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Evidence of endothermy in the extinct macropredatory osteichthyan *Xiphactinus audax* (Teleostei, Ichthyodectiformes)

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RH: Ferrón—Endothermy in *Xiphactinus*

Xiphactinus audax is the largest macropredatory osteichthyan ever known (Everhart et al., 2010). Some of the largest specimens exceed 5 m in total length, though the discovery of a few large, isolated teeth suggests that this teleost could reach even larger body sizes (Vavrek et al., 2016 and references therein). Fossil remains of this species have only been reported from the Upper Cretaceous of North America, across the Western Interior Basin (Schwimmer et al., 1997; Vavrek et al., 2016). The discovery of several virtually complete individuals in this area has provided valuable information about the anatomy, the dimensions, and the ecology of this species (Cope, 1872; Bardack, 1965). *Xiphactinus audax* displayed a tarpon-like body plan with a semi-lunate caudal fin and large caniniform teeth (Hay, 1898; Bardack, 1965; Carrillo-Briceño et al., 2012), suggestive of a highly active predatory lifestyle (Cavin et al., 2013). In fact, the emblematic 'fish-within-a-fish' specimen, containing an entire 2-m-long *Gillicus arcuatus*, provides evidence of the ability of *X. audax* to prey upon large, rapidly swimming fishes (Bardack, 1965).

Predation entails a high energetic demand (Brown and Kotler, 2004). Ferrón et al. (2017) recently proposed that, because mass-specific metabolic rate decreases with increasing body size, highly active lifestyles (such as macropredation) cannot be maintained by an ectothermic metabolism over a specific body size. From this perspective, they argued that the punctual evolution of gigantism among macropredators was closely linked to metabolic-level shifts promoted by various factors (i.e., endothermy, highly efficient respiratory systems, warm temperatures, and high oxygen levels), and suggested that several extinct aquatic macropredators, including *Xiphactinus*, could have been meso- or endotherms on the basis of their body size and life history. Later, Ferrón (2017) established a useful methodology to assess the swimming energetics of extinct aquatic organisms, which can be used to interpret their metabolic levels and thermoregulatory strategies. This study presents an equivalent methodology developed for assessing locomotion energetics in extinct osteichthyans, and provides evidence of endothermy in *X. audax*.

MATERIALS AND METHODS

The thermoregulatory strategy of *X. audax* was examined by comparing its estimated energy budget and cost of locomotion under an ectothermic and regionally-endothermic scenario at different water temperatures. This allowed for the determination of a range of potentially habitable water temperatures under each scenario (i.e., the temperature range is only viable when the estimated energy budget is greater than the cost of locomotion). In parallel, the actual range of water temperatures inhabited by this species was calculated from paleobiogeographical and paleoclimatic data. Comparison between potential and actual temperature ranges enabled exploration of the thermophysical strategy most likely adopted by *X. audax*.

Energy Budget Estimates

Energy budget of *X. audax* was assessed using routine metabolic rate (RMR) estimates given that both parameters can be considered equivalent in a broad sense (Willmer et al., 2009; Clarke, 2013). RMR records of 24 active extant osteichthyans were compiled from FishBase (Oxygen Consumption Studies Tables; Froese and Pauly, 2017) and Watanabe et al. (2015) (Table S1 in Supplemental Data 1), and were temperature adjusted from 0ºC to 32ºC (at 4ºC increments) with a Q_{10} of 1.83 (according to Clarke and Johnston, 1999). Two additional analyses including species with different levels of activity were also undertaken (see Appendix S1 in Supplemental Data 1). Where multiple records of RMR and body mass were available for the same species in FishBase the mean value was taken and subsequently treated as a single data point. RMR records expressed in joules per second ($J*s^{-1}$) were transformed to oxygen consumption units (mgO_2*h^{-1}) assuming an oxycaloric value of 13.54 $J*mgO_2^{-1}$ (following Brett and Groves, 1979). The scaling relationship between RMR and body mass was independently established in ectothermic and regional endothermic taxa by means of regression analysis, and differences between both groups were tested by ANCOVA analysis in PASW Statistics software version 18.0.0. The RMR of *X. audax* was then inferred at various temperatures in the ecto- and endothermic scenarios assuming body masses between 1,300 kg and 1,430 kg. Mass range was established assuming a body volume of 1,300,000 cm^3 and a possible range of body densities from 1.0 $g*cm^{-3}$ to 1.1 $g*cm^{-3}$ (according to the typical values from living teleosts; see Lowndes, 1955, and Davenport, 1999). Body volume was calculated in Nettfab Basic version 7.4.0 from a 3D virtual model of *X. audax* (Supplemental Data 2; available for use under a Creative Commons license in the Sketchfab platform, https://sketchfab.com) after scaling the model to 5.1 m total length (following Shimada and Everhart, 2004).

