Allometric Scaling of Anaerobic Capacity Estimated from a Unique Field-Based Data Set of Fish Swimming

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ABSTRACT

Locomotion is a defining characteristic that can dictate many aspects of an organism's life history in the pursuit of maximizing fitness, including escaping predators, capturing prey, and transitioning between habitats. Exhaustive exercise can have negative consequences for both short-term and long-term energetics and life history trade-offs, influencing fish survival and reproduction. Studies of swimming performance and exhaustive exercise in fish are often conducted on individual species, but few multispecies analyses exist and even fewer in field settings. In fish, swimming performance and exercise have historically been studied in the laboratory using swim tunnels, but an increasing body of work in recreational fisheries science provides a novel way to examine swimming capacity and exhaustion. Using fight time, the time it takes for a hooked fish to be landed on rod and reel fishing gear, as an opportunistic proxy for fish exhaustion, a multispecies meta-analysis of data from studies on recreational fisheries was conducted to elucidate the factors that most influence capacity for exhaustive exercise. Data from 39 species of freshwater and marine fish were aggregated, and negative binomial mixed effects models as well as phylogenetic least squares regression were used to identify the factors that most influenced exhaustive exercise in the field. Fish total length, aspect ratio of the caudal fin, and body form were significant factors in explaining the capacity for exhaustive exercise. Large migratory fish with high aspect ratios were able to fight, and therefore exercise, the longest. These results illustrate that body form and physiology are both deeply intertwined to inform function across fish species and point to angling fight time as a useful approximation of fish swimming capabilities that can be further developed for understanding the limits of fish exercise physiology.

Keywords: exhaustion, fish, recreational angling, fisheries, locomotion, anaerobiosis.

Introduction

Movement is integral to many animals as they accomplish life history tasks (Nathan et al. 2008; Bro-Jørgensen 2013). The precise ways animals move, including avoiding predators, acquiring food, and seeking reproductive opportunities that maximize lifetime fitness potential, are critical to their physical fitness (Brown et al. 2004; Chapman et al. 2015; Halsey 2016). Animals typically move within their aerobic scope, the range of aerobic metabolic activity above maintenance level (Fry 1947), but in rare instances they will recruit anaerobic exercise to accomplish specialized tasks such as chasing prey or escaping a predator and then incur the metabolic (Seymour et al. 1985; Kieffer 2000) and behavioral (Brownscombe et al. 2014*b*) costs of recovery. This exhaustive exercise has received attention as a key variable of interest for fundamental movement research (Wood et al. 1983; Wood 1991; Kieffer 2000). The energetic paradigms of exhaustive exercise have largely focused on a few species in laboratory settings exploring the fundamentals of scaling relationships, muscle energetics, and physical forces to calculate the limits of exercise across taxa (Kleiber 1947; Brett 1965; Webb 1971*a*, 1971*b*; West et al. 1997; White and Seymour 2005; Cloyed et al. 2021). Field research on exhaustive exercise is rare because of the challenges observing wild animals exercising at maximum capacity. As such, the relationships between animal form and function in the wild remain a significant knowledge gap with respect to the energetic capacity when confronted with a critical challenge.

Fish are an excellent model for studying exhaustive exercise across taxa, in part because they are a highly diverse group spanning a variety of morphologies optimized for various

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habitats. This diversity, however, can result in physiological trade-offs that influence locomotor performance, such as changes in the proportion of red to white muscle (see Garland et al. 2022 for a review on trade-offs in organismal biology). Indeed, fish have been studied extensively in laboratory settings to understand the behavioral and physiological determinants of anaerobic exercise (Goolish 1991; Hammer 1995; Kieffer 2000; Post and Parkinson 2001). Respirometry and other laboratory experiments have shown how fish recruit either aerobic red muscle for sustained swimming within the aerobic scope or anaerobic white muscle for burst exercise (Brett 1972; Goolish 1991; Blake 2004; Palstra and Planas 2011). Field experiments with accelerometry (e.g., Brownscombe et al. 2014*b*; Wright et al. 2014; Lennox et al. 2019) rarely capture sustained anaerobic swimming because animals seldom recruit these pathways in daily life and would even more uncommonly be recorded swimming to exhaustion. There is therefore a lingering gap in our understanding of how much exhaustive exercise fish can sustain in the wild that, if addressed, would provide new insights into how form and function are related within and among species.

Humans operate as predators in wild systems and use a variety of gears (e.g., fishing rods, nets, traps, guns) to target animals for harvest or recreation, which elicits an escape response from these animals. Recreational fishers in particular target a wide diversity of fish using rod and reel (Cowx 2002) that challenge the fish to swim to exhaustion before it can be landed. Literature on recreational fisheries provides a unique window into the swimming capabilities of different fish species and offers an opportunity to observe interspecific capacity for exhaustive exercise across taxa in response to an extreme challenge. We capitalized on the wide availability of accurately timed fights between recreational anglers and fish species around the world in scientific literature on recreational fisheries to investigate how species and individual traits contributed to the capacity to swim to exhaustion. Because metabolic rate increases with absolute body size (Clarke and Johnston 1999), we predicted that larger fish would have longer fight times across species. We also predicted that the aspect ratio of the caudal fin, a key morphological trait linked to swimming function, would influence fight time durations across species. Finally, we predicted that highly migratory fish, which are inherently more active over their life span than nonmigratory fish, would have higher exercise tolerance because their bodies are conditioned for the intense exercise, both aerobic and anaerobic, that migrations demand (Brownscombe et al. 2017).

Methods

Data Collection and Preparation

We reviewed the published literature from January 2007 to December 2017 covering fish caught with recreational angling equipment (rod and reel), which included studies focusing on physiological stress responses of angled fish. We emailed corresponding authors for the identified articles and colleagues working in recreational fisheries science for data from studies that recorded fish capture data, including fight time, defined as the amount of time elapsed from when a fish is first hooked on recreational fishing gear to when it is landed, and fish body size, measured in centimeters total length (table A1). We identified 23 studies in the published literature, and unpublished fish capture data from eight additional studies were shared with us, encompassing 42 species. The data extracted included fish species, length (fork length or total length), fight time, gear type (fly or conventional tackle), and location of capture (state/province and country). Fish shape (e.g., fusiform or elongate) and aspect ratio were added to the data set using data extracted from the global fish database FishBase (Froese and Pauly 2000) with the rfishbase package (Boettiger et al. 2012) in R (R Core Team 2020). Aspect ratio was defined as the squared height of the caudal fin divided by the surface area of the caudal fin (Froese and Pauly 2000). If multiple aspect ratios were found, values were averaged, and the mean value was used. Species were scored as highly migratory or nonmigratory according to designations for each species available in FishBase. While migration does exist on a spectrum, the binary classification was used for the purposes of these analyses. If necessary or if no information was provided in FishBase, these determinations were changed according to other support from the literature focused on species ecology. Species trophic level (level 3, level 4), food type (benthivore, piscivore, planktivore), and feeding strategy (ambush, chasing, crushers, mobile hunters, particulate feeding, stalking, suction feeders) were assigned according to the designations discussed by Gerking (1994) and notes on species biology from the included studies and FishBase. Determinations of the activity level (high, medium, low) and energy demand required (minimal, burst, sustained) for designated foraging strategies were assigned according to the descriptions of each feeding strategy (Gerking 1994). Some study species did not have measurable fork lengths because of the shape of their caudal fin. Because of this, all analyses were conducted with total length. For species whose total length was not directly measured in the original studies, fork lengths were converted to total length according to species-specific conversion equations found in the literature (table A2). When species-specific conversions could not be found, equations were used from closely related species to provide a best available approximation. This was done for eight species in the data set, mainly tunas (*Thunnus* spp.), false albacore (*Euthynnus alletteratus*), and skipjack (*Katsuwonus pelamis*; table A2). Some species had missing values for the gear type; haddock, bluefin tuna, largemouth bass, blue shark, and yellowfin tuna values were imputed to be conventional gear according to context. We excluded 23 Atlantic bonefish with missing values for tackle because gear was not known. Phylogenetic relationships among species were available for bony fish through the fishtree_phylogeny function in the fishtree R package, an application programming interface to the Fish Tree of Life (Chang et al. 2019).

