Evidence of endothermy in the extinct macropredatory osteichthyan *Xiphactinus audax*

(Teleostei, Ichthyodectiformes)

HUMBERTO G. FERRÓN; School of Earth Sciences, University of Bristol, BS8 1TQ

Bristol, United Kingdom, humberto.ferron@bristol.ac.uk

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 specimen 'fish within a fish,' 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, since 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 meters 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 utilised 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 1for 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 two latter 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, which 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.

ACKNOWLEDGMENTS

LITERATURE CITED

Arratia, G. 1999. The monophyly of Teleostei and stem-group teleosts. Consensus and Disagreements; pp. 265–334 in G. Arratia and H. P. Schultze, H.P. (eds.), Mesozoic Fishes 2—Systematics and Fossil Record. Verlag Dr. F. Pfeil, München.

Bardack, D. 1965. Anatomy and evolution of chirocentrid fishes. University of Kansas Paleontological Contributions 10:1–88.

Bernal, D., C. A. Sepulveda, and S.J. Beaupre. 2005. Evidence for temperature elevation in the aerobic swimming musculature of the common thresher shark, *Alopias vulpinus*. Copeia 2005:146–151.

Bernard, A., C. Lécuyer, P. Vincent, R. Amiot, N. Bardet, E. Buffetaut, G. Cuny, F. Fourel, F. Martineau, and J. M. Mazin. 2010. Regulation of body temperature by some Mesozoic marine reptiles. Science 328:1379–1382.

Block, B. A., and J. R. Finnerty. 1994. Endothermy in fishes: a phylogenetic analysis of constraints, predispositions, and selection pressures. Environmental Biology of Fishes 40:283–302.

Brett, J. R., and T. D. D. Groves. 1979. Physiological Energetics; pp. 280–352 in W. S. Hoar, D. J. Randall, and J. R. Brett (eds.), Fish Physiology. Academic Press, New York.

Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7:999–1014.

Cairns, D. K., A. J. Gaston, and F. Huettmann. 2008. Endothermy, ectothermy and the global structure of marine vertebrate communities. Marine Ecology Progress Series 356:239–250.

Carrillo-Briceño, J., J. Alvarado-Ortega, and C. Torres. 2012. Primer registro de *Xiphactinus leidy*, 1870 (Teleostei, Ichthyodectiformes) en el Cretácico superior de América del Sur (Formación la Luna, Venezuela). Revista Brasileira de Paleontologia 15:327–335.

Cavin, L., P. L. Forey, and S. Giersch. 2013. Osteology of *Eubiodectes libanicus* (Pictet and Humbert, 1866) and some other ichthyodectiformes (Teleostei): phylogenetic implications. Journal of Systematic Palaeontology 11:115–177.

Claireaux, G., C. Couturier, and A. L. Groison. 2006. Effect of temperature on maximum swimming speed and cost of transport in juvenile European sea bass (*Dicentrarchus labrax*). Journal of Experimental Biology 209:3420–3428.

Clarke, A. 2013. Dinosaur energetics: setting the bounds on feasible physiologies and ecologies. The American Naturalist 182:283–297.

Clarke, A., and N. M. Johnston. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. Journal of animal ecology 68:893–905.

Cope, E. D. 1872. Sketch of an expedition in the valley of the Smoky Hill River in Kansas. Proceedings of the American Philosophical Society 12:174–176.

Davenport, J. 1999. Swimbladder volume and body density in an armoured benthic fish, the streaked gurnard. Journal of Fish Biology 55:527–534.

Dickson, K. A., and J. B. Graham. 2004. Evolution and consequences of endothermy in fishes. Physiological and Biochemical Zoology 77:998–1018.

Everhart, M. J. 2005. Rapid evolution, diversification and distribution of mosasaurs (Reptilia; Squamata) prior to the KT Boundary. Eleventh Annual Symposium in Paleontology and Geology. Tate Geological Museum, Casper College, Casper, Wyoming, U.S.A.

