Title
Causes and consequences of body size-specific vulnerability to warming in fishes.

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Publication Date
2022

UNIVERSITY OF CALIFORNIA

Santa Barbara

Causes and consequences of body size-specific vulnerability to warming in fishes.

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Ecology, Evolution, and Marine Biology

by

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Krista Kraskura

ACKNOWLEDGEMENTS

First and foremost, thank you to my amazing advisor, Erika Eliason. Erika, you have taught me so very much. Thank you, Erika, for mentoring me on how to become a better lab member, researcher, teacher, mentor, communicator, and troubleshooter. Thank you for your dedication to diversity, inclusion, equity, and justice. You culture a safe, welcoming, and caring work environment and I deeply appreciate your advocacy of me. Thank you for the hundreds of hours that you have invested in providing feedback to my writing and preparing presentations. A bit more: Thank you for emphasizing the importance of collaborative work, to help others, and outreach. Thank you for the daily reminders that our work is important and should be fun! Thank you for helping me understand what a work-life balance is and for being such a positive person. I do not know how you do it all and I will always look up to you and your efforts with the deepest respect. Erika, you have inspired me through your leadership as you continue to lead by example.

Thank you to my graduate committee members. Chris Jerde, thank you for bringing in statistics and math to my graduate experience. I could not believe it was really possible, and I realize there is so much more to learn. Thank you for placing the emphasis on the "so what" in all our work, and for helping me to think about biologically meaningful inference. Thank you, Gretchen Hofmann, for making me think about the environment in which all the lovely creatures we study live. Thank you for helping me think outside my specific system of study, about the ecology and impact of ecological physiology in broader, but still local, scales. Thank you, Erika, Chris, and Gretchen, for the encouragement and support.

Thank you, Eliason Lab. Graduate student crew: Emily Hardison, Terra Dressler, Jacey Van Wert, Maddie Heard, Jasmine Childress, Jessica Madden, Bashir Ali, James Lichtenstein, also Noa Mayer. You all are an inspiring group of empowering, caring, and kind people that I am proud to call friends. You all have brought to the forefront the importance of work-life balance. You all are involved, engaged team players, and are artists, singers, dancers, frisbee players, weightlifters, runners, doggie parents, and much more. Let's not leave it out, you all are incredible young scientists on top of that with novel and impactful research ideas. Thank you, postdocs Gail Schwieterman, Kim Birnie-Gauvin, and Alex Little! Thank you for your welcoming openness to talk about your experiences, and the advice that stems from climbing up your career ladders.

Thank you to my fellow graduates and EEMB postdocs, you are rockstars. Thank you, Michelle Lee, Dana Cook, Sam Csik, Amelia Ritger, Joanna Tang, Bart DiFiore, Lisa Mesrop, Jason Johns, Terence Leach, Erin Winslow, Caroline Owens, Kate Culhane, Ferdi Pfab, and Grace DiRenzo for your friendship, support, and welcoming memorable times. I look up to you as you follow your passions. Each one of you has opened my mind to new ways of thinking, and I will continue to learn from you as you achieve great things. Thank you for creating EEMB a welcoming space and your advocacy. Thank you also graduate advisors of EEMB, Azure Stewart and Brittney Dinelli, and thank you to the International Student Office at UCSB.

Thanks to all those with whom I had a chance to go fishing. Special thanks to Jenny Dugan and her lab. You not only let me join in to help as a straggler on your survey trips, but also educated me about the beach zone ecosystem and kelp! Special thanks to Jessica Madden and Kyle Emery, you came out to help seine for barred surfperch every other morning until we collected enough fish for the thesis experiment, and you brought your seine net! I cannot thank you enough. Thank you, Justin and thank you to the SONGS survey group – I never knew I would get to seine in a salt marsh and study little gobies later! Altogether, these fishing trips with friends are forever memorable, even when we packed up empty coolers.

I am grateful for all my experiences being a mentor and a teacher. Undergraduate students Claire Anderson, Lucy Johnson, Yvette Gaytan, and Thomas Lenihan, thank you for your help and independence when tackling lab, field, data collection, analysis, writing, and computer tasks! I am grateful that I had the opportunity to work with such a large group of capable undergraduate students. You were ready to come on board to help with fishing, animal husbandry, a fishy day in the lab, or a building day in the lab. Thank you also, Yasmine Soliman, Vincent Han Lee, Bella Giglio, Cam Blair, Andrea Chandler, Bhavan Dhillon, Tina Nguyen, Maggie Slein, Haley Glasmann, Mason Tittle, Alicia Magliato, and Alex Vita. It has been a pleasure to work and learn with all of you along the way!

Thank you to our collaborating researchers introduced by Erika, Kara Anlauf-Dunn and David Patterson. Working with you outside of California deeply enriched my graduate experience. Thank you, Sam Csik, Bart DiFiore, Joe Curtis for the great times chasing a lobster around our tanks and teaching me how to hold it right. Thank you, James Lichtenstein, and Thomas Lenihan for lightening up my curiosity about ants.

Thank you to all my gym friends and communities -– CrossFit Santa Barbara and Push511 in Baltimore. There have been too many laughs, struggles, failures, and successes to count, all experienced during our daily grind at the gym. Your friendship has made me a better person, and a happier, healthier, and more focused graduate student.

I want to express a heartfelt gratitude to my family, mana ģimene, mamma Aija, brālis Mārtiņš, māsiņa Maija ar maziem Alenīti un Aleksīti (mom, brother, sister, and nephews). And to my grandparents, omamma un opaps, Velta un Aldis, thank you for being with me, for believing I could do it, and for seeding and fostering my curiosity about how life works. Paldies.

And a true and heartfelt thank you to my husband, Bradley Anderson. Thank you also to the Anderson family for your genuine support. Thank you, Bradley, for cooking zoom dates and zoom workouts, for pictures, for visits, for laughs, for cries, for the silly times and for the serious times. Words on paper will not do us justice. You have provided me with a new way to look at life. I love you.

Thank you, Everyone, for being you.

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Anlauf-Dunn, K., Kraskura, K., Eliason, E. J. (2022) Intraspecific variability in thermal tolerance: Linking physiological performance and climate adaptation. Conservation Physiology, Volume 10, Issue 1, coac029, https://doi.org/10.1093/conphys/coac029

Hardison E.A., Kraskura, K., Van Wert, J., Nguyen, T.#, and Eliason, E.J. (2021) Diet mediates thermal performance traits: implications for marine ectotherms. Journal of Experimental Biology. Volume 224, Issue 21, https://doi.org/10.1242/jeb.242846

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Oufiero, C. E., Kraskura, K., Bennington, R.#, and Nelson, J. A. (2020) Individual repeatability of locomotor kinematics and swimming performance in a gymnotiform swimmer. Physiological and Biochemical Zoology. Volume 94, Number 1. https://doi.org/10.1086/712058.