Cost of Locomotion Estimates

Costs of locomotion of *X. audax* were assessed from estimates of net cost of swimming (NCS), as this is a suitable parameter for assessing energy expenditure of thrust generation during swimming (Korsmeyer et al., 2002), and has been successfully utilized for this purpose in both extant (Sundström and Gruber, 1998; Semmens et al., 2013) and extinct groups (Ferrón, 2017; Ferrón et al., 2018). Power-performance curves for small fishes, calculated using conventional respirometers, represent useful tools for inferring energy expenditure in larger species (e.g., Sundström and Gruber, 1998; Semmens et al., 2013), particularly when the studied taxa share similar lifestyles (see references and a detailed discussion in Ferrón, 2017). Estimates of NCS for *X. audax* were calculated under ectothermic and endothermic scenarios from power-performance curves from two extant pelagic species, *Sarda chiliensis* (an ectotherm) (Sepulveda et al., 2003) and *Thunnus albacares* (a regional endotherm) (Korsmeyer and Dewar, 2001), as the difference between total metabolic rate (TMR, oxygen consumption at a particular swimming speed) and standard metabolic rate (SMR, oxygen consumption at resting) (Appendix S2 in Supplemental Data 1). NCS values were inferred assuming a cruising swimming speed of 3.65 $m*s^{-1}$ (equivalent to 0.57 body lengths per second, $BL*s^{-1}$), calculated from the method of Sambilay (1990) and considering a body length of 5.1 m (Shimada and Everhart, 2004) and an aspect ratio of the caudal fin of 5.93 (specimen FHSM VP-333 from Schwimmer et al., 1997:fig. 1; see Appendix S2 in Supplemental Data 1 for further details on how this parameter was calculated). NCS was considered identical for all temperature scenarios according to William and Beamish (1990), Claireaux et al. (2006) and Ohlberger et al. (2007).

Actual Temperature Range

The actual range of water temperatures inhabited by of *X. audax* was extrapolated from a global map of Late Cretaceous mean sea surface temperatures (Tabor et al., 2016) overlain with the current known paleobiogeographic distribution of this species (Vavrek et al., 2016). The paleoclimatic map considered in this study constitutes the most recently published global reconstruction of the Late Cretaceous, being based in multiproxy models that combine both climatic modelling and isotopic records (see Tabor et al., 2016 for further detail).

Validation Test

The predictive power of the established framework for inferring thermophysiological strategy in active pelagic osteichthyans was tested in a selection of living taxa from simultaneous records of cruising swimming speeds, water temperatures, and body masses (Table S2 in Supplemental Data 1). Two different validation tests were performed, the first considering all RMR records from the original dataset for establishing the RMR scaling relationship, and the second one performing a cross-validation analysis where the RMR scaling regression was recreated without inclusion of the particular species being tested in the each case.

RESULTS

Scaling relationship of RMR for both ectothermic and regional endothermic osteichthyans fits well to a linear model ($R^2_{ecto} = 0.95$; $R^2_{endo} = 0.97$) (Fig. 1; see equations calculated for each scenario in Appendix S3 in Supplemental Data 1). ANCOVA analysis detected significant differences between both groups, suggesting that regional endothermic osteichthyans exhibit a higher RMR than similar-sized ectotherms ($p < 0.000$) (Fig. 1). Low dispersion of the data allows for reliable RMR estimates for *X. audax* assuming ecto- and endothermy under different temperature scenarios (Table 1). NCS values of 57.09 $mgO_2{*}h^{-1}{*}kg^{-1}$ and 81.56 $mgO_2{*}h^{-1}{*}kg^{-1}$ are predicted for *X. audax* swimming at 0.57 $BL{*}s^{-1}$ assuming ecto- and endothermy, respectively (Appendix S2 in Supplemental Data 1). When contrasting RMR and NCS estimates, the model predicted that the range of potential habitable water temperatures would vary depending on the thermophysiological strategy of *X. audax* (Table 1). Thus, under the assumption of endothermy, this species could potentially live at considerably colder temperatures (waters above 4ºC) than in an ectothermic scenario (waters above 28ºC), which translates to disparate potential paleogeographical distributions (Fig. 2). When accounting for actual paleobiogeographic and paleoclimatic data, the estimated real distribution and range of water temperatures (12–32ºC) was inferred for *X. audax* that is congruent with the endothermic scenario (compare Fig. 2B, C). Furthermore, the validation tests support the high predictive power of this approach, as it is capable of correctly determining the thermophysiological strategy of all the living species included (Table 2).