Everhart, M. J., S. A. Hageman, and B. L. Hoffman. 2010. Another Sternberg "fish-within-a-fish" discovery: first report of *Ichthyodectes ctenodon* (Teleostei; Ichthyodectiformes) with stomach contents. Transactions of the Kansas Academy of Science 113:197–205.

Ferrón, H. G. 2017. Regional endothermy as a trigger for gigantism in some extinct macropredatory sharks. PloS One 12:e0185185.

Ferrón, H. G., C. Martínez-Pérez, and H. Botella. 2017. The evolution of gigantism in active marine predators. Historical Biology 30:712–716.

Ferrón, H. G., B. Holgado, J. J. Liston, C. Martínez-Pérez, and H. Botella. 2018. Assessing metabolic constraints on the maximum body size of actinopterygians: locomotion energetics of *Leedsichthys problematicus* (Actinopterygii: Pachycormiformes). *Palaeontology* 61:775–783.

Froese, R., and D. Pauly. 2017. Fishbase. Available at www.fishbase.org. Accessed February 14, 2017.

Giorgioni, M., H. Weissert, S. M. Bernasconi, P. A. Hochuli, C. E. Keller, R. Coccioni, M. R. Petrizzo, A. Lukeneder, and T. I. Garcia. 2015. Paleoceanographic changes during the Albian–Cenomanian in the Tethys and North Atlantic and the onset of the Cretaceous chalk. Global and Planetary Change 126:46–61.

Harrell, T. L., A. Pérez-Huerta, and C. A. Suarez. 2016. Endothermic mosasaurs? Possible thermoregulation of Late Cretaceous mosasaurs (Reptilia, Squamata) indicated by stable oxygen isotopes in fossil bioapatite in comparison with coeval marine fish and pelagic seabirds. Palaeontology 59:351–363.

Hay, O. P. 1898. Observations on the genus of fossil fishes called by Professor Cope, *Portheus*, by Dr. Leidy, *Xiphactinus*. Zoological Bulletin 2:25–54.

Huber, B. T., D. A. Hodell, and C. P. Hamilton. 1995. Middle–Late Cretaceous climate of the southern high latitudes: stable isotopic evidence for minimal equator-to-pole thermal gradients. Geological Society of America Bulletin 107:1164–1191.

Jenkyns, H. C., L. Schouten-Huibers, S. Schouten, and J. S. Damsté. 2012. Warm Middle Jurassic-Early Cretaceous high-latitude sea-surface temperatures from the Southern Ocean. Climate of the Past 8:215–226.

Korsmeyer, K. E., and H. Dewar. 2001. Tuna metabolism and energetics. Fish Physiology 19:35–78.

Korsmeyer, K. E., J. F. Steffensen, and J. Herskin. 2002. Energetics of median and paired fin swimming, body and caudal fin swimming, and gait transition in parrotfish (*Scarus schlegeli*) and triggerfish (*Rhinecanthus aculeatus*). Journal of Experimental Biology 205:1253–1263.

Lowe, C. G., and K. J. Goldman. 2001. Thermal and bioenergetics of elasmobranchs: bridging the gap. Environmental Biology of Fishes 60:251–266.

Lowndes, A. G. 1955. Density of fishes: Some notes on the swimming of fish to be correlated with density, sinking factor and load carried. Journal of Natural History 8:241–256.

Maisey, J. G., A. W. Bronson, R. R. Williams, and M. Mckinzie. 2017. A Pennsylvanian 'supershark' from Texas. Journal of Vertebrate Paleontology 37:e1325369.

Motani, R. 2009. The evolution of marine reptiles. Evolution: Education and Outreach 2:224–235.

Myers, C. E., and B. S. Lieberman. 2010. Sharks that pass in the night: using Geographical Information Systems to investigate competition in the Cretaceous Western Interior Seaway. Proceedings of the Royal Society B: Biological Sciences 278:rspb20101617.