Little, A., Hardison, E., Kraskura, K., Dressler, T., Prystay, T., Hendriks, B., Pruitt N. J., Farrell, A. P., Cooke, S. J., Patterson, D. A., Hinch, S. G. and Eliason, E. J. (2020) Reduced metabolic capacity of the heart and suppressed sex hormone levels are associated with female-biased mortality during thermal stress in Pacific salmon. Journal of Experimental Biology 223: jeb214841. DOI: 10.1242/jeb.214841

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Little, A., Dressler, T., Kraskura, K., Hardison, E., Hendricks, B., Prystay, T., Farrell, A. P., Cooke, S. J., Patterson, D. A., Hinch, S. G. and Eliason, E. J. (2020) Maxed out: Optimizing accuracy, precision and power for field measures of maximum metabolic rate in fishes. Physiological and Biochemical Zoology 93:3, 243-254. DOI: https://doi.org/10.1086/708673

Jerde, C. L., Kraskura, K., Eliason, E. J., Csik, S., Stier, A. C., Taper, M. L. (2019) Strong evidence for an intraspecific metabolic scaling coefficient near 0.89 in fish. Frontiers in Physiology 10:1166. DOI: 10.3389/fphys.2019.01166

Nelson, J. A., Kraskura, K. and Lipkey, G. K. (2019) Repeatability of hypoxia tolerance of individual juvenile striped bass *Morone saxatilis* and effects of social status. Physiological and Biochemical Zoology 92(4):396-407. https://doi.org/10.1086/704010

Kraskura, K. and Nelson, J. A. (2018) Hypoxia and sprint swimming performance of juvenile striped bass, *Morone saxatilis.* Physiological and Biochemical Zoology 91(1):682–690. https://doi.org/10.1086/694933

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Kraskura, K., Jerde, C., Eliason, E., 2021. Data from: Strong evidence for an intraspecific metabolic scaling coefficient near 0.89 in fish. Dryad. https://doi.org/10.25349/D9SP6V

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2014 Summer Intern. Institute of Marine Environmental Technology (IMET), Baltimore, MD. Crustacean Endocrinology Lab. Supervisor: Dr. Chung. J. Sook. *Monitored growth and mortality of blue crab larvae; exposed larvae to an environmental toxin; performed RNA extractions and gene expression analyses.*

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PRESENTATIONS

Kraskura, K., Hardison E., Eliason, E.J. Temperature influences intra-specific scaling of metabolic and heart performance in an indicator beach zone species, barred surfperch. 14th International Congress on the Biology of Fish (ICBF) Montpellier, France. June 2022 (delivered virtually).

Kraskura, K., Jerde C.L., Eliason, E.J. Variation in metabolic scaling relationships of diverse fish across temperatures. Canadian Society of Zoology. (CSZ) Annual (Virtual) Meeting. May 2021.

Kraskura, K., Jerde C.L., Eliason, E.J. Active and resting metabolic rate scaling relationships in fishes across ecologies, salinity, and body shapes. Society of Integrative and Comparative Biology (SICB) Annual (Virtual) Meeting. January 2021.

Kraskura, K., Patterson, D.A., Eliason, J.E. Swimming performance in adult Pacific salmon - presentation of metadata analysis. Big Bar Rockslide Science Workshop at Pacific Salmon Commission (PSC), Vancouver, Canada. March 2020.

Kraskura, K., Little, A.G., Dressler, T., Hardison, E., Prystay, T.S., Patterson, D.A., Hinch, S.G., Farrell, A.P., Cooke, S.J. and Eliason, E.J. Sex -specific differences in swimming performance, aerobic scope, and post-exercise oxygen consumption during temperature and handling stress in coho salmon (*Oncorhynchus kisutch).* International Congress on the Biology of Fish (ICBF), Calgary, Canada. May 2018.

Kraskura, K. and J.A. Nelson. Fitness components of individual fish that experience hypoxic dead zones under normoxia and hypoxia. Society of Integrative and Comparative Biology (SICB) Annual Meeting, San Francisco, California. January 2018.

Kraskura, K. and J.A. Nelson. Sprint, fast start and prey capture performance of juvenile striped bass under levels of hypoxia encountered in nature. Society of Integrative and Comparative Biology (SICB) Annual Meeting, New Orleans, Louisiana. January 2017.

Kraskura, K. Hypoxia diminishes sprint swimming performance in juvenile striped bass. 12th International Congress on the Biology of Fish (ICBF), San Marcos, Texas. June 2016.

Poster presentations: # undergraduate student, * Presenter

Gaytan, Y. *#, Kraskura, K., Johnson, L. #, Eliason, E.J. The shape and size of red blood cells in local fish across body size: does it relate with performance under warming? Undergraduate Symposium, Ecology, Evolution and Marine Biology Dpt. UCSB. March 2022

Kraskura, K.*, Jerde C.L., Eliason, E.J. Variation in metabolic scaling relationships of diverse fish across temperatures. Society of Experimental Biology (SEB) Annual (Virtual) Meeting. June/July 2021.

Kraskura, K.*, J. A. Nelson, C. E. Oufiero, and K. Ricci #. Allometry and repeatability of gymnotiform swimming performance in black ghost knifefish (*Apteronotus albifrons*). Society of Integrative and Comparative Biology (SICB) Annual Meeting Portland, Oregon. Poster. January 2016.

Kraskura, K.*, M. H. Schwarz, S. Urick, M. L. Jahncke, and Z. A. Horodysky. Effects of feeding rate and feeding frequency on growth of juvenile tilapia (*Oreochromis niloticus/O. aureus*). Ocean Sciences Meeting Honolulu, Hawaii. Poster. February 2014.

ABSTRACT

Causes and consequences of body size-specific vulnerability to warming in fishes.

by

Krista Kraskura

Temperature and body size are two fundamental factors shaping physiological and ecological processes across all levels of biological organization. Understanding the relationship between these two factors is therefore essential to our ability to understand how species are responding to climate change, especially as one response of ectotherms to warming is a decline in body size. Declining body size in fishes can consequently lead to declining economic and recreational fisheries value, declining population productivity, declining food security, and altered size-structure function of communities. My thesis explored the physiological mechanisms and the ecological consequences of body size and life-stage specific vulnerability to warming. First, I used a meta-analysis approach to determine species- and group-specific vulnerability to warming in fishes. I evaluated how aerobic metabolism scales with body mass in fishes across temperature and how these changes in scaling may differ with species ecology and morphology. Further, to better understand the mechanisms behind temperature-modulated scaling of aerobic metabolism, I tested how metabolism and maximum heart rates change with acute temperature change and body size in a model species, barred surfperch (*Amphistichus argenteus*). I then reviewed aerobic swim performance in adult salmon to determine the potential ecological consequences of shifting body sizes. By combining work both across and within species, and examining ecologically relevant physiological performances and contexts, my thesis demonstrates that relationships between body size and performance can provide a mechanistic platform to identify climate change vulnerability in fishes.