DISCUSSION

Regional endothermy is the ability of some living fishes to maintain the temperature of certain body areas over that of the surrounding water (Block and Finnerty, 1994; Dickson and Graham, 2004). Among chondrichthyans, regional endothermy has been documented within alopiids (Weng and Block, 2004; Bernal et al., 2005; Sepulveda et al., 2005; Patterson et al., 2011) and lamnids (Lowe and Goldman, 2001), and was likely present in two other extinct families of lamniforms (Otodontidae and Cretoxyrhinidae) (Ferrón, 2017; see also Maisey et al., 2017). Within osteichthyans, regional endothermy has been described in tunas (tribe Thunnini, Scombridae), billfishes (Xiphiidae and Istiophoridae), and *Gasterochisma*, although the last two taxa possess the ability to heat only the brain and the eyes (i.e., cranial endothermy) (Block and Finnerty, 1994). Recently, whole-body endothermy has also been recorded in the opah (*Lampris guttatus*) (Wegner et al., 2015). In the present study, a useful methodology for predicting the most likely thermophysiological strategy of extinct osteichthyans has been developed, also revealing the possible existence of endothermy in *X. audax*, a basal teleost belonging to the extinct order Ichthyodectiformes (Nelson et al., 2016). This study constitutes the first evidence of endothermy in a stem teleost (Arratia, 1999), and would represent the earliest case of an endothermic taxon among osteichthyans, pushing the appearance of this adaptation within this group back to the Turonian period (Late Cretaceous) (Cavin et al., 2013). However, endothermy could also be present in other older large ichthyodectiforms with similar macropredatory lifestyles.

Thermal niche expansion, promoted by oceanic cooling and tropical compression during the Late Paleocene and Early Eocene, has been proposed as the most likely explanation for the radiation and diversification of extant endothermic fishes (Dickson and Graham, 2004; but see also Ferrón, 2017). The selective pressures that drove the evolution of endothermy in *X. audax* cannot be reliably assessed until it is known whether this adaptation evolved in this species punctually or, conversely, if it was a generalized condition among ichthyodectiforms, and was also present in older forms. The thermal niche expansion hypothesis itself seems insufficient for explaining the evolution of endothermy in this group, given the warm climate and the reduced vertical and latitudinal temperature gradients present during most of the Jurassic and Cretaceous (Huber et al., 1995; Jenkyns et al., 2012; Giorgioni et al., 2015). Notwithstanding, other selective pressures acting in unison in a similar way to endothermic cretoxyrhinid sharks (Ferrón, 2017) could offer more convincing explanations. In this sense, competition with other predators, most of them endothermic taxa with higher prey capture rates (Wegner et al., 2015), and the elevated cruising speed hypothesis should be also considered in future studies. These are possible related factors given the evolution, rapid radiation, and diversification of various endothermic groups during the Cretaceous period (Everhart, 2005; Motani, 2009; Bernard et al., 2010; Harrell et al., 2016; Ferrón, 2017; Pimiento et al., 2019), the cosmopolitan distribution of the ichthyodectiforms, and their body and caudal fin morphology, which is suggestive of high locomotory capacity (Cavin et al., 2013). In any case, it is important to emphasize that niche expansion, competition, and elevated cruising speeds are not mutually exclusive hypotheses (see Watanabe et al., 2015; Wegner et al., 2015).

