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THERMOREGULATION OR HABITAT SELECTION? ENVIRONMENTAL PREDICTORS OF THE BODY SHAPE VARIATION IN SHARKS (CHONDRICTHYES: SELACHIMORPHA)

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Abstract: Ecomorphology is the study of the relation between organisms' shape and environmental factors. It assumes that variations in the organisms' shape lead to functional differences, resulting in changes in resource and habitat use. Here, we aimed to evaluate the effects of environmental variables, representing hypotheses of thermoregulation and habitat selection, over the sharks' body shape on a global scale. According to the thermoregulation hypothesis, the more fusiform species should be more commonly found in colder waters, and regarding the habitat selection hypothesis, we expected that the flatter species would occur nearest to the shore, and in the shallowest waters. Based on the body shape and occurrences of the shark species, we estimated the mean and median body shape index (body height: length ratio) of shark species on each cell in a 400 x 400 km grid, and applied a model selection by AIC approach to identify the relative importance of four environmental factors faced by the shark species: minimum temperature of the coldest month (Tc), maximum temperature of the warmest month (Tw), bathymetry (Bathy), and distance to shore (DistShr). Our results indicate a consistent trend of dorsoventral flattening towards coastal zones and shallow areas. A second detected trend was the increase in the body shape index values towards the tropical regions all over the globe, while flattened species were more common above 30º latitude in both hemispheres. Minimum temperature of the coldest month was included in all the best fitted models, but it did not follow our initial predictions of negative relation to body shape index, thus we did not find support for the thermoregulation hypothesis. On the other hand, Bathy and DistShr presented a positive relation to body shape index, thus consistent with our initial predictions. Our results indicate that the sharks body shape is not a response to a selective pressure for heat conservation in cold environments, but rather to where they live and how they obtain their food, contrary to what has been reported to ecologically equivalent marine mammals (suborder Odontoceti).

Keywords: ecomorphology; Elasmobranchii; macroecology; spatial ecology; spatial gradients.

INTRODUCTION

Ecomorphology is the study of the relation between morphology and environmental physical and biotic factors that in some way relate to the organism (Bock 1965). Ecomorphological analyses assume that variations in the organisms' shape lead to functional and performance differences, resulting in changes in resource and habitat use (Motta *et al.* 1995). Ultimately, these changes impact on individuals' fitness and relate to the species' ecology (Sampaio & Goulart 2011).

Morphology comprises a complex range of external and internal structural forms, and changes in these forms reflect in organism changes as a whole (Arratia & Johnson 2015). Environmental pressures strongly influence fish body shape (Breda *et al.* 2005), affecting their behavior, swimming mode, and habitat selection (Assumpção 2010). Species' swimming performance may be influenced by the type of locomotion, shape and body size, behavior, physiology, and temperature (Hammer 1995, Assumpção 2010). Body shapes that reduce dragging increase swimming capacity, enabling faster speeds to be achieved with lower energy consumption (Harris 1965, Walker & Westneat 2002).

Body shape also reflects on the organism's ability to exchange heat with its surrounding environment (Peters 1983, Schmidt-Nielsen 1984). The body has the ability to absorb or release heat through the skin, and the organism's surface area is directly proportional to the amount of heat exchanged (Tilkens *et al.* 2007). This relation has consequences on foraging time and strategies and on the tolerance to environmental climatic extremes (Peters 1983).

The relation between the diversity of organisms' body characteristics and latitude is as old as the perception of a geographical gradient of species diversity (Blackburn *et al.* 1999), noted since the early naturalists' studies (Wallace 1878). In spite of the huge efforts made to study the gradients of species diversity (see review in Hawkins *et al.* 2003) and body size variation (Rodríguez *et al.* 2006, Torres-Romero *et al.* 2016), few studies associating species' shape variation and environmental factors on broad geographic scale have been conducted (*e.g.*, Shepherd 1998, Shepherd & Kelt 1999, Roy *et al.* 2001). Analyses considering this interrelation between body shape and environmental conditions can provide valueble insight into the pressures that are structuring biological communities, as the shape of organisms lead to functional and performance differences, resulting in changes in resource and habitat use (Motta *et al.* 1995).