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CHAPTER 1: INTRODUCTION

Temperature and size are two fundamental factors that intricately shape a vast array of physiological and ecological processes across all levels of biological organization and spatial and temporal scales (Atkinson, 1994; Brown et al., 2004; Fry, 1971; Gillooly et al., 2001; Schmidt-Nielsen, 1984; Sunday et al., 2011). However, temperatures are increasing at unprecedented rates, with a predicted sea surface temperature increase of 1.5ºC over the next few decades (Intergovernmental Panel on Climate Change, 2022), which is particularly concerning for ectotherms that cannot regulate their body temperature (Morley et al., 2019; Pinsky et al., 2019; Sunday et al., 2012). One response to warming is a decline in body size, observed across and within species and described as a *universal* response to climate change (Daufresne et al., 2009; Gardner et al., 2011). Therefore, larger and mature animals may be more vulnerable to climate change and anthropogenic stressors than smaller ones (Audzijonyte et al., 2020; Carey and Sigwart, 2014; Dahlke et al., 2020; Forster et al., 2012; Olden et al., 2007; Rubalcaba and Olalla-Tárraga, 2020; Urbina and Glover, 2013). Fishes are no exception to this trend (Audzijonyte et al., 2020, 2016, 2013; Dulvy and Reynolds, 2002; Lindmark et al., 2022, 2018; Rubalcaba et al., 2020). Declining body size in fishes comes along with concerning ecological consequences, including but not limited to changing size structure of populations and communities (Lindmark et al., 2018), changing predator-prey and trophic interactions (Audzijonyte et al., 2013), and growth rates (Lindmark et al., 2022), fecundity (Barneche et al., 2018). Furthermore, fisheries provide food security, support economies, and bring important recreational resources supporting human well-being (Intergovernmental Panel on Climate Change, 2022). Given this collective importance and being driven by understanding the function of biological processes, I asked: *What [mechanistically] would make larger fish more vulnerable under climate change than smaller fish? How would the size-related vulnerability differ at inter-specific compared to intra-specific levels? And lastly, what can be the ecological consequences of declining size?*

1.1. BODY SIZE AND TEMPERATURE IN ECOLOGICAL PHYSIOLOGY

Temperature and body size intersect in intricate ways that have led to the establishment of several *common* patterns describing biological processes (Atkinson et al., 2006; Atkinson, 1994; Brown et al., 2004; Gillooly et al., 2001). The biochemical rates and, thus, physiological processes within an individual animal depend on the ectotherm's intrinsic temperature (Schulte, 2015). And growing in size requires physiological and morphological features that allow the body to function as one integrated system (e.g., West, 1999). Allometric metabolic scaling is a *common* relationship that describes that larger organisms have higher absolute metabolic rates (MR) and thus energy demands but lower metabolic rates per unit of their body mass (BM). It is classically described as $\mathrm{MR} = a*\mathrm{BM}^b$ ($ln\mathrm{MR} = ln(a) + b*\mathrm{BM}$ in its linear form; (Kleiber, 1932), Figure 1), where '*a'* is a normalization constant, log-intercept; '*b*' is scaling exponent, slope. Allometric metabolic scaling is a shared phenomenon across life, e.g., unicellular, multicellular, modular organisms, eusocial animals, and even whole ecosystems (Brown et al., 2004; Kleiber, 1932; Perl and Niven, 2018; West et al., 2002).

Another *common* suite of patterns is the non-linear relationships between the temperature and biological rates, which are described by thermal performance curves (TPCs) (Schulte, 2015). Resting metabolic rates (RMR) in ectotherms – at a calm, non-feeding, non-reproductively active state – follow the tight control of temperature and typically increase exponentially until the maximum thermal limit is reached (Schulte, 2015). Allometric metabolic scaling and exponential increase of metabolism (RMR) are central relationships in a foundational framework, Metabolic Theory of Ecology, MTE (Brown et al., 2004), which further links individual physiology to predict ecosystem level processes, such as population dynamics, survival rates, reproductive rates (Brown et al., 2004; Enquist et al., 2003). However, MTE assumes animals are under "*normal operating temperatures*" or within optimal ranges for the given population and species (Brown et al., 2004). Under temperatures beyond the optimal for ectotherms, their vital performances (e.g., growth, locomotion, feeding capacity, reproduction) will decline (Eliason et al., 2011; Jutfelt et al., 2021; Pörtner and Farrell, 2008; Sinclair et al., 2016). Therefore, in the context of climate change, the metabolic scaling and temperature sensitivity of metabolic rates may change, consequently changing ecological and ecosystem functions.

In the wild, animals are rarely resting. Instead, fish may engage in various activities – hovering, bursting, migrating, foraging, chasing prey, digesting, competing for mates, mating, defending territories, escaping predation, and even playing – during which the metabolic rates will change dynamically to match the immediate needs (Hall and Clark, 2016; Steell et al., 2019; Wilson et al., 2013). Metabolic rates are whole organism level performances representing a sum of all biochemical reactions within the body at the time (Nelson, 2016) and intrinsically encompass any compensatory mechanisms to maintain optimal performance (reviewed by Somero, 2004). Since activity is a different physiological state, the TPC of active or maximum metabolic rates (MMR) deviates from the exponential pattern (Schulte, 2015). MMR increases with temperature and then may plateau or decline before reaching the absolute thermal limit. Therefore, TPCs are specific to a given performance trait (Kellermann et al., 2019; Sinclair et al., 2016). Furthermore, TPCs can change with environmental contexts (Claireaux and Lagardère, 1999), timescales of thermal exposures (Eliason et al., 2011; Schulte, 2015), and importantly also, life stages, thus body size (e.g., Pörtner and Farrell, 2008; Twiname et al., 2020; Wheeler et al., 2021). Recognizing this context specificity of TPC, especially with life-stage specific, I predict that scaling relationships will change with temperatures, be different for different metabolic rate performance metrics, and vary across and within species.