Data Analysis

The response variable, fight time, is essentially a count variable of seconds to exhaustion. If an appropriate fishing line test is used, a fish will not be landed before it experiences exhaustion and can no longer fight against the line. As a count variable, the data were initially modeled by generalized linear regression with a Poisson distribution. To account for evidence of overdispersion in our Poisson models, a negative binomial distribution was ultimately used. Two models were constructed and compared, both using the glmer.nb function in the R package lme4 (Bates et al. 2015). The first model included multiple putative explanatory variables hypothesized to contribute to time to exhaustion: total length, aspect ratio, body shape (elongated or fusiform), energy demand (minimal, burst, sustained), food type (piscivore, benthivore, planktivore), migratory trait, and gear type. The second model included only total length and gear type. Both models included species as a random effect, in part to account for unbalanced observations among species, as is common in ecology studies (Schielzeth et al. 2020). The models were compared by Akaike information criterion (AIC; Akaike 1974), a commonly used metric for selecting the model that best balances goodness of fit and parsimony from a candidate model set. Predictions were drawn with the predict.merMod function in lme4 without random effects to provide generic predictions for fight times.

In consideration of potential phylogenetic relations among species and the influence on violation of independence, an especially important consideration when comparing species for metabolic scaling (White and Kearney 2014), the full model was repeated using phylogenetic generalized least squares regression using the gls function in the nlme package (Pinheiro et al. 2020). The nlme package does not take a family argument, so neither Poisson nor negative binomial distributions were supported. Using the ape package (Paradis and Schliep 2019), we included a Brownian motion correlation structure (Felsenstein 1985; Martins and Hansen 1997) based on the phylogenetic tree drawn by the fishtree package. Because not all of the species were included in the possible trees, only 30 species were used in this model. The corBrownian function assumes only one line per phylogenetic grouping, so random effects are not supported. Therefore, the mean fight time and mean total length for each species were fitted along with aspect ratio, shape, energy demand, food type, and migratory tendency; fishing gear was not used in this analysis. Again, a full model and reduced model were fitted and compared by AIC based on maximum likelihood estimation (method = “ML”).

Results

A total of 5,749 fight time records were extracted from recreational fishing studies on 42 different species of bony and cartilaginous fish, 30 of which were available in fishtree for phylogenetic analysis (fig. 1). After removal of three species with only one observation and observations without length records, 5,652 records from 39 species were available for modeling. The longest average fight times were for white marlin (*Kajikia albida*), the largest species in the data set (230.9 ± 11.6 cm total length; mean ± SD) and Atlantic tarpon (*Megalops atlanticus*), averaging 37 and 25 min, respectively (figs. 2, 3). Fat snook (*Centropomus parallelus*), peacock bass (*Cichla ocellaris*), and brook trout (*Salvelinus fontinalis*) were landed in 11, 14, and 22 s, respectively, on average, representing the shortest fight times. These were the three smallest species in the data set, measuring 26.9 ± 9.3, 26.4 ± 4.4, and 18.2 ± 5.2 cm total length, respectively. The full model performed better than the simple model with only total length and gear type, so the full model was retained (ΔAIC = 3.65). The full model revealed a strong positive relationship to total length ($z = 39.93$, $P < 0.01$; fig. 4) and aspect ratio ($z = 2.01$, $P = 0.04$). Fight times for the fusiform body form were not quite significantly longer than for the elongated body forms ($z = 1.83$, $P = 0.07$; fig. 4). Fish captured by fly fishing also took longer to land ($z = -3.77$, $P < 0.01$). Food type, energy demand, and migratory trait were not significant.

The phylogenetic (fig. 1) generalized least squares regression analysis had results similar to the negative binomial mixed effects model. In this case, there was no clear difference between the full model and the reduced model (ΔAIC = 1.96), so the simple model, which included only total length, was retained. In this case, total length was a strong significant positive predictor of fight time ($t = 15.06$, $P < 0.01$).

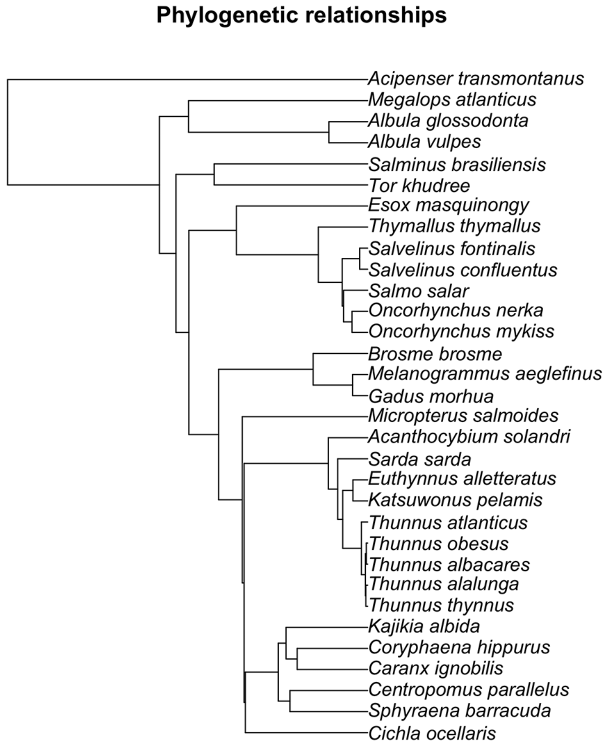

Figure 1. Phylogenetic relationships among bony fish species covered in this article, excluding 10 not in the fishtree database, primarily sharks. These 32 species were used for the phylogenetic generalized least squares model. The origin (root) of the tree represents the most recent common ancestor linking the phylogenetic tree of bony fish.

Discussion

Animals have evolved physiological systems adapted to their environments and the challenges that confront them in staying alive (Bro-Jørgensen 2013). The musculature of a fish and the