Although the oceans cover about 70% of the planet's surface, only 10-15% of biogeographical studies published in the last two decades concern the marine environment (Barros 2016). In marine habitats, in contrast to terrestrial and freshwater habitats, physical barriers to dispersal are considered weak or often absent (Richardson *et al.* 1995). Nevertheless, persistent transoceanic currents and intermittent large-scale oceanographic events produce large variations in current flows, contributing to produce very different macroecological patterns among marine organisms compared to those observed in both freshwater and terrestrial species (Macpherson *et al.* 2009). Marine environments present higher density, higher thermal conductivity, lower oxygen concentration, and greater osmotic variation when compared to terrestrial environments (Torres-Romero *et al.* 2016), which represent different environmental pressures from those normally addressed in studies with terrestrial organisms.

About 44% of the species classified as Elasmobranchii belong to the sharks' clade (superorder Selachimorpha), which origin dates back to about 400 million years (Weigmann 2016). They compose a diverse group, representing one of the most speciose lineages of predators on the planet that play important functional roles in the top-down control of coastal and oceanic ecosystem structure and function (Compagno 1990, Ferretti *et al.* 2010, Heithaus *et al.* 2012). This successful evolutionary trajectory can be explained by their sharp sensorial ability, reproductive strategies diversification, and great interspecific variability in body morphology, resulting in a great variety in the swimming mode and niche (feeding and habitat) among cartilaginous species (Camhi *et al.* 1998, Scacco *et al.* 2010, Irschick & Hammerschlag 2015). Selachimorpha species are the focus of multiple ecological, physiological and morphological studies (Garcia *et al.* 2008, Vélez-Zuazo & Agnarsson 2011, Espinoza *et al.* 2014, Irschick & Hammerschlag 2015, Davidson *et al.*

2016). They are widely distributed along the latitudinal gradient, being present in diverse habitats, from the surface to the bottom, in nearly all seas and oceans, occupying diverse ecological niches (Compagno 1990, Szpilman 2004, Espinoza *et al.* 2014). Furthermore, sharks are one of the most threatened groups of marine animals worldwide and has arguably one of the worst status of conservation reported for any major vertebrate lineage except amphibians (Dulvy *et al.* 2014).

Currently, 509 species of sharks are known around the planet. They are divided into nine orders, 34 families, and 105 genera (Weigmann 2016), whose body shapes range from flat to more rounded species. Most shark species have a fusiform body varying from elongated, such as the bamboo shark (*Hemiscyllium halmahera*), to torpedo shape of the white shark (*Carcharodon carcharias*), and there are also those dorsoventrally compressed, such as the angel shark (*Squatina* sp.) (Maia *et al.* 2012).

Here, we aimed to evaluate the environmental factors related to the sharks' body shape variations on a global scale through an assembly macroecological approach. We analyzed the effects of four environmental variables, representing two different hypotheses (thermoregulation and habitat selection), over the sharks' body shape. According to the thermoregulation hypothesis, we expected that more fusiform species should be more commonly found in colder waters, as they should be able to retain heat better than the flatter ones, once the reduced surface-volume ratio of large bodied species is a selective advantage to better retain body heat in cold environments (Peters 1983, Brown *et al.* 2017). Regarding the habitat selection hypothesis, we expect that flatter species would occur nearest to the shore, and in the shallowest waters, as fish morphology affects its swimming performance (Haas *et al.* 2015) and, consequently, habitat selection (Breda *et al.* 2005).

MATERIAL AND METHODS

Species data

The species set included in this study was based on the most recent list of Chondrichthyes of the world (Weigmann 2016). Sharks (Selachimorpha, Chondrichthyes) from freshwater and extinct species were excluded from the analysis. Distribution maps of shark species were obtained from the International Union for Conservation of Nature (IUCN) Red List (http://www.iucnredlist.org, accessed in July 2016). The maps were processed using ArcGIS 10.5 to extract presences–absences of each species and map them onto a Behrmann equal-area global grid at spatial resolution of 400 km x 400 km (approximately 4° near the Equator). The exclusion of grid cells containing continental area resulted in a total of 1,817 grid cells with at least one shark species record. For one species (*Etmopterus compagnoi*) the extent of occurrence was not available in the IUCN database. Hence, for this species, we built it in ArcGIS 10.5 through the Minimum Convex Polygon approach, encompassing all the species occurrence points obtained from the online databases Fishbase (Froese & Pauly 2016) and GBIF (www.gbif.org).