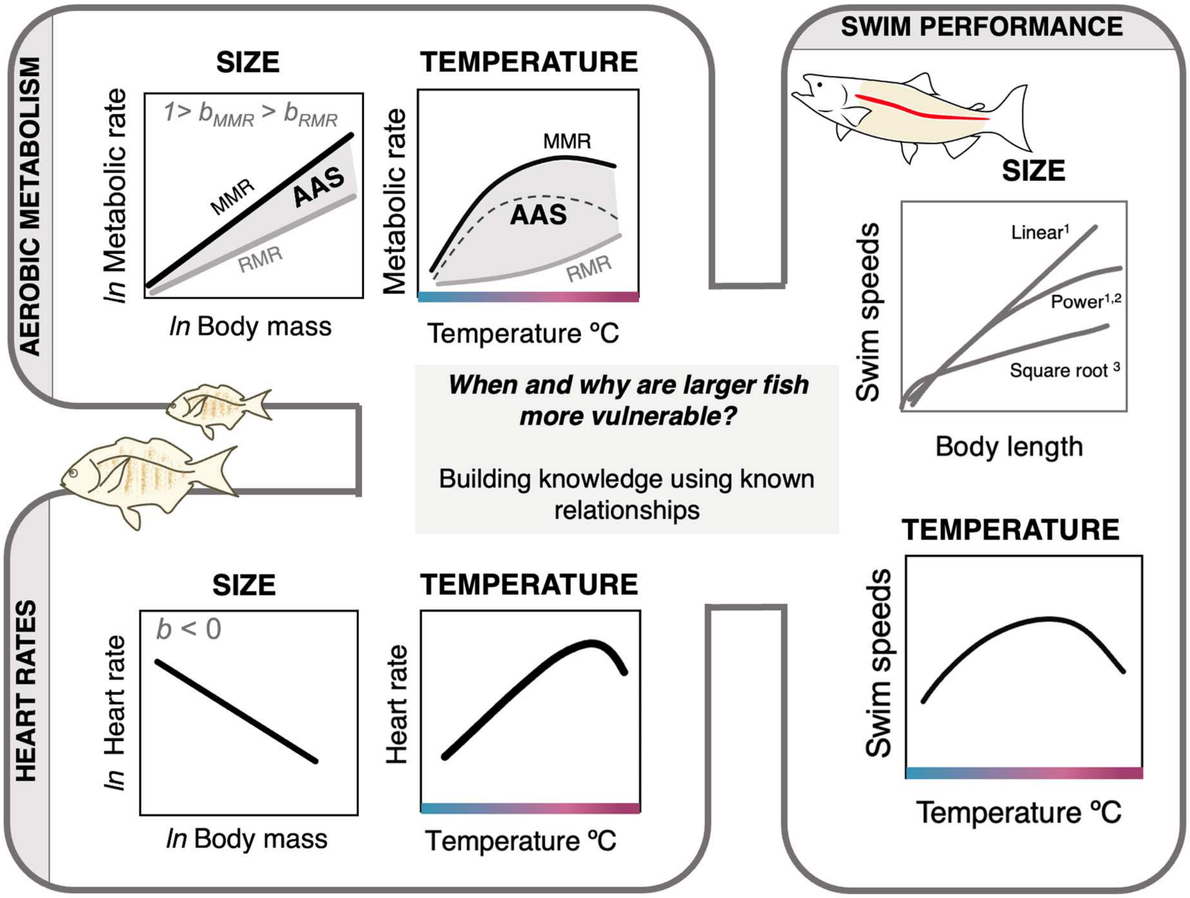

Figure 1. The central relationships between body size, temperature, and physiological performances essential in fish biology.
Recognized scaling relationships of aerobic metabolic performances (top left) that are directly underlined by cardiac performance and specifically relates with thermal response of maximum heart rates (bottom left). Aerobic capacity further influences vital performances, including swimming in fishes (right). Therefore, body size and thermal performance of presented performances are all ecologically relevant, and mechanistically linked. I used the presented relationships to design and

conceptualize my thesis work with an aim to study physiological mechanisms that could underscore size-specific vulnerability in fishes. It must be noted - each of these relationships contain appreciated amount of inter-and intra-specific variation, which also is addressed in my thesis. MMR = maximum metabolic rates, RMR = Resting metabolic rates, AAS = absolute aerobic scope (AAS = MMR – RMR). Swim speeds depict predominantly aerobic performances ([1] Cano□Barbacil et al. 2020, [2] Brett and Glass 1973, [3] Katopodis and Gervais 2016).

1.2. INTERSPECIFIC AND INTRASPECIFIC VARIATION

As established in the previous section, both metabolic scaling relationships and temperature sensitivity of metabolic performances contain variation. Regarding metabolic scaling relationships, the variation of MMR scaling is still less understood, as fewer empirical studies have measured it. MMR and RMR define the Absolute Aerobic Scope (AAS = MMR - RMR), a renowned ecologically relevant measure of aerobic capacity in ectotherms (Clark et al., 2013; Farrell, 2016, 2013). AAS represents the metabolic capacity for activity above resting levels, i.e., move, forage, digest, grow, reproduce, and evade predators (Holt and Jorgensen, 2015). The growing evidence that ectotherms are getting smaller under climate change has accelerated the attention to the metabolic scaling relationships and, now, with a sharper focus on temperature effects and aerobic performances beyond RMR, like MMR and AAS (Ballesteros et al., 2018; Carey and Sigwart, 2014; Glazier et al., 2020; Lindmark et al., 2022; Rubalcaba et al., 2020; Tan et al., 2019; Wootton et al., 2022). These scaling relationships are evaluated experimentally at intra-specific and inter- and intra-specific levels in meta-analyses.

Scaling relationships that cover diverse animals (fish and other taxa) suggest that MMR scales with steeper slopes than RMR; more specifically, that b_{MMR} approaches 1, while $b_{\mathrm{RMR}} < 1$ and $b_{\mathrm{RMR}} < b_{\mathrm{MMR}}$ (Barbosa et al., 2006; Darveau et al., 2002; Gillooly and Allen, 2007; Glazier, 2009; Hochachka et al., 2003; Killen et al., 2007; Weibel and

Hoppeler, 2005). With the further addition of temperature, the broadscale trends reveal that scaling slopes decrease with increasing temperature (Lindmark et al., 2022; Rubalcaba et al., 2020). This decline could suggest a metabolic capacity constraint in larger fish. Temperature can also change metabolic scaling so that $b_{\mathrm{MMR}} < b_{\mathrm{RMR}}$, indicating declining AAS with size (Figure 1). However, experimentally measured scaling relationships provide mixed evidence on how MMR and RMR scale with mass and, thus, how both collectively change aerobic capacity in fishes (Figure 2). This body of work affirms that scaling is contextual and suggest that size-specific metabolic constraint may not develop in all fishes. Declining body size has been observed in some fishes and not in others (Audzijonyte et al., 2020; Baudron et al., 2014; Oke et al., 2020). Therefore, the question: *What underlines this variation and possible species-specific vulnerability?*

Many factors can underline aerobic physiological performance in animals, and thus metabolic scaling relationships. To name a few, taxonomic classification (species, family, order; Capellini et al., 2010; Isaac and Carbone, 2010; Killen et al., 2016; White et al., 2019), lifestyles, life history, or ecological roles (Glazier, 2014; Killen et al., 2016; Kozłowski et al., 2020; Tan et al., 2019), morphology and body shapes (Burgess et al., 2017; Killen et al., 2016), and also ontogeny (Killen et al., 2007; Maino and Kearney, 2014; Moran and Wells, 2007; Tan et al., 2019). Although, it has not been described how metabolic scaling of fish characterized by these outlined factors changes with temperatures, especially those passed optimal (chronic, acute, across generations; e.g., Messmer et al., 2017). Metabolic scaling relationships across temperatures can help identify biologically relevant groups of fish in which the vulnerability to climate change can be body size specific.