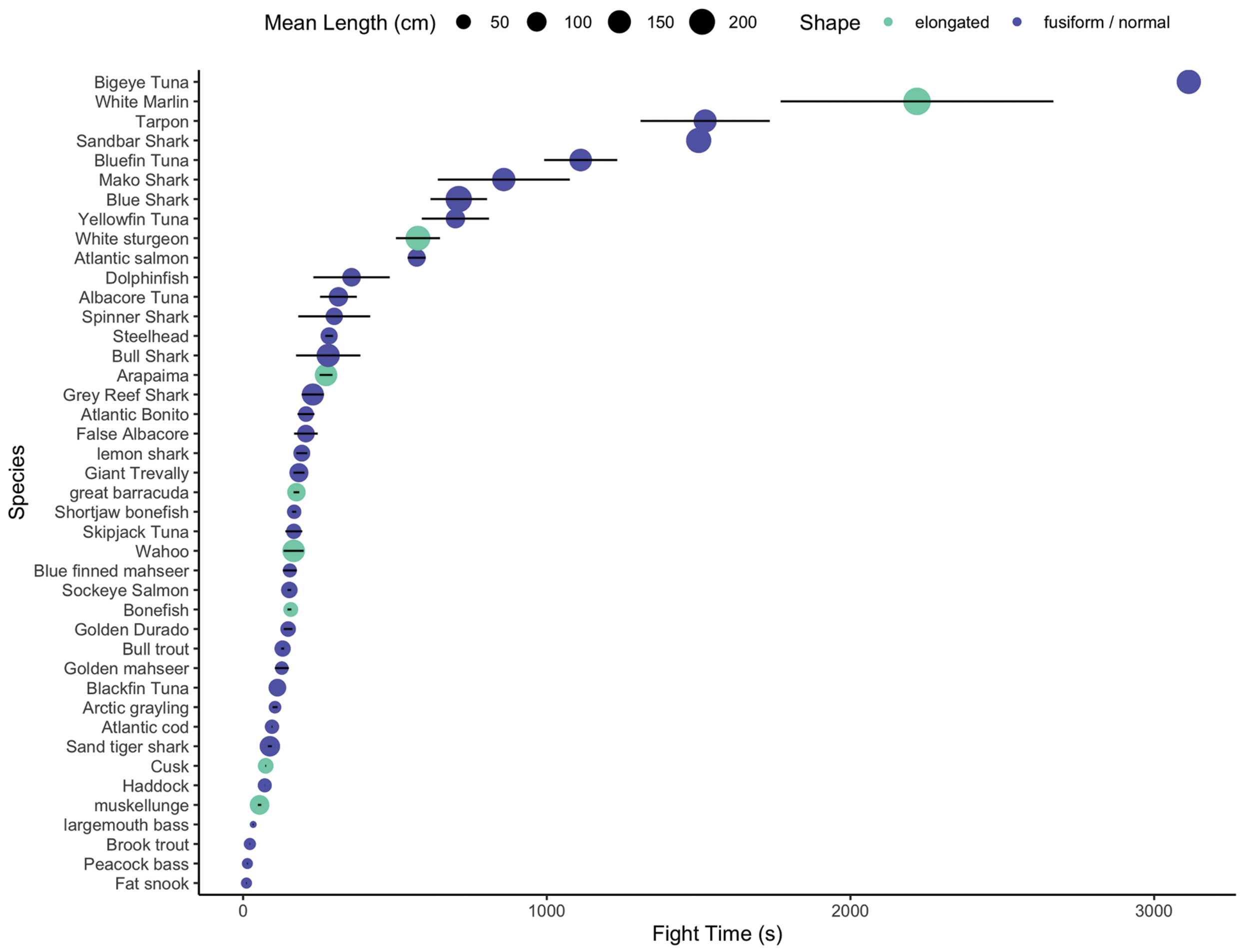

Figure 2. Summary of fish fight times, mean and standard error, with mean fish length and body shape scaled and colored to the plot. Fat snook and butterfly peacock bass had on average the briefest fight times, whereas bigeye tuna and white marlin had on average the longest fight times to exhaustion.

associated physiological systems that limit exercise potential, especially the cardiorespiratory system, are shaped by evolution of the species, with some interindividual variation in performance (Albert and Johnson 2012). Fish phylogenetic groups vary dramatically in musculature, shape, fin placement, and metabolic capabilities, demonstrating how body form reflects function and performance (Goolish 1991; Altringham and Ellerby 1999; Langerhans and Reznick 2010). Among species, the amount of anaerobic performance required for an ambush predator to forage efficiently will be less than the amount of white muscle required for cursorial counterparts (Childress and Somero 1990), leading active species to exhibit stronger positive trends of body size with anaerobic capacity (e.g., Centrarchidae [Kieffer et al. 1996]; Cyprinidae [Ohlberger et al. 2005]). In our analysis of field responses to an extreme challenge, fish anaerobic performance had significant variation among species groupings reflecting these interspecific differences in lifestyle, but high variation was associated with individual body size. These results are suggestive of a strong allometric scaling of exhaustive energy potential across taxa.

Body size alone is a strong predictor of metabolic rate across vertebrate species (Nagy 2005; Cloyed et al. 2021). Larger fish inherently have more muscle mass and access to larger energy reserves through both aerobic and anaerobic metabolism (Kieffer 2000) and, correspondingly, have a greater capacity for exhaustive exercise in laboratory trials (Ferguson et al. 1993;

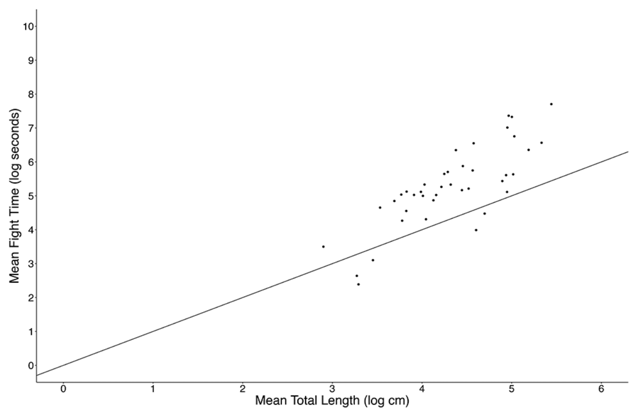

Figure 3. Mean and standard error of fight times on the log scale for all species by mean total length also on the log scale.

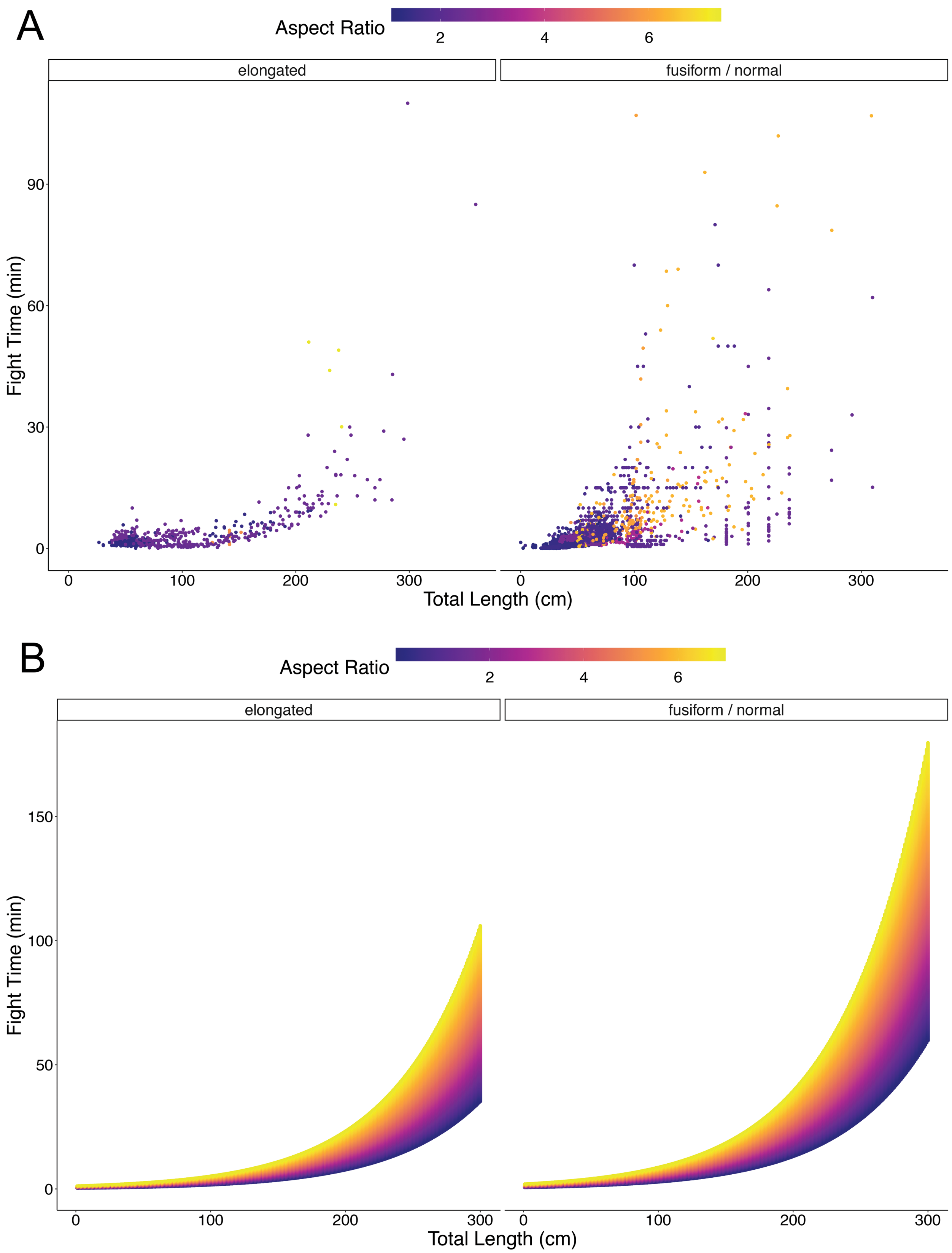

Figure 4. *A*, Raw observations of fight times recorded for 42 fish species with total length, aspect ratio, and body shape mapped. *B*, Model-predicted fight times at given total lengths for fish according to the full negative binomial mixed effects regression. Predictions are drawn across lengths and aspect ratios and for elongated and fusiform body shapes. Gear type is fixed to spinning gear, food type is fixed to piscivore, energy demand is fixed to sustained, and the migratory trait is fixed to positive. Random effects are turned off for the prediction.