To describe the variation in body shape, we applied a Body Shape index (hereafter BSi), described as the ratio between body height and length. The lower the value of the index, the flatter the body shape. Whenever available we obtained this information directly from the Fishbase. For those species that the information was not readily available, we estimated BSi from measurements taken on images obtained from Fishbase, IUCN (www.iucnredlist.org/), and WoRMS (www.marinespecies.org/) websites. We only considered those images which showed the animal in lateral plane, disregarding the ventral or dorsal fins. The digital images were processed in the software TpsDig version 2.25 (Rohlf 2016) to place landmarks for the morphometric analysis. Four landmarks were set on standardized anatomic locations on the fish image to determine body measurement of the total length (including the caudal fin) and height (excluding the pelvic and dorsal fins), according to the Fishbase standard metrics. A scaled distance was measured on each image to give a scale factor that converts the pixels to millimetres, in order to set all individual fish to the same scale (Viscosi & Cardini 2011).

Based on the BSi and occurrences of the shark species, we estimated the mean and median body shape of shark species on each cell and these two statistics were used as response variables in the following analyses. As both mean and median have been used in ecomorphological studies (Garcia *et al.* 2008, Fisher *et al.* 2010, Berke *et al.* 2013, Feldman & Meiri 2014, Torres-Romero *et al.* 2016), we decided to include both in our analyses, since the mean is usually a better descriptor of the data, but it is also more sensitive to extreme values than the median (Zar 1999).

Environmental variables

We used four variables as descriptors of the environmental conditions faced by the shark species. They were obtained from the AquaMaps' global marine coverage environmental layers (Kesner-Reyes *et al.* 2013) at a resolution of 0.58°, and were processed in ArcGIS 10.5 to fit the 400 x 400 km cell grid described above. We selected minimum temperature of the coldest month (Tc) and maximum temperature of the warmest month (Tw) to represent the thermoregulation hypothesis, as these two variables are extreme or limiting climatic factors. To support the thermoregulation hypothesis, we would expect a negative relation between BSi and temperature, as more fusiform species should be more commonly found in colder waters. To represent the habitat selection hypothesis, we selected bathymetry (Bathy) and distance to shore (DistShr), as both predictors are associated to different environmental conditions which can be related to sharks' swimming mode and habitat selection. To support this hypothesis, we would expect a positive relation between BSi and bathymetry or distance to shore, as flatter species would occur nearest to the shore, and in the shallowest waters.

Spatial autocorrelation

The lack of independence between pairs of observations due to geographic proximity (spatial autocorrelation) increases Type I errors, resulting in spurious relations and jeopardising the interpretation of observed patterns (Borcard *et al.* 1992, Legendre 1993). In order to control the effects of spatial autocorrelation, we used spatial filters (Borcard & Legendre 2002), generated in the software SAM 4.0 (Rangel *et al.* 2006). A matrix of connectivity based on the central coordinates of each grid cell was built to obtain the filters, and a principal coordinates analysis was applied on this matrix. This analysis resulted in a set of eigenvectors (the filters) representing the grid geometric structure in different spatial scales. To avoid excessive numbers of explanatory variables and overcorrection for spatial autocorrelation (Diniz-Filho & Bini 2005), we derived a thinned set of spatial filters, retaining in the analysis only filters with spatial autocorrelation (Moran's I) greater than 0.1. Hence, 53 filters were added to the models related to body shape, which were enough to remove spatial autocorrelation in all distance classes.