Nelson, J. S., T. C. Grande, and M. V. Wilson (eds.). 2016. Fishes of the World, fifth edition. John Wiley and Sons, Hoboken, New Jersey, 652 pp.

Ohlberger, J., G. Staaks, and F. Hölker. 2007. Effects of temperature, swimming speed and body mass on standard and active metabolic rate in vendace (*Coregonus albula*). Journal of Comparative Physiology B 177:905–916.

Patterson, J. C., C. A. Sepulveda, and D. Bernal. 2011. The vascular morphology and in vivo muscle temperatures of thresher sharks (Alopiidae). Journal of Morphology 272:1353–1364.

Pimiento, C., J. L. Cantalapiedra, K. Shimada, D. J. Field, and J. B. Smaers. 2019. Evolutionary pathways toward gigantism in sharks and rays. Evolution 73:588–599.

Sambilay, V. C. 1990. Interrelationships between swimming speed, caudal fin aspect ratio and body length of fishes. Fishbyte 8:16–20.

Schwimmer, D. R., J. D. Stewart, and G. D. Williams. 1997. *Xiphactinus vetus* and the distribution of *Xiphactinus* species in the eastern United States. Journal of Vertebrate Paleontology 17:610–615.

Semmens, J. M., N. L. Payne, C. Huveneers, D. W. Sims, and B. D. Bruce. 2013. Feeding requirements of white sharks may be higher than originally thought. Scientific Reports 3:1471.

Sepulveda, C. A., K. A. Dickson, and J. B. Graham. 2003. Swimming performance studies on the eastern Pacific bonito *Sarda chiliensis*, a close relative of the tunas (family Scombridae) I. Energetics. Journal of Experimental Biology 206:2739–2748.

Sepulveda, C. A., N. C. Wegner, D. Bernal, and J. B. Graham. 2005. The red muscle morphology of the thresher sharks (family Alopiidae). Journal of Experimental Biology 208:4255–4261.

Shimada, K., and M. J. Everhart. 2004. Shark-bitten *Xiphactinus audax* (Teleostei: Ichthyodectiformes) from the Niobrara Chalk (Upper Cretaceous) of Kansas. The Mosasaur 7:35–39.

Sundström, L. F., and S. H. Gruber. 1998. Using speed-sensing transmitters to construct a bioenergetics model for subadult lemon sharks, *Negaprion brevirostris* (Poey), in the field. Hydrobiologia 371:241–247.

Tabor, C. R., C. J. Poulsen, D. J. Lunt, N. A. Rosenbloom, B. L. Otto-Bliesner, P. J. Markwick, E. C. Brady, A. Farnsworth, and R. Feng. 2016. The cause of Late Cretaceous cooling: a multimodel-proxy comparison. Geology 44:963–966.

Vavrek, M. J., A. M. Murray, and P. R. Bell. 2016. *Xiphactinus audax* Leidy 1870 from the Puskwaskau Formation (Santonian to Campanian) of northwestern Alberta, Canada and the distribution of *Xiphactinus* in North America. Vertebrate Anatomy Morphology Palaeontology 1:89 –100.

Vermeij, G. J. 2002. Evolution in the consumer age: predators and the history of life. The Paleontological Society Papers 8:375–394.

Walker, S. E., and C. E. Brett. 2002. Post-Paleozoic patterns in marine predation: was there a
Mesozoic and Cenozoic marine predatory revolution? Paleontological Society Papers
8:119–194.

Watanabe, Y. Y., K. J. Goldman, J. E. Caselle, D. D. Chapman, and Y. P. Papastamatiou.
2015. Comparative analyses of animal-tracking data reveal ecological significance of
endothermy in fishes. Proceedings of the National Academy of Sciences 112:6104–
6109.

Wegner, N. C., O. E. Snodgrass, H. Dewar, and J. R. Hyde. 2015. Whole-body endothermy in
a mesopelagic fish, the opah, *Lampris guttatus*. Science 348:786–789.