Clarke and Johnston 1999). The scaling of anaerobic capacity with body size has been documented in many commonly tested laboratory species (brook trout [Kieffer et al. 1996; McDonald et al. 1998], kelp bass [*Paralabrax clathratus*; Somero and Childress 1990], rainbow trout [*Oncorhynchus mykiss*; Somero and Childress 1990; McDonald et al. 1998], and Atlantic salmon [*Salmo salar*; McDonald et al. 1998]), with some exceptions (largemouth bass [*Micropterus salmoides*; Kieffer et al. 1996] and Dover sole [*Solea solea*; Somero and Childress 1990]). The scaling of fight time with individual size was predicted according to laboratory and theoretical models explaining animal exercise but nevertheless represents a unique quantification of patterns of exhaustive exercise in wild, unconditioned animals and across a wide breadth of species.

The strong influence of body size on the fight time response potentially dominated other important variables. Body shape was marginally significant, suggesting a shorter expected time to exhaustion for elongated swimmers. We predicted that high aspect ratio, which maximizes the amount of thrust that can be generated (Blake 2004) by increasing the aerodynamic efficiency of the caudal fin (Nursall 1958), would allow a fish to fight harder against an angler while using less energy than fish with lower aspect ratio. This was the case according to the random effects model but not the phylogenetic model. Tunas, sharks (in this article mainly Carcharhinidae but also *Isurus oxyrinchus* and *Carcharias taurus*), and other cursorial piscivores (Gerking 1994) had a mean aspect ratio of 4.11, and these species had significantly longer fight times than ambush predators and particulate feeders whose mean aspect ratios were 1.79 and 1.75, respectively. Aspect ratio is also linked to fish migratory behavior, with most highly migratory fish having high aspect ratios to maximize their performance as steady body and caudal fin swimmers that often consume widely dispersed prey (Blake 2004). For fish in our data set, the mean aspect ratio (using unique values) for migratory fish was nearly double that of nonmigratory fish (3.89 and 2.05, respectively).

The Fry (1947) paradigm outlined the controlling factors that govern an animal's metabolic rate in relation to exhaustive exercise, including temperature. Water temperature is missing from our analysis and likely would have had some effect within studies. However, much of the variation in water temperature is likely collinear with species because of the nested nature of data collection. Furthermore, all of the temperate fish across studies were caught during the summer, predominantly centrally within their global range, making fish unlikely to be exposed to their thermal minima or maxima. Therefore, the variation driven by temperature is likely captured in our model random effects and correlation structures. Water temperature was not available for all of the studies in the meta-analysis, and imputing these values would likely further contribute to collinearity. The effects of water temperature on the resting metabolic rate of fish varies at the inter- and intraspecific levels (Killen et al. 2010; Ohlberger et al. 2012), with metabolic rate often scaling significantly with body mass, lifestyle, and swimming mode regardless of temperature (Killen et al. 2010). In other ectotherms, specifically various species of lizard, temperature and body size have been shown to affect locomotor capacity, with higher temperatures allowing for higher maximum speeds (Bennett 1987; Garland 1994). However, the effects of temperature vary across species and among individuals, and more research is needed in a variety of taxa to fully support the thermodynamic constraint hypothesis (Angilletta et al. 2009).

Our study addressed field aspects of exhaustive exercise, as opposed to a laboratory setting, and offers insight into different species across environmental contexts. The taxonomically diverse species presented here, while of importance to recreational fisheries, are not often tested in the laboratory, in part because of the challenges of maintaining large-bodied individuals, such as sharks, tarpon (*Megalops atlanticus*), arapaima (*Arapaima* spp.), marlins (Istiophoridae), and tunas (Scombridae), in a research setting. When time to fatigue was available in controlled critical velocity swim tunnel trials, comparisons between time to fatigue in swimming challenges and fight times for comparably sized fish were similar for brook trout (mean fight time: 22.2 ± 14.3 s; time to fatigue range: 18–90 s; Kieffer et al. 2011) and sockeye salmon (*Oncorhynchus nerka*; mean fight time: 2.53 ± 1.12 min; time to 50% of fish fatigued at constant 3.0 L/s flow velocity: 5 min; Brett 1967). Laboratory studies conduct manipulations to better resolve the mechanisms underlying physiological performance, whereas our data are observational from the field given ambient, unmanipulated fish and environmental conditions. Fish in swim tunnel experiments are often exposed to incremental increases in water velocity (Brett 1965; Nowell et al. 2015), allowing fish to gradually engage in anaerobic exercise, while hooked fish will immediately engage in burst swimming and may reach fatigue more rapidly, as seen in a swim trial of comparably sized Atlantic cod (*Gadus morhua*) that fatigued after 151 ± 1.2 min on average (Reidy et al. 1995), compared with our observed mean fight time of 1.58 ± 0.59 min.

Phylogeny is important to consider when comparing locomotor performance across taxa (Cloyed et al. 2021), and we produced two models that accounted for phylogeny differently. The random effects model had no structure to account for species relatedness and performed slightly differently from the phylogenetic generalized least squares regression analysis. The phylogenetic analysis excluded a few rare species, including arapaima (*Arapaima* cf. *arapaima)*, whose taxonomy is relatively new (Watson and Stewart 2020), and all sharks that were not included in the Fish Tree of Life. The advantage of the random effects model was the ability to model residual error with a negative binomial distribution, which was most appropriate given our data structure. However, the phylogenetic relationships violated the assumption of independence (Cloyed et al. 2021). There are credible reasons why each model may be considered better, so we presented both. Ultimately, the relationship between fish size and time to exhaustion was strong and significant regardless of the model. We considered that this relationship between fight time and fish size may be nonlinear (i.e., exponential), and predictions from the negative binomial model suggest some nonlinearity.

Limitations

We posit that fight times represent a robust and comparable metric for measuring field exercise capabilities of wild animals. Capturing a fish via recreational angling simulates a predator-prey interaction (Carpenter et al. 1994; Johnson and Carpenter 1994), and the angling process exercises fish to exhaustion (Brobbel et al. 1996; Kieffer et al. 2002; Currey et al. 2013). This process is physiologically comparable to more controlled laboratory analyses of exhaustive exercise, with angled fish exhibiting the same changes in blood physiology as those exercised in the lab (Wood 1991; Suski et al. 2007; Thompson et al. 2008; Kneebone et al. 2013). Like the body of literature for lab-based physiology studies, our data set is not a comprehensive representation of fish diversity. The fish species included in our analyses were commonly targeted in recreational fisheries and biased toward higher-trophic-level consumers. While the fish sampled ranged in size from 10.5 to 358.5 cm total length and had a variety of feeding strategies, from particulate feeders to mobile hunters, small, low-trophic-level fish were underrepresented in the study.

We showed that fight times predictably scale with individual and species-level metrics of fish. We acknowledge that there are some limitations to this approach and suggest that these offer insights into important further studies in movement ecology research and exercise physiology of wild animals. Research on artificially selected largemouth bass shows that vulnerability to capture via recreational angling during the breeding season is heritable and tied to resting metabolic rate, with more aggressive and attentive nest guarders having a higher resting metabolic rate and being more vulnerable to capture (Cooke et al. 2007). Sampling fish via recreational angling may bias samples toward individuals with a higher resting metabolic rate and thus a need to forage more regularly, which could reduce their metabolic scope. However, fish fighting on a line against an angler can use currents, shelter, and other strategies beyond simply maximal swimming, such that their level of exercise is not necessarily fully exhaustive. Fight times may not represent the fastest possible onset of exhaustion as swim tunnel trials can, but this has the advantage of being more representative of a true predator-prey encounter where fish use their environment to maximize escape probability. However, for small species such as fat snook, peacock bass, and brook trout, fight time probably underestimates exhaustive exercise capacity because the angler can pull harder than the fish and retrieve it before it is fully spent. Indeed, fight times can depend on angler skill, fishing method (especially the amount of line out when the fish is hooked), and fishing gear. Fly gear took significantly longer to exhaust fish than spinning gear. Other nonreported aspects of the gear, especially rod length and strength and line test, would probably affect fight time and should be considered to introduce some level of error into the estimates that we were not able to model. Generally, recreational angling research is conducted by experienced anglers using gear that is appropriate for the target species and not ultralight or ultraheavy gear that would prolong or truncate fight times, but there is variation among studies that could affect estimates. Further research should be conducted to investigate recreational fishing through the lens of exhaustive exercise, including how fish balance red and white muscle activation when hooked to maximize their capacity to escape.