Data analysis

To identify the effect of environmental variables over the Selachimorpha's body shape, we applied linear regressions over additive models based on all possible combinations among the four environmental variables, except those that combined highly correlated variables ($r > |0.6|$), to avoid collinearity between the predictors. Therefore, only one of the temperature variables (Tc or Tw) could be included in each model. The species richness was included in the grid cells as a covariate for all the analysed models, aiming to control the effect of the number of species on the calculation of mean and median BSi. Based on the combinations of the variables and restrictions applied, we obtained 11 explanatory models plus a null model. To evaluate if the geographical patterns could have arisen at random, the null model did not contain any environmental variable, being composed only by the model intercept.

The model (or models) with better fit to the data was (were) selected based on the Akaike Information Criterion (AIC) (Burnham & Anderson 2002). This approach proposes to compare a large number of models at once and to identify the simplest one that yet provides the best fit to the data (Johnson & Omland 2004). We selected models with good empirical support ($\Delta AICc \leq 2$), while models with $\Delta AICc > 10$ have no empirical support and can be disregarded (Burnham & Anderson 2002). We also calculated the Akaike weights (w_i) for each model, which can be interpreted as the probability that it really is the best explanatory model. From those weights, we calculated the relative importance of each variable ($w+$) summing the Akaike weights across all models that included each explanatory variable. This approach usually presents robust results regardless of the autocorrelation control method

(Diniz-filho *et al.* 2008). Both the regressions and the AIC values calculations were performed on the platform R 3.3.2 (R Core Team 2015). We also evaluated the direction of the relation between the variables present in the best model and the response variables to assess whether the proposed hypothesis would be confirmed or disproved.

RESULTS

We could obtain information regarding both shape and geographic range for 359 shark species, and the calculated BSi ranged from 6.3% (most flattened - *Parascyllium variolatum*) to 22% (most fusiform - *Somniosus antarcticus*). The spatial variation in the mean body shape index shows a clear latitudinal gradient, in which species in temperate regions tend to have flatter bodies than those in tropical regions. The highest mean BSi values were found around oceanic archipelagos, while the lowest values were found at higher latitudes (Figure 1).

Among the 12 models that were analysed, only one stood out, with values of ΔAICc ≤ 2 (Table 1). The most plausible model (ΔAICc = 0.00, $w_i = 0.759$) was composed of three variables - distance to shore, temperature of the coldest month and bathymetry - and was considerably more plausible than the null model (ΔAICc = 231.57, $w_i = 0.000$). The distance to shore (w+ = 0.853) and the temperature of the coldest month (w+ = 1.000) showed a positive relation with the sharks mean BSi, while the bathymetry (w+ = 0.901) presented a negative relation (Table 3).

Regarding the spatial variation in the median BSi, we did not find a clear latitudinal gradient as we did when the mean was evaluated. However, the highest BSi values (more fusiform) were also found around oceanic archipelagos, whereas the lowest values (more flattened) were found at higher latitudes. We observed lower medians near the continents comparing to those found in the middle of the oceans (Figure 2).

Concerning the median BSi, two of the 12 models were considered plausible (Table 2), with values of ΔAICc ≤ 2, and both were more plausible than the null model (ΔAICc = 37.00, $w_i = 0.000$). The temperature of the coldest month was included in the two most plausible models