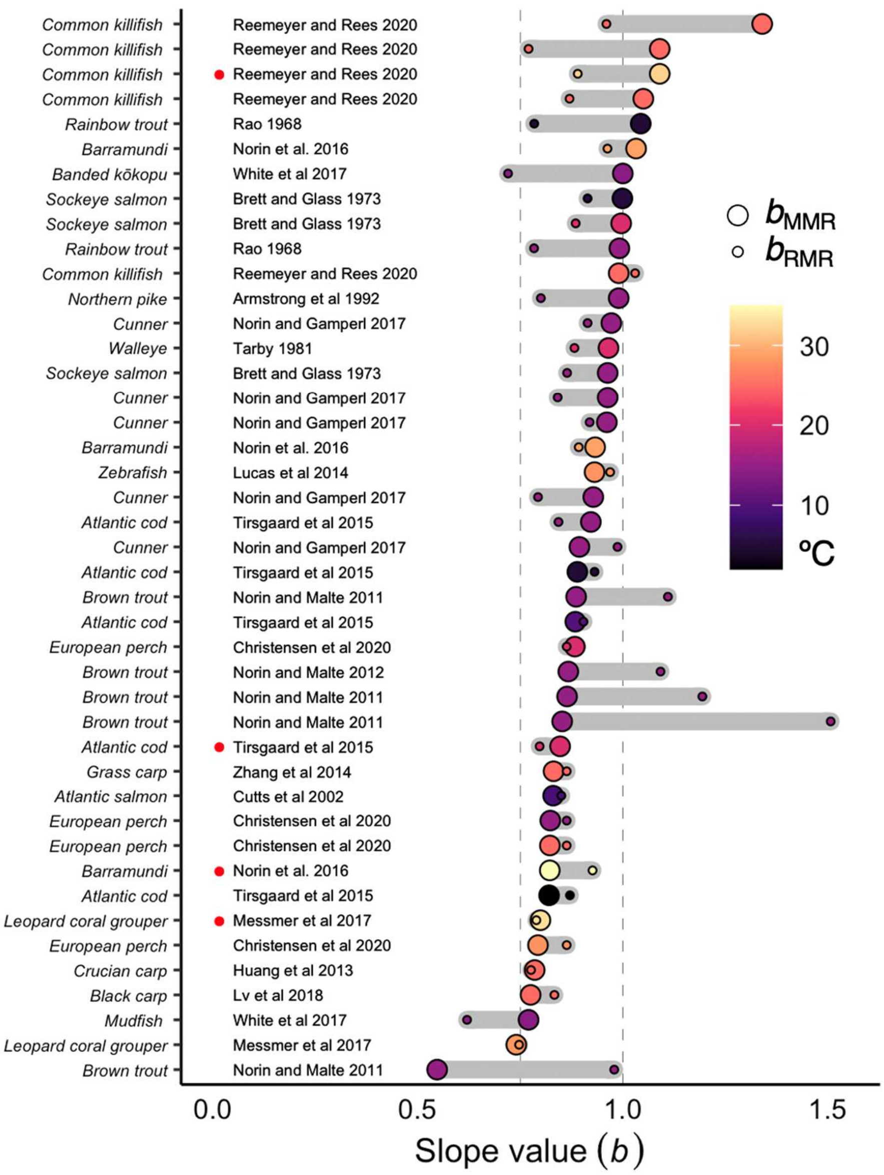

Figure 2. Intraspecific variation in metabolic scaling slopes of resting and maximum metabolic rates.

All connected MMR (large dots) and RMR (small dots) scaling slopes (b) belong to the same group of fish. The red dots mark studies that test fish under warm conditions. The left 'tail' relationships show $b_{RMR} < b_{MMR}$ indicating cases where absolute aerobic scope, AAS (MMR – RMR) may not be constrained with body size. The right "tail" shows cases where $b_{RMR} > b_{MMR}$ indicating cases where larger individuals may experience aerobic constraint. This is not a comprehensive review of all studies that have estimated scaling of MMR and RMR.

In systems where temperature modulates metabolic scaling relationships, either MMR or RMR, it begs the question: *what are the underlying mechanisms of this* *temperature-induced variation*? Metabolism is a whole animal performance that depends on many cascading physiological functions at a lower level of biological organization. Cardiovascular performance is essential for maintaining aerobic capacity across temperatures in ectotherms, and particularly critical is the function of the heart (Eliason and Anttila, 2017; Farrell, 1997). Another *common* physiological scaling relationship is a negative scaling of resting heart rates, a reciprocal of metabolic rate scaling, i.e., MTE suggests $b_{\mathrm{MR}} = 0.75$ and $b_{\mathrm{heart\ rate}} = -0.25$ (Brown et al., 2004) (Figure 1). In fishes, temperature regulates cardiac performance, where the change in heart rates is the leading response to meet the rising aerobic metabolic demands (Eliason and Anttila, 2017; Lillywhite et al., 1999).

Scope for heart rate directly underscores the aerobic capacity in fishes (e.g., Eliason et al., 2013a). The resting heart rates generally increase with acute warming, often until the absolute thermal maximum of the species. Maximum heart rates, however, increase with temperature and then tend to plateau several ºC before species thermal maximum (Eliason and Anttila 2017; the acute response of both resting and maximum heart rates vary intra-specifically). Therefore, the scope for the heart rate declines at the warmest temperatures triggering a collapse of the cardiac function and, consequently, aerobic capacity at the whole animal level (Eliason et al., 2013a). The acute TPC of maximum heart rates is particularly revealing of an individual's aerobic capacity because the temperature where the increase of maximum heart rate first begins to decline (Arrhenius breakpoint temperature) overlaps with species optimal temperature for AAS (Casselman et al., 2012). Additionally, the individual's upper thermal limits overlay with temperature where the maximum heart rate peaks and loses rhythmicity (cardiac arrhythmia) (Anttila et al., 2013; Casselman et al., 2012; Eliason and Anttila, 2017). If scaling of aerobic metabolism interactively changes with temperatures, this change could be mechanistically linked with size- and temperature-specific scaling of maximum heart rates and size-specific thermal tolerance of the heart. Evidently, a study on chinook salmon found that larger fish suffered from cardiac failure at lower temperatures than their smaller counterparts (e.g., cardiac arrhythmia; Clark et al., 2008). Cardiac performance can provide mechanisms for the size-specific vulnerability of fish under warming.