Weng, K. C., and B. A. Block. 2004. Diel vertical migration of the bigeye thresher shark
(*Alopias superciliosus*), a species possessing orbital retia mirabilia. Fishery Bulletin
102:221–229.

William, F., and H. Beamish. 1990. Swimming metabolism and temperature in juvenile
walleye, *Stizostedion vitreum vitreum*. Environmental Biology of Fishes 27:309–314.

Willmer, P., G. Stone, and I. Johnston (eds.). 2009. Environmental Physiology of Animals.
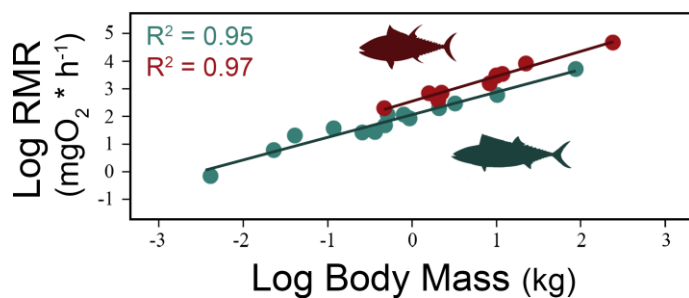Blackwell, Carlton, 768 pp.

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]
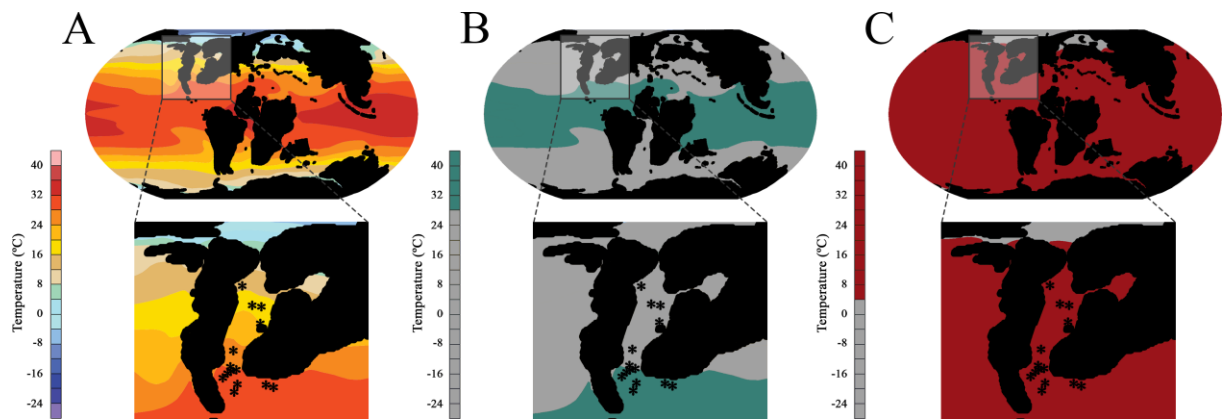
FIGURE 2. **A**, paleogeographic reconstruction of the entire Late Cretaceous globe and Western Interior Basin (zoomed, below), indicating mean sea surface temperatures (SST) (modified from Tabor et al., 2016). The range of potential habitable water temperatures (i.e., range of water temperatures within 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]

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. Data in italics indicate cases where RMR exceeded NCS.

			Prediction		
Body mass (kg)	Water temp. (°C)	$NCS_{ectotherm}$ ($mgO_2 * h^{-1} * kg^{-1}$)	$RMR_{ectotherm}$ ($mgO_2 * h^{-1} * kg^{-1}$)	$NCS_{endotherm}$ ($mgO_2 * h^{-1} * kg^{-1}$)	$RMR_{endotherm}$ ($mgO_2 * h^{-1} * kg^{-1}$)
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. *I. platypterus* and *M. nigricans* can be considered ectothermic fishes in terms of locomotion performance, as 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