Conclusions

Predation has a strong influence on animal phenotypes and physical fitness via natural selection as well as conditioning (Davison 1997) of individuals. Evading a predator, such as a recreational angler, is one of the most demanding events that an animal will experience in its life, and these activities require burst-speed bouts of energy and cannot be sustained for prolonged periods of time (Goolish 1991; Kieffer 2000). In this study, we aggregated data on field exhaustive exercise of fish from around the world to understand how functional traits of species and individuals contribute to swimming capabilities. Across species, we found that an individual fish's body size prolongs the duration of the fight with an angler with a linear response based on a negative binomial error distribution. Functional performance of swimming fish in response to extreme challenges therefore follows predictable patterns, which also have important implications for fisheries management given that larger fish develop greater anaerobic debt and may therefore be more prone to postrelease mortality (Wood et al. 1983). This is not surprising given how swimming power and speed scale with animal size but provides insight into the functional ecology of exhaustive exercise that has not been adequately resolved in laboratory trials or from observations of free-swimming fish using accelerometry devices.

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APPENDIX

Table A1: Species, sample size, and sources of data included in this analysis

Common name	Scientific name	Sample size (*n*)	Data source
Albacore tuna	*Thunnus alalunga*	4	Skomal 2007
Arapaima	*Arapaima arapaima*	17	R. J. Lennox, unpublished data
Arapaima	*A. arapaima*	27	Lennox et al. 2018
Arctic grayling	*Thymallus thymallus*	39	Lennox et al. 2016
Atlantic bonito	*Sarda sarda*	20	Skomal 2007
Atlantic cod	*Gadus morhua*	614	Capizzano et al. 2016
Atlantic salmon	*Salmo salar*	264	Lennox 2017*a*
Atlantic salmon	*S. salar*	264	Lennox et al. 2017*c*
Bigeye tuna	*Thunnus obesus*	1	Skomal 2007
Blackfin tuna	*Thunnus atlanticus*	1	Skomal 2007
Blue-finned mahseer	*Tor khudree*	37	Bower et al. 2016*b*
Blue shark	*Prionace glauca*	75	Skomal 2007
Bluefin tuna	*Thunnus thynnus*	109	Skomal 2007
Bonefish	*Albula glossodonta*	40	A. J. Danylchuk, unpublished data
Bonefish	*Albula vulpes*	86	Danylchuk et al. 2007
Bonefish	*A. vulpes*	23	Brownscombe et al. 2015
Brook trout	*Salvelinus fontinalis*	172	Kerr et al. 2017
Brook trout	*S. fontinalis*	146	Lizee et al. 2017
Bull shark	*Carcharhinus leucas*	3	Skomal 2007
Bull trout	*Salvelinus confluentus*	127	Gutowsky et al. 2011
Cusk	*Brosme brosme*	435	C. W. Capizzano, unpublished data
Dolphinfish	*Coryphaena hippurus*	3	Skomal 2007
False albacore	*Euthynnus alletteratus*	5	Skomal 2007
Fat snook	*Centropomus parallelus*	31	Lennox 2015
Gaint trevally	*Caranx ignobilis*	71	A. J. Danylchuk, unpublished data
Golden durado	*Salminus brasiliensis*	47	Gagne et al. 2017
Golden mahseer	*Tor putitorra*	41	S. D. Bower, unpublished data
Gray reef shark	*Carcharhinus amblyrhynchos*	4	Skomal 2007
Great barracuda	*Sphyraena barracuda*	62	O'Toole et al. 2010
Haddock	*Melanogrammus aeglefinus*	2,305	Capizzano et al. 2019
Largemouth bass	*Micropterus salmoides*	86	Brownscombe et al. 2014*a*
Lemon shark	*Negaprion brevirostris*	32	Danylchuk et al. 2014
Mako shark	*Isurus oxyrinchus*	7	Skomal 2007
Muskellunge	*Esox masquinongy*	69	Landsman et al. 2011
Peacock bass	*Cichla ocellaris*	55	Bower et al. 2016*a*
Sand tiger shark	*Carcharias taurus*	83	Kneebone et al. 2013
Sandbar shark	*Carcharhinus plumbeus*	1	Skomal 2007
Shortjaw bonefish	*Albula glossodonta*	57	Lennox et al. 2017*b*
Skipjack tuna	*Katsuwonus pelamis*	26	Skomal 2007
Sockeye salmon	*Oncorhynchus nerka*	130	M. Donaldson, unpublished data
Spinner shark	*Carcharhinus brevipinna*	5	Skomal 2007
Steelhead	*Oncorhynchus mykiss*	159	Twardek et al. 2018
Tarpon	*Megalops atlanticus*	28	L. P. Griffin, unpublished data
Wahoo	*Acanthocybium solandri*	7	Skomal 2007
White marlin	*Kajikia albida*	5	Skomal 2007
White sturgeon	*Acipenser transmontanus*	126	M. F. McLean, unpublished data
Yellowfin tuna	*Thunnus albacares*	65	Skomal 2007

Table A2: Equations used to convert fork length (FL) to total length (TL) when TL data were not available based on the best available literature at the time of publication

Species	Conversion equation	Source
Albacore tuna	TL = (FL + .081)/1.026	Used bluefin tuna conversion
Arctic grayling	TL = .0622 + .1.052(FL)	Reed and McCann 1971
Atlantic bonito	TL = (FL + .081)/1.026	Used bluefin tuna conversion
Bigeye tuna	TL = (FL + .081)/1.026	Used bluefin tuna conversion
Blackfin tuna	TL = (FL + .081)/1.026	Used bluefin tuna conversion
Blue shark	TL = (FL − 1.39)/.8313	Skomal and Natanson 2003
Bluefin tuna	TL = (FL + .081)/1.026	Perçin and Akyol 2009
Bonefish (*Albula glossodonta*)	TL = (FL + 1.3813)/.8619	Used conversion for *Albula vulpes*; Larkin 2011
Bull shark	TL = 1.21(FL) + 13.84	Neer et al. 2005
Dolphinfish	TL = 1.205(FL) − 2.648	Campbell 1984
False albacore	TL = (FL + .081)/1.026	Used bluefin tuna conversion
Giant trevally	TL = .182081(FL) + .421882	Smallwood et al. 2017
Gray reef shark	TL = 3.087 + 1.198(FL)	Used conversion for Caribbean reef shark *Carcharhinus perezi*; Tavares 2009
Mako shark	TL = (FL + 1.7101)/.9286	Kohler et al. 1996
Sand tiger shark	TL = (FL + .592)/.8471	Goldman et al. 2006
Sandbar shark	TL = (FL − 2.5675)/.8175	Kohler et al. 1996
Skipjack tuna	TL = (FL + .081)/1.026	Used bluefin tuna conversion
Sockeye salmon	TL = 1.0202(FL) + .3363	Used conversion for brown trout *Salmo trutta*; Arslan et al. 2004
Spinner shark	TL = 1.17(FL) + 3.05	Branstetter 1987
Steelhead	TL = 1.0202(FL) + .3363	Used conversion for brown trout *S. trutta*; Arslan et al. 2004
Tarpon	TL = (FL + 1.062607)/.896584	Ault et al. 2007
Wahoo	TL = 2.452 + 1.016(FL)	Oxenford et al. 2003
White marlin	TL = (FL + .720)/.760	Prager et al. 1995
White sturgeon	TL = 1.110(FL)	Beamesderfer 1993
Yellowfin tuna	TL = (FL + .081)/1.026	Used bluefin tuna conversion

Note. If conversions were not available for the specific species, a best approximation was made using a conversion available from a closely related species.