1.3. TIGHTLY LINKED PERFORMANCE TO METABOLISM: SWIMMING IN SALMONIDS

Swimming is an aerobically supported activity that is essential for fish as they swim to forage, chase prey, avoid predation, find and secure a mate, or move to avoid unfavorable conditions. The swimming behaviors range from hovering stationary, darting, maneuvering, cruising, and even leaping outside the water (Beamish, 1978; Webb, 1984). Some species, including the remarkable and valuable salmon, undergo impressive – up to several thousand kilometers long – migrations (Binder et al., 2011). Larger fish will be more powerful swimmers as they can produce more thrust and contribute more muscle to power swimming (Bainbridge, 1958; Beamish, 1978; Brett, 1965b; Rubio-Gracia et al., 2020). At the inter-specific level across taxa, this can be depicted by the positive relationship between migration distance and adult body size (fishes, mammals, and birds: Hein et al., 2012). Also, at the intra-specific level, larger adults will 'outswim' their smaller counterparts (Bainbridge, 1958; Cano-Barbacil et al., 2020). Some swimming behaviors, like bursting, jumping, and escaping predation, are *an*-aerobic and may have different [non-linear] relationships with size (Goolish, 1991). Yet, contingent on anaerobic swimming is recovery, which is necessarily aerobic (Zhang et al., 2018). The close links between swimming and aerobic capacity lay out an important reason to study the swimming capacity of fish across body size and ecological contexts.

Wild migrating adult Pacific salmon is the ideal model for studying the interactive effects of body size (and other factors) and swim performance (Cooke et al., 2012; Eliason and Farrell, 2016; Farrell, 2009). In Pacific salmon, the spawning migration is once in a lifetime journey supported by finite energy stores. Therefore, the physiological and morphological traits that enable successful migration or hinder it are under strong selection (e.g., swimming, body size, aerobic and cardiovascular performance; Crossin et al., 2003; Eliason et al., 2011; Hinch and Bratty, 2000). And importantly, salmon are iconic species bringing special cultural, recreational, and economic value (Atlas et al., 2021). Yet, the ecological challenges that migrating adult salmon must face during spawning migrations are increasing in severity. Among those are drought, river discharge, and other catastrophic events such as landslides that restrain migration paths (Bett et al., 2020; Crozier et al., 2019; Government of Canada, 2019). Furthermore, salmon species are no exception to the pervasive trend of declining size with temperature, as observed across and within species (Cox and Hinch, 1997; Oke et al., 2020). If salmon cannot complete their spawning migration, their lifetime fitness is zero leading to a declining population.

Salmon rely on predominantly aerobic swimming during migration but must also swim anaerobically to overcome rapids or climb fishways (Burnett et al., 2014a; Hinch and Bratty, 2000; Hinch and Rand, 1998). Aerobic swimming scales positively with body size (Figure 1; Brett, 1965b); therefore, larger and faster salmon may benefit from a size-associated advantage. However, Pacific salmon with the most strenuous and longest migrations tend to be smaller than the more coastal populations and species (Crossin et al., 2004). One reason may be a size-specific recovery performance. For example, a study on coho salmon showed that larger individuals took longer to recover, which was related to higher total metabolic costs of recovery from burst (anaerobic) swimming at elevated temperatures (Clark et al., 2012). This finding could be associated with more significant physiological disturbance after strenuous exercise in larger fish compared to smaller fish (Clark et al., 2012; Gingerich and Suski, 2012; Goolish, 1991; Kieffer, 2000). These competing observations illustrate that biologically important factors beyond body size (e.g., sex, temperature, maturity state, body shape, somatic energy reserves) affect migration success and, thus, swim performance in Pacific salmon (Crossin et al., 2004). Therefore, large adult salmon may be more vulnerable to secondary stressors while swimming to reach the spawning ground, though the evidence for this hypothesis is not systematically evaluated. Therefore, a holistic picture depicting how maximum swimming performance varies inter- and intra-specifically and under the influence of secondary factors, including body size, is necessary to develop and implement the best practices to manage valuable salmon.

1.4. MOTIVATION AND OUTLINE OF MY THESIS

Fishes span across ~ five magnitudes of order with smallest vertebrate species (*Paedocypris progenetica*, cyprinid, 7.9 mm length, Kottelat et al., 2006) to the largest fish species, the whale shark (*Rhincodon typus,* up to 20000 mm in length, and weight of 34 t; ("Rhincodon typus, Whale shark : fisheries," fishbase.org), they have evolved a fascinating spectrum of lifestyles, from nearly sedentary and burrowing, to highly active and migratory, which has allowed fishes to thrive across diverse habitats from poles to tropics. Different fish species must possess a metabolic phenotype (MMR, RMR, and AAS; Metcalfe et al., 2016) that supports their energetic demands and responds to environmental changes within appropriate timescales. Metabolic scaling relationships could inform us how energy demand changes across size and under any selected stressors, including warming. In addition, scaling of performances beyond metabolism – heart rate that supports aerobic capacity or swimming (and recovery) that is predominantly supported by aerobic capacity – can allow us to understand the ecological consequences and vulnerability of fish across body size and life stages. My thesis research is comprised of three chapters.

In chapter two, I develop metabolic scaling relationships (MMR, RMR, and aerobic scope) in fishes and identify how ecology, morphology, and temperature alter them at inter- and intra-specific levels. This chapter was a collaboration between myself, Dr. Christopher L. Jerde, and Dr. Erika J. Eliason. An earlier version of this work has gone through a peer review in two journals: "Fish and Fisheries" and "The Canadian Journal of Fisheries and Aquatic Sciences." The work continues to be improved with considerations from reviews.

In chapter three, I experimentally test how aerobic metabolic performances (MMR, RMR, and aerobic scopes) and maximum heart rates change with acute temperature change and body size in barred surfperch, *Amphistichus argenteus.* I also test cardiac thermal tolerance across body sizes in the same individuals. This chapter was a collaboration between myself, a Ph.D. Candidate Emily A. Hardison, and Dr. Erika J. Eliason. It is written in preparation for the "Journal of Experimental Biology."

In chapter four, I consolidate and review swim performance in adult salmon. This chapter was a collaboration between myself, David A. Patterson, and Dr. Erika J. Eliason. It will be submitted to “The Canadian Journal of Fisheries and Aquatic Sciences” as an invited review article.

CHAPTER 2: METABOLIC SCALING RELATIONSHIPS IN FISHES: THE ROLES OF TEMPERATURE, SPECIES, AND THEIR ECOLOGY.

2.1. INTRODUCTION

Body mass is a powerful trait that modulates energy flow and ecological interactions within ecosystems (Brose et al., 2012; Brown et al., 2004). The ubiquitous metabolic scaling law and its relationship with ecosystem processes are receiving renewed attention because anthropogenic impacts such as climate change, overharvesting, and pollution affect biodiversity, population, and community size structures across ecosystems (Gardner et al., 2011; Pecl et al., 2017). Meanwhile, a decline in body size has been recognized as the third *universal* response to climate change (Daufresne et al., 2009; Gardner et al., 2011). The observational evidence to support this phenomenon is growing in fishes, key taxa with high economic and ecological value (Audzijonyte et al., 2020; Jeffrey et al., 2017; Oke et al., 2020). Yet, the underlying physiological mechanisms leading to this change are largely unknown. The metabolic scaling law in the context of a warming world could provide a mechanistic framework to explain decreasing body size in ectotherms.