Marine predators have experienced a tendency toward larger, faster, and more mobile forms from the Paleozoic to the present (Vermeij, 2002). Extant communities of marine vertebrates, especially those inhabiting comparatively high latitudes, usually include highly active meso- or endothermic top predators such as tunas, lamnid sharks, birds, or marine mammals (Cairns et al., 2008). The results presented here provide evidence of *X. audax* representing an endothermic taxon, which constitutes further evidence supporting endothermy already being a common trait among Cretaceous marine vertebrate top predators, including ichthyosaurs (Bernard et al., 2010), mosasaurs (Bernard et al., 2010; Harrell et al., 2016), cretoxyrhinid sharks (Ferrón, 2017), and now ichthyodectiform osteichthyans. In fact, representatives from the majority of these taxa coexisted not only temporally, but also geographically in non-tropical latitudes, as occurred in the Western Interior Sea (Shimada and Everhart, 2004; Myers and Lieberman, 2010). Altogether, these aspects highlight the singularity of Cretaceous marine ecosystems, where vertebrate predator communities not only acquired unprecedented levels of taxonomic diversity (Walker and Brett, 2002), but were also characterized by the independent evolution of highly active lifestyles and energetically costly thermophysiological strategies among phylogenetically distant taxa.

CONCLUSIONS

This study presents a useful approach for assessing the thermophysiological strategy of extinct osteichthyans by comparing energy budgets and cost of locomotion estimates under ecto- and endothermic scenarios. By applying this framework, the presence of endothermy is supported in *X. audax*, the largest macropredatory osteichthyan ever known. This finding constitutes the first evidence of endothermy in a stem teleost, and represents the earliest case of an endothermic taxon among osteichthyans—pushing the appearance of this adaptation in such groups back to the Late Cretaceous. These results also highlight the singularity of Cretaceous marine ecosystems, further supporting that vertebrate predator communities were already dominated by endothermic taxa belonging to several phylogenetically distant groups during this period.

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FIGURE CAPTIONS

FIGURE 1. Routine metabolic rate (RMR) scaling relationships established for living ecto- and regionally endothermic osteichthyans (in green and red, respectively) temperature adjusted to 16 °C. [planned for column width]

FIGURE 2. **A**, paleogeographic reconstruction of the entire Late Cretaceous globe and Western Interior Basin (zoomed, below), indicating mean sea surface temperatures (SST) (modified from Tabor et al., 2016). The range of potential habitable water temperatures (i.e., range of water temperatures within which energetic budget surpasses the net costs of swimming) and potential paleobiogeographic distribution of *Xiphactinus audax* are shown assuming **B**, ectothermy (in green) and **C**, endothermy (in red). Fossil occurrences of this taxon, representing its real distribution, are denoted with asterisks (according to Vavrek et al., 2016). [planned for page width]