Literature Cited

Akaike H. 1974. A new look at statistical model identification. IEEE Trans Autom Control 19:716–723.

Albert J.S. and D.M. Johnson. 2012. Diversity and evolution of body size in fishes. Evol Biol 39:324–340.

Altringham J.D. and D.J. Ellerby. 1999. Fish swimming: patterns in muscle function. J Exp Biol 202:3397–3403.

Angilletta M., Jr., R.B. Huey, and M.R. Frazier. 2009. Thermodynamic effects on organismal performance: is hotter better? Physiol Biochem Zool 83:197–206.

Arslan M., A. Yildirim, and S. Bektas. 2004. Length-weight relationship of brown trout, *Salmo trutta* L., inhabiting Kan Stream, Coruh Basin, North-Eastern Turkey. Turk J Fish Aquatic Sci 4:45–48.

Ault J.S., R. Humston, M.F. Larkin, E. Perusquia, N.A. Farmer, J. Luo, and J.M. Posada. 2007. Population dynamics and resource ecology of Atlantic tarpon and bonefish. Pp. 217–258 in J.S. Ault, ed. Biology and management of the world tarpon and bonefish fisheries. CRC, Boca Raton, FL.

Bates D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48.

Beamesderfer R.C. 1993. A standard weight (W_s) equation for white sturgeon. Calif Fish Game 79:63–69.

Bennett A.F. 1987. Evolution of the control of body temperature: is warmer better? Pp. 421–431 in P. Dejours, L. Bolis, C.R. Taylor, and E.R. Weibel, eds. Comparative physiology: life in water and on land. Fidia Research Series 9. Liviana, Padova, Italy.

Blake R.W. 2004. Functional design and swimming performance. J Fish Biol 65:1193–1222.

Boettiger C., D.T. Lang, and P.C. Wainwright. 2012. rfishbase: exploring, manipulating and visualizing FishBase data from R. J Fish Biol 81:2030–2039.

Bower S.D., A.J. Danylchuk, J.W. Brownscombe, J.D. Thiem, and S.J. Cooke. 2016*a*. Evaluating effects of catch-and-release angling on peacock bass (*Cichla ocellaris*) in a Puerto Rican reservoir: a rapid assessment approach. Fish Res 175:95–102.

Bower S.D., A.J. Danylchuk, R. Raghavan, S.E. Clark-Danylchuk, A.C. Pinder, and S.J. Cooke. 2016*b*. Rapid assessment of the physiological impacts caused by catch-and-release angling on blue-finned mahseer (*Tor* sp.) of the Cauvery River, India. Fish Manag Ecol 23:208–217.

Branstetter S. 1987. Age and growth estimates for blacktip, *Carcharhinus limbatus*, and spinner, *C. brevipinna*, sharks from the northwestern Gulf of Mexico. Copeia 1987:964–974. https://doi.org/10.2307/1445560.

Brett J.R. 1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). J Fish Res Board Can 22:1491–1501. https://doi.org/10.1139/f65-128.

———. 1967. Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue time and temperature. J Fish Res Board Can 24:1731–1741.

———. 1972. The metabolic demand for oxygen in fish, particularly salmonids, and a comparison with other vertebrates. Respir Physiol 14:151–179. https://doi.org/10.1016/0034-5687(72)90025-4.

Brobbel M.A., M.P. Wilkie, K. Davidson, J.D. Kieffer, A.T. Bielak, and B.L. Tufts. 1996. Physiological effects of catch and release angling in Atlantic salmon (*Salmo salar*) at different stages of freshwater migration. Can J Fish Aquat Sci 53:2036–2043.

Bro-Jørgensen J. 2013. Evolution of sprint speed in African savannah herbivores in relation to predation. Evolution 67:3371–3376.

Brown J.H., J.F. Gillooly, A.P. Allen, V.M. Savage, and G.B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Brownscombe J.W., S.J. Cooke, D.A. Algera, K.C. Hanson, E.J. Eliason, N.J. Burnett, A.J. Danylchuk, S.G. Hinch, and A.P. Farrell. 2017. Ecology of exercise in wild fish: integrating concepts of individual physiological capacity, behavior, and fitness through diverse case studies. Integr Comp Biol 57:281–292.

Brownscombe J., L.P. Griffin, T. Gagne, C.R. Haak, S.J. Cooke, and A.J. Danylchuk. 2015. Physiological stress and reflex impairment of recreationally angled bonefish in Puerto Rico. Environ Biol Fishes 98:2287–2295.

Brownscombe J.W., K. Marchand, K. Tisshaw, V. Fewster, O. Groff, M. Pichette, M. Seed, L.F.G. Gutowsky, A.D.M. Wilson, and S.J. Cooke. 2014*a*. The influence of water temperature and accelerometer-determined fight intensity on physiological stress and reflex impairment of angled largemouth bass. Conserv Physiol 2:cou057.

Brownscombe J.W., L. Nowell, E. Samson, A.J. Danylchuk, and S.J. Cooke. 2014*b*. Fishing-related stressors inhibit refuge-seeking behavior in released subadult great barracuda. Trans Am Fish Soc 143:613–617.

Campbell P. 1984. Weight-total length and length-length relationships for four saltwater fishes. Texas Parks and Wildlife Department Management Data Series 62. Texas Parks and Wildlife Department Coastal Fisheries Branch, Austin, TX.

Capizzano C.W., J.W. Mandelman, W.S. Hoffman, M.J. Dean, D.R. Zemeckis, H.P. Benoît, J. Kneebone, et al. 2016. Estimating and mitigating the discard mortality of Atlantic cod (*Gadus morhua*) in the Gulf of Maine recreational rod-and-reel fishery. ICES J Mar Sci 73:2342–2355. https://doi.org/10.1093/icesjms/fsw058.

Capizzano C.W., D.R. Zemeckis, W.S. Hoffman, H.P. Benoît, E. Jones, M.J. Dean, N. Ribblett, J.A. Sulikowski, and J.W. Mandelman. 2019. Fishery-scale discard mortality rate estimate for haddock in the Gulf of Maine recreational fishery. North Am J Fish Manag 39:964–979.

Carpenter S.R., A. Muñoz-del-Rio, S. Newman, P.W. Rasmussen, and B.M. Johnson. 1994. Interactions of anglers and walleyes in Escanaba Lake, Wisconsin. Ecol Appl 4:822–832.

Chang J., D.L. Rabosky, S.A. Smith, and M.E. Alfaro. 2019. An R package and online resource for macroevolutionary studies using the ray-finned fish tree of life. Methods Ecol Evol 10:1118–1124.

Chapman D.D., K.A. Feldheim, Y.P. Papastamatiou, and R.E. Hueter. 2015. There and back again: a review of residency and return migrations in sharks, with implications for population structure and management. Annu Rev Mar Sci 7:547–570.

Childress J.J. and G.N. Somero. 1990. Metabolic scaling: a new perspective based on scaling of glycolytic enzyme activities. Am Zool 30:161–173. https://doi.org/10.1093/icb/30.1.161.

Clarke A. and N.M. Johnston. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. J Anim Ecol 68:893–905.

Cloyed C.S., J.M. Grady, V.M. Savage, J.C. Uyeda, and A.I. Dell. 2021. The allometry of locomotion. Ecology 102:e03369.

Cooke S.J, C.D. Suski, K.G. Ostrand, D.H. Wahl, and D.P. Philipp. 2007. Physiological and behavioral consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. Physiol Biochem Zool 80:480–490.

Cowx I.G. 2002. Recreational fishing: handbook of fish biology and fisheries. Fisheries 2:367–390.

Currey L.M., M.R. Heupel, C.A. Simpfendorfer, and T.D. Clark. 2013. Blood lactate loads of redthroat emperor *Lethrinus miniatus* associated with angling stress and exhaustive exercise. J Fish Biol 83:1401–1406.

Danylchuk S.E., A.J. Danylchuk, S.J. Cooke, T.L. Goldberg, J. Koppelman, and D.P. Philipp. 2007. Effects of recreational angling on the post-release behavior and predation of bonefish (*Albula vulpes*): the role of equilibrium status at the time of release. J Exp Mar Biol Ecol 346:127–133.