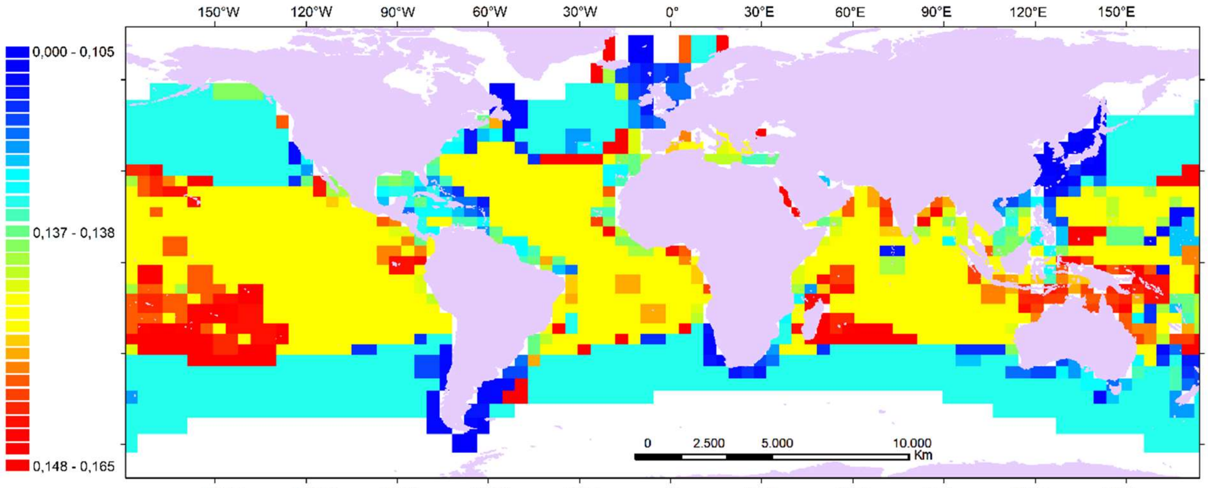

Figure 1. Geographic distribution of the mean body shape index of species from the superorder Selachimorpha in the world. The resolution of the grid cells is 400 km x 400 km (about 4° in the Equator). In blue and red are the smallest and largest values of mean body shape index, respectively.

Table 1. Adjustment of the models predicting shark mean body shape index based on environmental variables, on the 400 x 400 km grid. DistShr: distance to shore; Tc: minimum temperature of the coldest month; Tw: maximum temperature of the warmest month; Bathy: bathymetry.

Order	Models	ΔAICc	K	W_i
1	DistShr + Tc + Bathy	0.00	59	0.752
2	Tc + Bathy	3.35	58	0.094
3	DistShr + Tcr	4.17	58	0.094
4	Tc	10.16	57	0.005
5	DistShr + Tw + Bathy	58.00	59	0.000
6	Tw + Bathy	71.59	58	0.000
7	DistShr + Tw	75.12	58	0.000
8	Tw	98.96	57	0.000
9	DistShr + Bathy	160.52	58	0.000
10	Bathy	177.82	57	0.000
11	DistShr	196.95	57	0.000
12	Null	231.57	56	0.000

Table 2. Adjustment of the models predicting the shark median body shape index based on environmental variables, on the 400 x 400 km grid. DistShr: distance to shore; Tc: minimum temperature of the coldest month; Tw: maximum temperature of the warmest month; Bathy: bathymetry.

Order	Models	ΔAICc	K	W_i
1	Tc + Bathy	0.00	58	0.469
2	Tc	1.12	57	0.268
3	DistShr + Tc + Bathy	2.08	59	0.166
4	DistShr + Tc	3.24	58	0.093
5	Tw + Bathy	10.65	58	0.002
6	DistShr + Tw + Bathy	12.59	59	0.001
7	Tw	16.43	57	0.000
8	DistShr + Tw	17.40	58	0.000
9	Bathy	25.39	57	0.000
10	DistShr + Bathy	27.09	58	0.000
11	DistShr	36.72	57	0.000
12	Null	37.00	56	0.000

combined with bathymetry in the best model (ΔAICc = 0.00, w_i = 0.469), and alone in the second-best model (ΔAICc = 1.12, w_i = 0.268). The temperature of the coldest month (w+ = 0.997) was positively related to the shark's median BSi, while the bathymetry (w+ = 0.638) was negatively related (Table 3).

DISCUSSION

Our results indicate that both the mean and the median BSi presented congruent responses of spatial variation of the Selachimorpha body shape. We could detect a consistent trend of dorsoventral flattening towards coastal zones and shallow areas, while fusiform species were more common in deep waters far from the shore, and the transition between these two situations was occasionally abrupt. This trend was more clearly represented by the median than by the mean. A second, less conspicuous, trend detected was the increase in the BSi values (more fusiform species) towards the tropical regions all over the globe, while flattened species were more common above 30° latitude in both hemispheres. This trend was more clearly perceived by the mean than by the median. Overall, the results presented by our models were similar for the two response variables. The order of importance of the environmental variables was the same either for mean or for the median, although there were some differences in the relative importance values. The direction of the relationship was also the same for both, mean and median. So, except when noted, the results here were discussed based on the general trend presented by the two response variables.