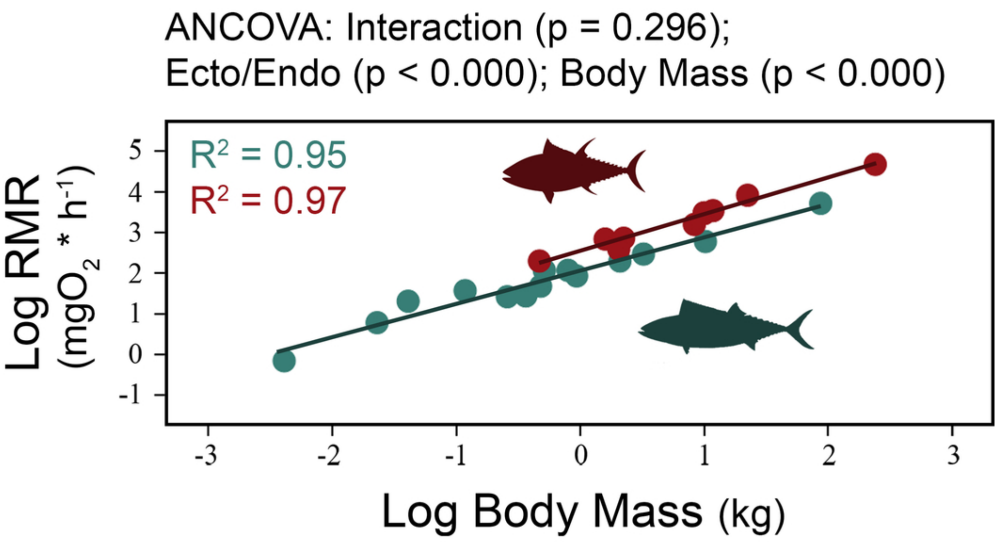

Figure 1

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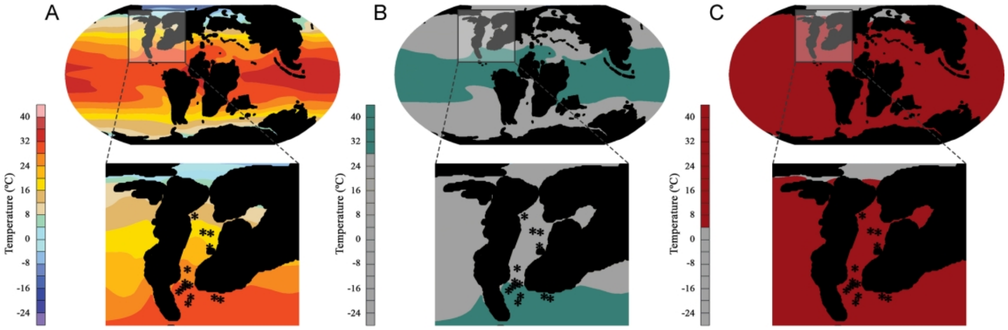

Figure 2

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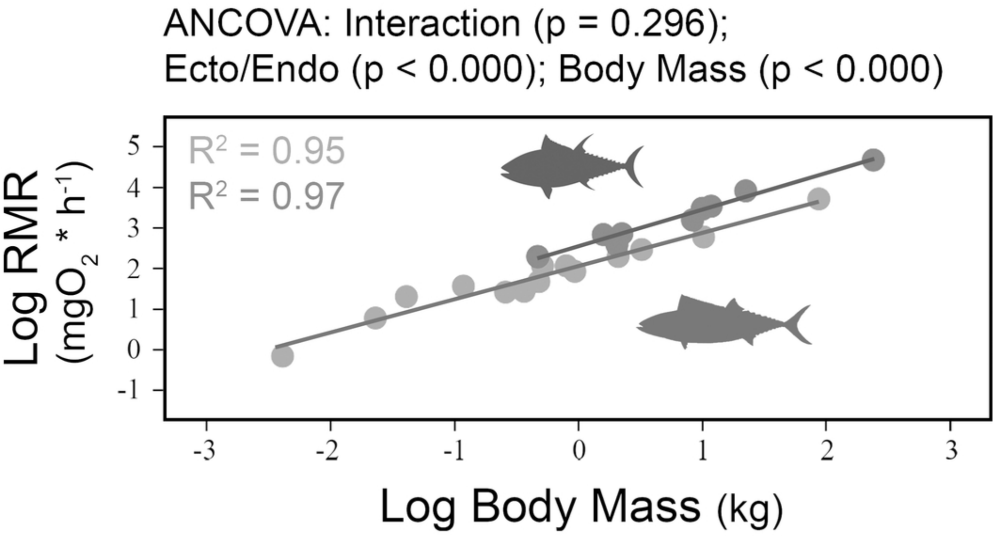

Figure 1 for print

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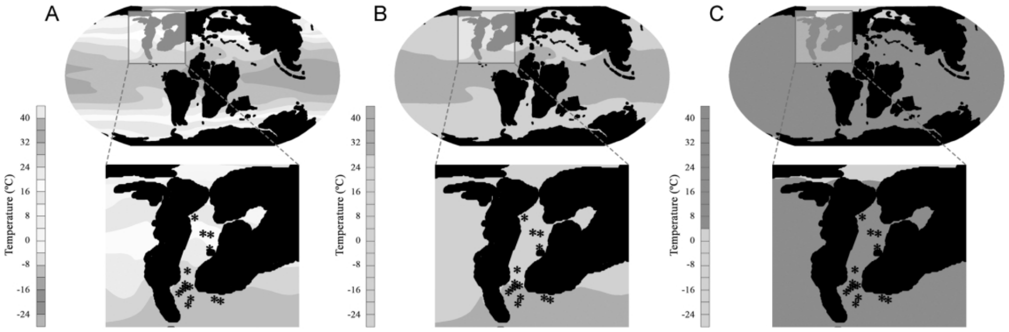

Figure 2 for print

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TABLE 1. Predicted values for net cost of swimming (NCS) and routine metabolic rate (RMR) in *Xiphactinus audax* assuming ectothermy and endothermy, different body masses, and multiple water temperature scenarios. Asterisks (*) indicate cases where RMR exceeded NCS.