Danylchuk A.J., C.D. Suski, J.W. Mandelman, K.J. Murchie, C.R. Haak, A.M.L. Brooks, and S.J. Cooke. 2014. Hooking injury, physiological status and short-term mortality of juvenile lemon sharks (*Negaprion bevirostris*) following catch-and-release recreational angling. Conserv Physiol 2:cot036. https://doi.org/10.1093/conphys/cot036.

Davison W. 1997. The effects of exercise training on teleost fish, a review of recent literature. Comp Biochem Physiol A 117:67–75. https://doi.org/10.1016/S0300-9629(96)00284-8.

Felsenstein J. 1985. Phylogenies and the comparative method. Am Nat 125:1–15.

Ferguson R.A., J.D. Kieffer, and B.L. Tufts. 1993. The effects of body size on the acid-base and metabolite status in the white muscle of rainbow trout before and after exhaustive exercise. J Exp Biol 180:195–207.

Froese R. and D. Pauly. 2000. FishBase 2000: concepts, design and data sources. ICLARM, Los Baños, Philippines.

Fry F.E.J. 1947. Effect of the environment on animal activity. Univ Tor Stud Biol Ser 55:1–62.

Gagne T.O., K.L. Ovitz, L.P. Griffin, J.W. Brownscombe, S.J. Cooke, and A.J. Danylchuk. 2017. Evaluating the consequences of catch-and-release recreational angling on golden dorado (*Salminus brasiliensis*) in Salta, Argentina. Fish Res 186:625–633.

Garland T., Jr. 1994. Phylogenetic analyses of lizard endurance capacity in relation to body size and body temperature. Pp. 237–259 in L.J. Vitt and E.R. Pianka, eds. Lizard ecology: historical and experimental perspectives. Princeton University Press, Princeton, NJ.

Garland T., Jr., C.J. Downs, and A.R. Ives. 2022. Trade-offs (and constraints) in organismal biology. Physiol Biochem Zool 95:82–112.

Gerking S.D. 1994. Feeding ecology of fish. Academic Press, San Diego.

Goldman K.J., S. Branstetter, and J.A. Musick. 2006. A reexamination of the age and growth of sand tiger sharks, *Carcharias taurus*, in the western North Atlantic: the importance of ageing protocols and use of multiple back-calculation techniques. Dev Environ Biol Fishes 25:241–252. https://doi.org/10.1007/s10641-006-9128-y.

Goolish E.M. 1991. Aerobic and anaerobic scaling in fish. Biol Rev 66:33–56.

Gutowsky L.F.G., P.M. Harrison, S.J. Landsman, M. Power, and S.J. Cooke. 2011. Injury and immediate mortality associated with recreational troll capture of bull trout (*Salvelinus confluentus*) in a reservoir in the Kootenay-Rocky Mountain region of British Columbia. Fish Res 109:379–383.

Halsey L.G. 2016. Do animals exercise to keep fit? J Anim Ecol 85:614–620.

Hammer C. 1995. Fatigue and exercise tests with fish. Comp Biochem Physiol A 112:1–20. https://doi.org/10.1016/0300-9629(95)00060-K.

Johnson B.M. and S.R. Carpenter. 1994. Functional and numerical responses: a framework for fish-angler interactions? Ecol Appl 4:808–821. https://doi.org/10.2307/1942010.

Kerr S.M., T.D. Ward, R.J. Lennox, J.W. Brownscombe, J.M. Chapman, L.F.G. Gutowsky, J.M. Logan, et al. 2017. Influence of hook type and live bait on the hooking performance of inline spinners in the context of catch-and-release brook trout *Salvelinus fontinalis* fishing in lakes. Fish Res 182:642–647.

Kieffer J.D. 2000. Limits to exhaustive exercise in fish. Comp Biochem Physiol A 126:161–179.

Kieffer J.D., R.A. Ferguson, J.E. Tompa, and B.L. Tufts. 1996. Relationships between body size and anaerobic metabolism in brook trout and largemouth bass. Trans Am Fish Soc 125:760–767.

Kieffer J.D., R.S. Kassie, and S.G. Taylor. 2011. The effects of low-speed swimming following exhaustive exercise on metabolic recovery and swimming performance in brook trout (*Salvelinus fontinalis*). Physiol Biochem Zool 84:385–393.

Kieffer J.D., A.M. Rossiter, C.A. Kieffer, K. Davidson, and B.L. Tufts. 2002. Physiology and survival of Atlantic salmon following exhaustive exercise in hard and softer water: implications for the catch-and-release sport fishery. North Am J Fish Manag 22:132–144.

Killen S.S., D. Atkinson, and D.S. Glazier. 2010. The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. Ecol Lett 13:184–193.

Kleiber M. 1947. Body size and metabolic rate. Physiol Rev 27:511–541.

Kneebone J., J. Chisholm, D. Bernal, and G. Skomal. 2013. The physiological effects of capture stress, recovery, and post-release survivorship of juvenile sand tigers (*Carcharias taurus*) caught on rod and reel. Fish Res 147:103–114.

Kohler N.E., J.G. Casey, and P.A. Turner. 1996. Length-length and length-weight relationships for 13 shark species from the western North Atlantic. NOAA Technical Memorandum NMFS-NE-110. Northeast Fisheries Science Center, Woods Hole, MA.

Landsman S.J., H.J. Wachelka, C.D. Suski, and S.J. Cooke. 2011. Evaluation of the physiology, behaviour, and survival of adult muskellunge (*Esox masquinongy*) captured and released by specialized anglers. Fish Res 110:377–386.

Langerhans R.B. and D.N. Reznick. 2010. Ecology and evolution of swimming performance in fishes: predicting evolution with biomechanics. Pp. 200–235 in P. Domenici, ed. Fish locomotion: an eco-ethological perspective. CRC, Boca Raton, FL.

Larkin M.R. 2011. Assessment of South Florida's bonefish stock. PhD diss. University of Miami, Coral Gables, FL.

Lennox R.J., J.W. Brownscombe, S.J. Cooke, and A.J. Danylchuk. 2018. Post-release behaviour and survival of recreationally-angled arapaima (*Arapaima arapaima*) assessed with accelerometer biologgers. Fish Res 2017:197–203.

Lennox R.J., J.W. Brownscombe, S.J. Cooke, A.J. Danylchuk, P.S. Moro, E.A. Sanches, and D. Garrone-Neto. 2015. Evaluation of catch-and-release angling practices for the fat snook *Centropomus parallelus* in a Brazillian estuary. Ocean Coast Manag 113:1–7.

Lennox R.J., J.M. Chapman, W.M. Twardek, F. Broell, K. Bøe, F.G. Whoriskey, I.A. Fleming, M. Robertson, and S.J. Cooke. 2019. Biologging in combination with biotelemetry reveals behavior of Atlantic salmon following exposure to capture and handling stressors. Can J Fish Aquat Sci 76:2176–2183.

Lennox R.J., S.J. Cooke, C.R. Davis, P. Gargan, L.A. Hawkins, T.B. Havn, and I. Uglem. 2017*a*. Pan-Holarctic assessment of post-release mortality of angled Atlantic salmon *Salmo salar*. Biol Conserv 209:150–158.

Lennox R.J., A. Filous, S.C. Danylchuk, S.J. Cooke, J.W. Brownscombe, A.M. Friedlander, and A.J. Danylchuk. 2017*b*. Factors influencing post-release predation for a catch-and-release tropical flats fishery with a high predator burden. North Am J Fish Manag 37:1045–1053.

Lennox R.J., T.B. Havn, E.B. Thorstad, E. Liberg, S.J. Cooke, and I. Uglem. 2017*c*. Behaviour and survival of wild Atlantic salmon (*Salmo salar*) captured and released while surveillance angling for escaped farmed salmon. Aquac Environ Interact 9:311–319.

Lennox R.J., I. Mayer, T.B. Havn, M.R. Johansen, K. Whoriskey, S.J. Cooke, E.B. Thorstad, and I. Uglem. 2016. Consequences of recreational angling and air exposure on the physiological status and reflex impairment of European grayling (*Thymallus thymallus*). Boreal Environ Res 21:461–470.