The minimum temperature of the coldest month was included in all the best fitted models and showed the highest value of importance amongst all the variables. However, contrary to our expectations, this positive relationship indicates that species with more fusiform bodies tend to occur in warmer waters, thus not supporting the thermoregulation hypothesis prediction (Peters 1983, Brown *et al.* 2017). Despite not adjusting to our hypothesis, the high relative importance of temperature on our models indicates that it is related to Selachimorpha body shape, but probably it is responding to a different mechanism rather the one initially hypothesized.

A possible mechanism which associates these two variables is related to the swimming performance in fishes. Swimming performance is an important capacity for fish, playing a role in food capture, predator avoidance and reproductive behavior (Zeng *et al.* 2009, Penghan *et al.* 2014). Several studies indicated that swimming performance increased significantly with temperature (Lee *et al.* 2003, Zeng *et al.* 2009, Yan *et al.* 2012, Penghan *et al.* 2014). According to this association, it would be expected that more fusiform species (body shape that makes swimming more efficient) tend to be more common in warmer waters. Our results that showed a positive relationship between minimum temperature of the coldest month and BSi seem to support this hypothesis.

An additional mechanism that can associate temperature and body shape is related to the diffusion of oxygen in water. Warmer waters are able to retain larger amounts of dissolved oxygen than colder waters. A decrease in dissolved oxygen may result in a more depressed swimming performance (Penghan *et al.* 2014). At the same time, the oxygen (O_2) consumption rate of an organism increases in allometric form with its size;

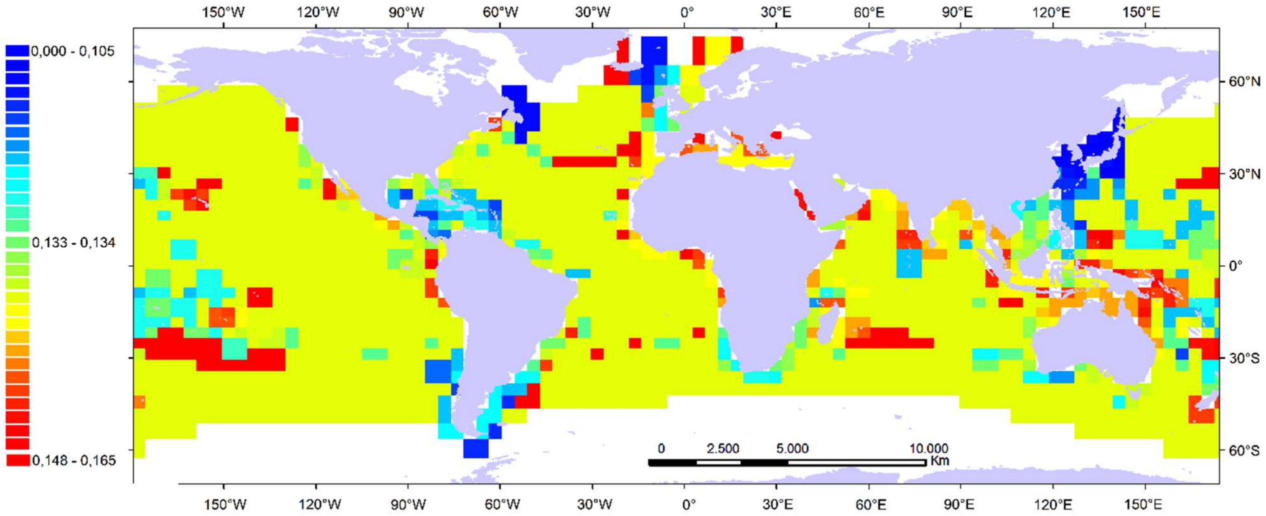

Figure 2. Geographic distribution of the median body shape index of species from the superorder Selachimorpha in the world. The resolution of the grid cells is 400 km x 400 km (about 4° in the Equator). In blue and red are the smallest and largest values of median body shape index, respectively.

organisms have a lower O_2 demand per unit mass than smaller organisms (West et al. 1997). Another possibility is the relation between the O_2 concentration in water and shark's gill morphology, and not body shape (Wootton *et al.* 2015). In either case, it is possible that the positive relation that we observed between temperature and body shape of Selachimorpha is related to the respiratory capacity of organisms, but we were not able to test this hypothesis directly and neither we have enough data to perform this analysis at the time.