		Prediction			
Body mass (kg)	Water temp. (ºC)	NCS$_{\mathrm{ectotherm}}$ (mgO$_2$*h^{-1}*kg^{-1})	RMR$_{\mathrm{ectotherm}}$ (mgO$_2$*h^{-1}*kg^{-1})	NCS$_{\mathrm{endotherm}}$ (mgO$_2$*h^{-1}*kg^{-1})	RMR$_{\mathrm{endotherm}}$ (mgO$_2$*h^{-1}*kg^{-1})
1300	0	57.09	11.57	81.56	68.31
1300	4	57.09	14.73	81.56*	86.99*
1300	8	57.09	18.76	81.56*	110.77*
1300	12	57.09	23.89	81.56*	141.06*
1300	16	57.09	30.42	81.56*	179.64*
1300	20	57.09*	38.74	81.56*	228.76*
1300	24	57.09	49.34	81.56*	291.31*
1300	28	57.09*	62.83*	81.56*	370.97*
1300	32	57.09*	79.99*	81.56*	472.41*
1430	0	57.09	11.37	81.56	67.75
1430	4	57.09	14.48	81.56*	86.27*
1430	8	57.09	18.44	81.56*	109.86*
1430	12	57.09	23.47	81.56*	139.91*
1430	16	57.09	29.89	81.56*	178.16*
1430	20	57.09*	38.07	81.56*	226.88*
1430	24	57.09	48.48	81.56*	288.92*
1430	28	57.09*	61.64*	81.56*	367.92*
1430	32	57.09*	78.60	81.56*	468.53*

TABLE 2. Routine metabolic rate (RMR) and net cost of swimming (NCS) estimates predicted from the established framework for living active pelagic species assuming ectothermy and regional endothermy. Note that ectothermy is discarded as a likely strategy in *Thunnus* species, as NCS exceeded RMR under an ectothermic scenario. *Istiophorus platypterus* and *M. nigricans* can be considered ectothermic fishes in terms of locomotion performance, because these species exhibit only eye and brain warming (i.e., cranial endothermy) and do not possess warmed red muscle.

ORIGINAL

	Species	$NCS_{ectotherm}$ ($mgO_2*h^{-1}*kg^{-1}$)	$RMR_{ectotherm}$ ($mgO_2*h^{-1}*kg^{-1}$)	$NCS_{endotherm}$ ($mgO_2*h^{-1}*kg^{-1}$)	$RMR_{endotherm}$ ($mgO_2*h^{-1}*kg^{-1}$)
Endotherm	*Thunnus albacares*	197.62	110.37	248.63	412.19
Endotherm	*Thunnus orientalis*	162.77	64.06	210.24	255.06
Endotherm	*Thunnus thynnus*	78.23	41.50	109.17	173.44
Ectotherm	*Istiophorus platypterus*	40.70	94.16	59.32	370.43
Ectotherm	*Makaira nigricans*	17.74	103.72	26.66	469.69

CROSS-VALIDATION

	Species	$NCS_{ectotherm}$ ($mgO_2*h^{-1}*kg^{-1}$)	$RMR_{ectotherm}$ ($mgO_2*h^{-1}*kg^{-1}$)	$NCS_{endotherm}$ ($mgO_2*h^{-1}*kg^{-1}$)	$RMR_{endotherm}$ ($mgO_2*h^{-1}*kg^{-1}$)
Endotherm	*Thunnus albacares*	197.62	110.37	248.63	403.87
Endotherm	*Thunnus orientalis*	162.77	64.06	210.24	251.65
Endotherm	*Thunnus thynnus*	78.23	41.50	109.17	190.93
Ectotherm	*Istiophorus platypterus*	40.70	93.69	59.32	370.43
Ectotherm	*Makaira nigricans*	17.74	92.94	26.66	469.69