Lizee T.W., R.J. Lennox, T.D. Ward, J.W. Brownscombe, J.M. Chapman, A.J. Danylchuk, L.B. Nowell, and S.J. Cooke. 2017. Influence of landing net mesh type on handling time and tissue damage of angled brook trout. North Am J Fish Manag 38:76–83.

Martins E.P. and T.F. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. Am Nat 149:646–667.

McDonald D.G., W.J. McFarlane, and C.L. Milligan. 1998. Anaerobic capacity and swim performance of juvenile salmonids. Can J Fish Aquat Sci 55:1198–1207.

Nagy K.A. 2005. Field metabolic rate and body size. J Exp Biol 208:1621–1625. https://doi.org/10.1242/jeb.01553.

Nathan R., W.M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P.E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci USA 105:19052–19059.

Neer J.A., B.A. Thompson, and J.K. Carlson. 2005. Age and growth of *Carcharhinus leucas* in the northern Gulf of Mexico: incorporating variability in size at birth. J Fish Biol 67:370–383. https://doi.org/10.1111/j.0022-1112.2005.00743.x.

Nowell L.B., J.W. Brownscombe, L.F.G. Gutowsky, K.J. Murchie, C.D. Suski, A.J. Danylchuk, A. Shulz, and S.J. Cooke. 2015. Swimming energetics and thermal ecology of adult bonefish (*Albula vulpes*): a combined laboratory and field study in Eleuthera, The Bahamas. Environ Biol Fishes 98:2133–2146

Nursall J.R. 1958. The caudal fin as a hydrofoil. Evolution 12:116–120.

Ohlberger J., T. Mehner, G. Staaks, and F. Hölker. 2012. Intraspecific temperature dependence of the scaling of metabolic rate with body mass in fishers and its ecological implications. Oikos 121:245–251.

Ohlberger J., G. Staaks, P.L. van Dijk, and F. Hölker. 2005. Modelling energetic costs of fish swimming. J Exp Zool A 303:657–664.

O'Toole A.C., A.J. Danylchuk, C.D. Suski, and S.J. Cooke. 2010. Consequences of catch-and-release angling on the physiological status, injury, and immediate mortality of great barracuda (*Sphyraena barracuda*) in the Bahamas. ICES J Mar Sci 67:1667–1675.

Oxenford H.A., P.A. Murray, and B.E. Luckhurst. 2003. The biology of wahoo (*Acanthocybium solandri*) in the western central Atlantic. Gulf Caribb Res 15:33–49. https://doi.org/10.18785/gcr.1501.06.

Palstra A.P and J.V. Planas. 2011. Fish under exercise. Fish Physiol Biochem 37:259–272.

Paradis E. and K. Schliep. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35:526–528.

Perçin F. and O. Akyol. 2009. Length-weight and length-length relationships of the bluefin tuna, *Thunnus thynnus* L., in the Turkish part of the eastern Mediterranean Sea. J Appl Ichthyol 25:782–784. https://doi.org/10.1111/j.1439-0426.2009.01288.x.

Pinheiro J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2020. nlme: linear and nonlinear mixed effects models. R package version 3.1–149. https://CRAN.R-project.org/package=nlme.

Post J.R. and E.A. Parkinson. 2001. Energy allocation strategy in young fish: allometry and survival. Ecology 82:1040–1051.

Prager M.H., E.D. Prince, and D.W. Lee. 1995. Empirical length and weight conversion equations for blue marlin, white marlin, and sailfish from the North Atlantic Ocean. Bull Mar Sci 56:201–210.

R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/.

Reed R.J. and J.A. McCann. 1971. Total length-weight relationships and condition factors for the Arctic grayling, *Thymallus arcticus* (Pallas), in Alaska. Trans Am Fish Soc 100:358–359. https://doi.org/10.1577/1548-8659(1971)100<358:TLRACF>2.0.CO;2.

Reidy S.P., J.A. Nelson, Y. Tang, and S.R. Keer. 1995. Post-exercise metabolic rate in Atlantic cod and its dependence upon the method of exhaustion. J Fish Biol 47:377–386.

Schielzeth H., N.J. Dingemanse, S. Nakagawa, D.F. Westneat, H. Allegue, C. Teplitsky, D. Réale, N.A. Dochtermann, L.Z. Garamszegi, and Y.G. Araya-Ajoy. 2020. Robustness of linear mixed-effects models to violations of distributional assumptions. Methods Ecol Evol 11:1141–1152.

Seymour R.S., A.F. Bennett, and D.F. Bradford. 1985. Blood gas tensions and acid-base regulation in the salt-water crocodile, *Crocodylus porosus*, at rest and after exhaustive exercise. J Exp Biol 118:143–159.

Skomal G.B. 2007. Evaluating the physiological and physical consequences of capture on post-release survivorship in large pelagic fishes. Fish Manag Ecol 14:81–89.

Skomal G.B. and L.J. Natanson. 2003. Age and growth of the blue sharks (*Prionace glauca*) in the North Atlantic Ocean. Fish Bull 101:627–639.

Smallwood C.B., A. Tate, and K.L. Ryan. 2017. Weight-length summaries for Western Australian fish species derived from surveys of recreational fishers at boat ramps. Fisheries Research Report 278. Department of Primary Industries and Regional Development, Western Australia, Perth.

Somero G.N. and J.J. Childress. 1990. Scaling of ATP-supplying enzymes, myofibrillar proteins ad buffering capacity in fish muscle: relationship to locomotory habit. J Exp Biol 149:319–333.

Suski C.D., S.J. Cooke, A.J. Danylchuk, C.M. O'Connor, M. Gravel, T. Redpath, K.C. Hanson, et al. 2007. Physiological disturbance and recovery dynamics of bonefish (*Albula vulpes*), a tropical marine fish, in response to variable exercise and exposure to air. Comp Biochem Physiol A 148:664–673.

Tavares R. 2009. Fishery biology of the Caribbean reef sharks, *Carcharhinus perezi* (Poey, 1876), in a Caribbean insular platform: Los Roques Archipelago National Park, Venezuela. Pan-Am J Aquat Sci 4:500–512.

Thompson L.A., S.J. Cooke, M.R. Donaldson, K.C. Hanson, A. Gingerich, T. Klefoth, and R. Arlinghaus. 2008. Physiology, behavior, and survival of angled and air-exposed largemouth bass. J Fish Manag 28:1059–1068.

Twardek W.M., T.O. Gagne, L.K. Elmer, S.J. Cooke, M.C. Beere, and A.J. Danylchuk. 2018. Consequences of catch-and-release angling on the physiology, behaviour and survival of wild steelhead *Oncorhynchus mykiss* in the Bulkley River, British Columbia. Fish Res 206:235–246.

Watson L.C. and D.J. Stewart. 2020. Growth and mortality of the giant arapaima in Guyana: implications for recovery of an over-exploited population. Fish Res 231:105692.

Webb P.W. 1971*a*. The swimming energetics of trout. I. Thrust and power output at cruising speeds. J Exp Biol 55:489–520.

———. 1971*b*. The swimming energetics of trout. II. Oxygen consumption and swimming efficiency. J Exp Biol 55:521–540.

West G.B., J.H. Brown, and B.J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. Science 276:122–126.

White C.R. and M.R. Kearney. 2014. Metabolic scaling in animals: methods, empirical results, and theoretical explanations. Compr Physiol 4:231–256.

White C.R. and R.S. Seymour. 2005. Allometric scaling of mammalian metabolism. J Exp Biol 208:1611–1619.

Wood C.M. 1991. Acid-base and ion balance, metabolism, and their interactions, after exhaustive exercise in fish. J Exp Biol 160:285–308.

Wood C.M., J.D. Turner, and M.S. Graham. 1983. Why do fish die after severe exercise? J Fish Biol 22:189–201.

Wright S., J.D. Metcalfe, S. Hetherington, and R. Wilson. 2014. Estimating activity-specific energy expenditure in a teleost fish, using accelerometer loggers. Mar Ecol Prog Ser 496:19–32.