The two variables that represent the habitat selection hypothesis (bathymetry and distance to shore), on the other hand, presented results consistent with our initial predictions. Viewed together, both variables suggest that more flatted body species (lower BSi values) occur in the shallower, closer to the shore areas, and that the more fusiform species occur in areas that are deeper and farther from the coast. According to Webb *et al.* (1996) and Breda *et al.* (2005), the fusiform body is hypothetically ideal for locomotion at high speeds in pelagic regions that do not present obstacles, since this body structure softens the forces contrary to the movement. This characteristic form is found in the species from the family Lamnidae, such as the white shark (*C. carcharias*) and the mako shark (*Isurus oxyrinchus*), which stand out for their great dispersal ability and use speed as their main strategy to obtain their food (Donley *et al.* 2004, Lingham-Soliar 2005). This body shape is considered a convergent trait with other lineages of top predatory marine vertebrates, such as dolphins, tunas, and extinct ichthyosaurs (Donley *et al.* 2004). On the contrary, the flattened body shape is more associated with the benthic habitat of several shark species, such as the spiny dogfish (*Squalus acanthias*), the tasselled wobbegong (*Eucrossorhinus dasypogon*), and the angel sharks (*Squatina* sp.). This flattened body shape is common in species thriving in shallower and coastal regions (Kriwet *et al.* 2010, Vaz & de Carvalho 2013) or in reef environments, where they await their prey in ambush strategies (Smith & Brown 2002, Baremore *et al.* 2009, Raoult *et al.* 2017). This type of morphology gives the species a slower and more manoeuvrable swim, typical of benthic species (Scacco *et al.* 2010).

Our results seem to indicate that the sharks' body shape is not a response to a selective pressure for heat conservation in cold environments, but rather to where they live and how they obtain their food. In a study associating the sharks' body shape to their ecology and taxonomic groups, Almeida (2016) showed that body shape does not seem to be structured throughout the phylogeny. Despite not explicitly testing for phylogenetic autocorrelation, this study demonstrated that several phylogenetically distant orders - such as Hexanchiformes and Carcharhiniformes (Vélez-Zuazo & Agnarsson 2011) - present similar body shapes, while other more closely related orders - such as Orectolobiformes and Squaliformes - have different body shapes. Therefore, the body shape of shark orders would not be a reflection of the evolutionary relationship between them, but rather an association with predation strategies and occupation of similar habitats, congruent with the idea that ecomorphological attributes tend to be related to locomotion (Cianciaruso *et al.* 2009) and habitat occupation, as it has already been demonstrated for several shark species (Scacco *et al.* 2010, Irschick & Hammerschlag 2015).

These patterns described for sharks were contrasting with those reported to other marine mammals (cetaceans and pinnipeds), which exhibit results supporting the heat conservation hypothesis, but not habitat preference and availability hypotheses (Torres-Romero *et al.* 2016). This difference among two taxa which live in the same environment and have similar ecologies, as sharks and toothed whales (suborder Odontoceti), suggests that they are responding to different selective pressures according to their physiological restrictions. According to Torres-Romero *et al.* (2016) the mechanism responsible by the pattern reported to marine mammals was their endothermy, and the negative relation between body size and water temperature was sustained even when only the toothed whales were analyzed. Fish morphology, on the other hand, is usually related to the type of habitat they preferentially explore (Piorski *et al.* 2006), and our results indicate that sharks clearly responded to habitat selection. But the strong positive relationship between body shape and temperature suggests that a physiological mechanism other than the hypothesized initially must be acting over shark body shape, possibly related to swimming performance. Future studies on macroecological marine patterns should include other variables which represent environmental pressures different from those usually addressed in terrestrial studies, especially those related to physiological mechanisms, since marine ecosystems are much less studied than terrestrial ones (Macpherson *et al.* 2009) and we know little about factors that structure marine communities on geographical scales (Torres-Romero *et al.* 2016).

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