Aside from body size, temperature is a master regulator of metabolism in ectotherms, including fish (Brett, 1971; Fry, 1971). Warming may impose a greater metabolic constraint on large compared to small individuals (Rubalcaba et al., 2020), which could reflect in temperature-dependent metabolic rate scaling relationships (Christensen et al., 2020). Several meta-analyses studies have begun to tackle this question aiming to identify *who* and *when* are the most vulnerable to climate change (Peralta-Maraver and Rezende, 2021; Rubalcaba et al., 2020; Rubalcaba and Olalla-Tárraga, 2020). The current evidence for temperature-dependent metabolic scaling is inconsistent across species, life stages (ontogeny), temperature ranges, and the type of temperature changes (e.g., acclimation versus acute exposure) (Gjoni et al., 2020; Glazier, 2020; Killen et al., 2010). Conceptualizing temperature-specific scaling relationships will enable an improved evaluation of changing ecological processes.

The most common scaling relationships implemented across biological disciplines rely on resting metabolic rates (RMR). However, metabolic scaling of active (or maximum) metabolic rate (MMR) is gaining recognition due to its ecological importance, particularly in the context of climate change (Bigman et al., 2021; Christensen et al., 2020; Rubalcaba et al., 2020; Scheuffele et al., 2021b). One can expect different scaling relationships between MMR and RMR because they reflect different physiological and metabolic states (Darveau et al., 2002; Suarez, 2005). Likewise, MMR and RMR scaling can show different levels of temperature dependence because these metabolic rates generally respond to changing temperature following varying non-linear patterns (e.g., increase, decrease, no change) (Kellermann et al., 2019; Scheuffele et al., 2021b; Schulte, 2015). Therefore, scaling relationships of MMR or RMR alone without accurately describing their response to temperature will be insufficient to predict biological processes at the level of individuals, populations, and ecosystems in the context of climate change.

The field requires a more refined understanding of how metabolic capacity changes across body size in wild fish. Animals routinely expend energy above the RMR level (e.g., foraging, defending territory) but below maximum metabolic capacity, MMR level (e.g., escaping a predator, strenuous migration). Aerobic scope (AS) is the difference between MMR and RMR, representing the energetic capacity to thrive (e.g., move, digest, reproduce). If RMR scales allometrically ($b < 1$) and MMR scales isometrically ($b = 1$), as has been proposed and empirically observed (Brett, 1965b; Glazier, 2005; Grula et al., 2021), then AS increases with increasing body size providing larger individuals with an energetic advantage ($b_{\mathrm{MMR}} > b_{\mathrm{RMR}}$, indicate increasing AS with size; e.g., Armstrong et al., 1992; Brett and Glass, 1973; Rao, 1968). Conversely, if MMR scales with lower slopes than RMR, AS decreases with increasing body size, and larger individuals would have an energetic disadvantage ($b_{\mathrm{MMR}} < b_{\mathrm{RMR}}$ indicate decreasing AS with size (Lv et al., 2018; Norin and Malte, 2011). Alternatively, these relationships may not differ ($b_{\mathrm{MMR}} \sim b_{\mathrm{RMR}}$), suggesting a negligible change in AS (Huang et al., 2013; Tirsgaard et al., 2015). In addition to AS, RMR and MMR can be used to calculate Factorial aerobic scope (FAS = MMR / RMR). FAS represents the proportion by which an individual can elevate its metabolic rate above resting level and represent a clear metabolic constraint (Eliason et al., 2022). A negative relationship between body size and FAS would indicate a direct metabolic constraint that increases with body size. To our knowledge, no comprehensive analyses have established how MMR and RMR scaling relationships shape metabolic capacity (AS and FAS) in fish across body sizes. These patterns need to be resolved to develop robust predictions about the ecological consequences of metabolic scaling.

Maximum and resting metabolic rates and the difference between the two, the aerobic scopes, are ecologically important traits (Eliason et al., 2011; Fry, 1971), and each varies intra- and inter-specifically (Glazier, 2005; Pettersen et al., 2018). A large portion of variability can be attributed to taxonomic classification (species, family, order; Clarke and Johnston, 1999) and phylogenetic relatedness of studied species (Capellini et al., 2010; Isaac and Carbone, 2010; Killen et al., 2016). Furthermore, metabolic demands can be influenced by different life histories (Eliason et al., 2011; Kozłowski et al., 2020) and ecologies (Killen et al., 2010; Tan et al., 2019), acclimatization histories (Carey and Sigwart, 2014), cross-generational thermal conditions (Wootton et al., 2022), species-specific general metabolic level (e.g., active lifestyle tuna *versus* more sluggish species like carp; Glazier, 2005; Killen et al., 2010; Killen et al., 2016; Tan et al., 2019), and morphology (Grula et al., 2021; Killen et al., 2016). If these factors affect individuals across body mass differently, scaling relationships (MMR and RMR) can be expected to change. Studies that have examined MMR scaling relationships (e.g., but not only: Christensen et al., 2020; Gillooly and Allen, 2007; Grula et al., 2021; Huang et al., 2013; Killen et al., 2016; Rao, 1968; Weibel and Hoppeler, 2005; White et al., 2008), often do not link scaling of RMR and MMR to evaluate the inter- and inter-specific variation in aerobic scope (but see: Gillooly et al., 2017; Gillooly and Allen, 2007). This context dependency of metabolic scaling of MMR, RMR, and aerobic scopes is critical to consider because resilience to size-structured harvesting and vulnerability to warming may differ across taxa.

Our synthesis focuses on fish in which a declining body mass can: 1) jeopardize food security through shifts or losses of fisheries (Oke et al., 2020; Pinsky et al., 2011; Rice and Garcia, 2011), and 2) cause unexpected shifts to food webs possibly leading to loss of ecosystem stability and loss of their functioning (Jeppesen et al., 2010; Rice and Garcia, 2011). Our specific objective was to estimate the metabolic scaling relationships of MMR and RMR, AS, and FAS in diverse fish across temperatures, particularly focusing on fish exposed to warm temperatures. We hypothesized that: *i*) Scaling relationships change with temperature, but the nature of ‘how’ depends on activity level (maximum metabolic rates, MMR *vs.* resting metabolic rates, RMR) and the level of temperature acclimation of fish (different thermal histories), *ii*) A fish's absolute and factorial aerobic scopes will vary depending on different temperatures and the level of temperature acclimation of the fish (different thermal histories), *iii*) The scaling slope of MMR would be statistically indistinguishable from $b_{\mathrm{MMR}} = 1.00$, thus leading to a positive or constant AS across body size ($b_{\mathrm{MMR}} > b_{\mathrm{RMR}}$; $b_{\mathrm{MMR}} \sim b_{\mathrm{RMR}}$) across fish species, *iv*) Mass independent measures of metabolism (MMR, RMR, AS, FAS) will differ between fish with different lifestyles, morphologies, climatic and salinity habitats, *v*) Mass independent MMR and RMR will have different thermal sensitivities, the rationale being that they have different thermal performance curves. Using the scaling relationships of MMR, RMR, and FAS under warming, we identified various patterns of emerging metabolic constraints in fishes across species and ecological contexts. As a novel contribution, we focus on FAS as an essential capacity metric because it directly identifies the constraints on elevating metabolic capacity.

