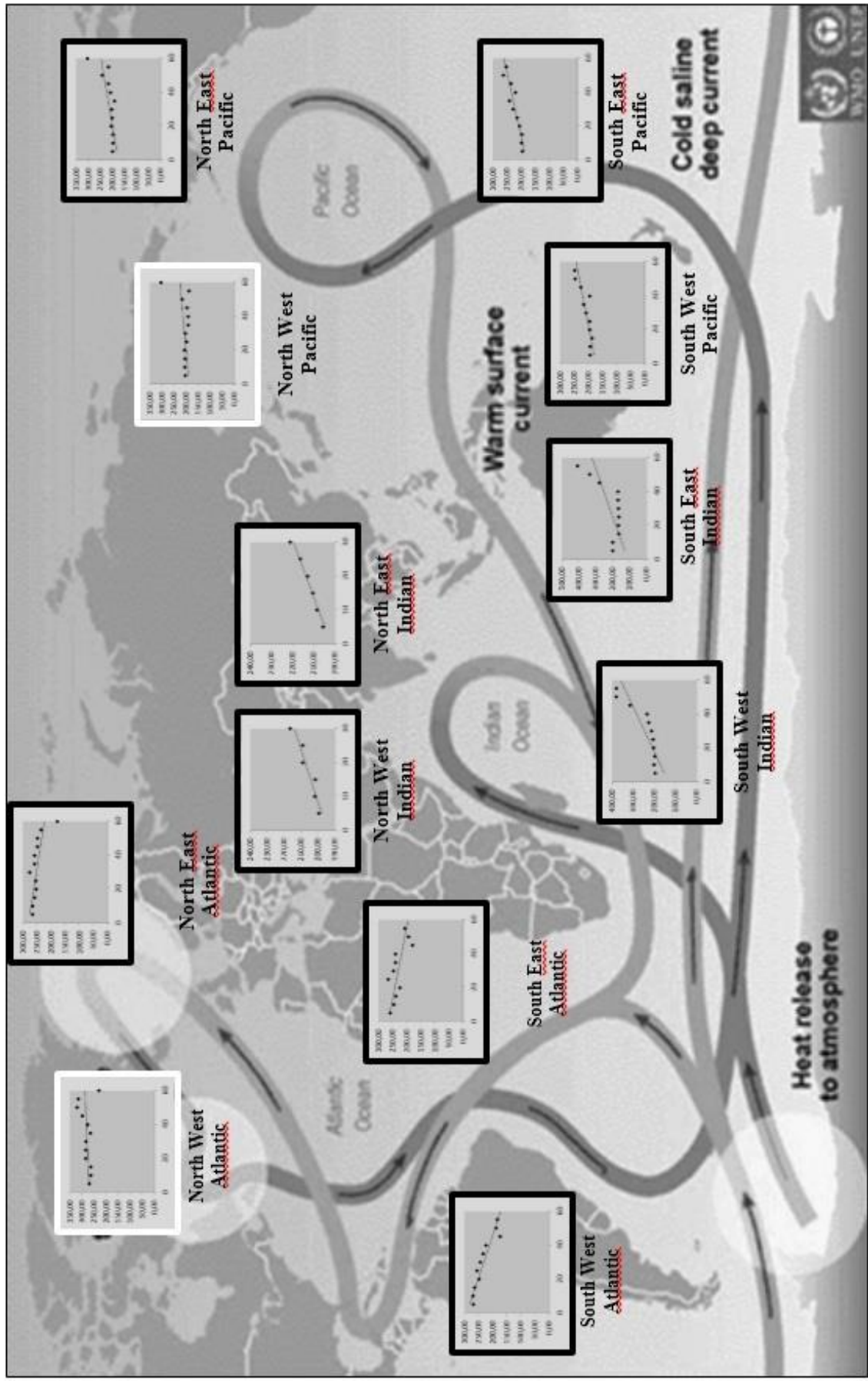


Figure 3: Linear regression graphics of Bergmann's rule analyses of cartilaginous fish assemblages for the latitudinal gradient. Graphs: X-axis, latitudinal gradient ( $5^\circ$  bands); Y-axis, mean body size (cm). Graphical edge: black, significant ( $p < 0.05$ ); white, non-significant ( $p > 0.05$ ). Map source: U.S. Government.



## CONSIDERAÇÕES FINAIS

Os testes efetuados para avaliar a aplicação da Regra de Bergmann mostraram a mesma controvérsia observada na extensa literatura sobre o assunto (Shelomi, 2012; Berke et al., 2013; Pincheira-Donoso & Meiri, 2013; Rypel, 2014).

Tanto na análise intraespecífica quanto na análise em assembleia, a ausência de uma tendência geral para a detecção do padrão, bem como os baixos valores observados para a inclinação ( $\beta$ ) das regressões lineares, sugere que tanto a Regra de Bergmann quanto a hipótese original para explicá-la, não possuem a generalidade inicialmente proposta na sua descrição original.

As inconsistências observadas sugerem que a observação do gradiente de tamanho corporal associado à latitude ainda carece de uma hipótese unificadora capaz de explicar a Regra de Bergmann e todas as suas variações (Olalla-Tárraga, 2011). Apesar de Blanckenhorn & Demont (2004) proporem única hipótese para explicar o aparecimento da Regra de Bergmann e da sua variação “Converse”, a forma como os componentes ambientais e genéticos elencados na sua proposta interagem para determinar o padrão, ainda não são conhecidos, e nem foram suficientemente testados para a sua validação.

Dentro da ideia dos componentes ambientais, os resultados alcançados nos estudos de caso observados no presente estudo, mostram como os diferentes mecanismos propostos para explicar o padrão podem ser aplicados na determinação deste gradiente, como por exemplo, as hipóteses de resistência à escassez de recursos, da produtividade e a da originalmente proposta por Bergmann. Além disso, os aspectos relacionados à história de vida dos organismos, como a forma do corpo, poderiam ser incluídos dentro do componente genético que poderia influenciar na determinação do padrão.

Os resultados alcançados por este estudo tornam evidente a importância que a adoção das escalas geográficas utilizadas por este estudo, à variedade de estratégias de vida empregadas pelos organismos analisados, bem como o emprego das diferentes abordagens para se testar o padrão, podem ajudar na sua elucidação. No futuro, a melhor investigação dos aspectos oceanográficos envolvidos na determinação do padrão, bem como as diferentes estratégias de vida adotadas pelos organismos, poderá auxiliar na compreensão da Regra de Bergmann, e de outras regras ecogeográficas associadas ao gradiente de latitude.

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