2.2. MATERIALS AND METHODS

2.2.1. Data

We compiled maximum metabolic rate (MMR, mg O_2 h^{-1}) and resting metabolic rate (RMR, mg O_2 h^{-1}) measurements of individual fish, their body mass (BM, g), and test temperature (ºC). We expanded the RMR dataset from Jerde et al. (2019) (Jerde et al., 2019; Kraskura et al., 2021) by adding additional RMR of more diverse species (e.g., polar and tropical species), adding MMR, and including metabolic rate data that were measured in fish that were exposed to above ecologically relevant temperatures. Data were gathered by carefully and individually examining publicly available datasets published in complement to peer-reviewed articles from 2000 or later using *i)* Google Dataset Search (https://datasetsearch.research.google.com/); we used the following keywords "maximum metabolic rate fish", "maximum metabolic rate fish", "oxygen consumption fish", "metabolism fish" and "metabolic rate fish", *ii)* using Mendeley search engine directly (https://data.mendeley.com/), *iii)* reviewing journal publication for supplemental data published directly on journal sites, or lastly, *iv)* several datasets were personally received from authors (Appendix 1, Table 1).

Metabolic rate data were included if: *i*) fish were at post-larval stages (juvenile or adult stage), *ii*) MMR was the metabolic rate measurement during locomotion; specifically, MMR was recorded either at the end of an exhaustive swim test while still swimming, immediately after the fish completed an exhaustive swim test but during recovery, or post chasing by hand or net. The representative metabolic rate measurement for 73 individuals should be more accurately defined as an active metabolic rate because the individual was not exercised to its aerobic maximum (Greenland shark, *Somniosus microcephalus*, n = 3; Neumayer's barb, *Enteromius neumayeri*, n = 70). Further, the data were included if the following criteria were met: *iii*) RMR was recorded in calm fish in a resting, post-absorptive (in fish fasted long enough to have completed digestion for a given species) state (Chabot et al., 2016), and *iv*) fish were acclimated (or raised) and tested in ecologically relevant, physiologically non-disturbing conditions (e.g., light, salinity, social environment, feeding regimens), and *v*) fish that were tested at temperatures that fall within their ecologically relevant ranges (throughout referred to as "optimal"), or in fish that were either acutely (< 1 day) exposed to, or acclimated to, temperatures above optimal before being tested. Data points (MMR and RMR) were excluded during data curation if the originally reported MMR estimate was lower than RMR (leading to negative metabolic scope).

Data from the same species were first grouped by the study, then sub-grouped based on specific study conditions, i.e., repeat test trials, population, generations, ecologically relevant salinity, flow and wave, light, food ratio, or diet conditions. This approach allowed us to account for variation due to study-specific and biotic and abiotic condition-specific conditions. To specifically examine temperature effects on metabolic scaling, the data were first classified into three thermal history categories: 1) 'optimal' (defined above), 2) 'acclimated warm' - fish in this category were acclimated and tested at a temperature that was above their optimal range (i.e., climate change scenario, or current maximum temperatures), and 3) 'acute warm', these fish were acclimated to one temperature but tested at a different acutely changed temperature (no more than 24 h under new thermal conditions). To examine how metabolic scaling relationships (MMR and RMR) change in fish with shared ecologies and morphologies, we extracted species-specific data from the online database (https://www.fishbase.com) and FishBase R interface (Boettiger et al., 2012) (Appendix 1 Table 2, Appendix 1 Table 3). All species were categorized based on inhabited environment: *i)* Climate (polar, temperate, tropical, subtropical), *ii)* Salinity conditions throughout an animal's lifespan (freshwater, marine, freshwater-brackish, marine-brackish, marine-freshwater-brackish (all salinities)), their *iii)* Lifestyle (demersal, benthopelagic, pelagic, reef-associated), and their *iv)* Morphology (elongated, fusiform, short-deep, eel-like, dorsoventrally flattened). If the classification was unavailable, the species were categorized following peer-reviewed literature (Appendix 1, Table 2). Ecology- and morphology-specific metabolic scaling relationships were established if the data subset had ≥ 100 data points and the body size range spanned at least one order of magnitude. These data subsets were suited for body size scaling studies (White and Kearney, 2014).

2.2.2. Models

Fish body mass, BM (g), maximum metabolic rate, MMR (mg O_2 h^{-1}), resting metabolic rate, RMR (mg O_2 h^{-1}), and aerobic scope, AS = MMR - RMR (mg O_2 h^{-1}), were natural log-transformed before analysis to comply with a linear homoscedastic form $ln\text{MR} = ln(a) + b*ln\text{BM}$ of a power function $\text{MR} = a*\text{BM}^b$; in these equations a = scaling intercept, and b = scaling slope, MR = metabolic rate (RMR or MMR). Additional fixed (temperature, or indicator variables) and random (species, trials) explanatory variables were added to this equation to evaluate sources of inter- and intra-specific variation in scaling relationships. All statistical approaches are detailed below. Data and statistical analyses were performed using R Studio (R version 4.0.4, 2021-02-15).

The temperature was included in all models. We used indicator variable statistics to examine if thermal history "acute-warm" and "acclimated-warm" lead to different scaling relationships. A new numeric variable was created and assigned either 1 (acute-warm) or 0 (acclimated), and all measurements under optimal conditions were excluded. Mixed-effects models were developed to test for significance that two warm exposed fish were statistically different (fixed factors: *ln*BM, temperature, indicator variable, and interaction between factors). The model with an interaction between *ln*BM and indicator variable was weaker than the more parsimonious model without the interaction, which served as evidence that scaling relationships between fish from the acute-warm and acclimate-warm groups did not differ. These thermal conditions were combined for the proceeding analyses and are called "warm" here forward.

The scaling relationships of each metabolic performance metric (MMR, RMR, AS, and FAS) were separately established on fish in two temperature history groups: "optimal" and “warm”. We examined five model suites for each metabolic rate metric. Each was defined by its unique random effect structures (sp = species, tr = trial, T_K = inverse temperature in Kelvin (1000/ºK), *ln*BMg = natural log body mass in grams):

i) (1|sp)

ii) (1|sp) + (1|sp:tr)

iii) (1|sp) + (0 + T_K|sp) + (1|sp:tr)

iv) (1|sp) + (0 + *ln*BM|sp) + (1|sp:tr)

v) (1|sp) + (0 + *ln*BM|sp:tr) + (1|sp:tr)

All models had two fixed effects, 1) body mass (*ln*BM, g) and 2) temperature term. For MMR, RMR, and AS, the temperature was included in an inverse unit scale of 1000/ºK to allow for the establishment of the Arrhenius relationship to estimate temperature sensitivity (Barneche et al., 2014; Downs et al., 2008; Rubalcaba et al., 2020) (equations 1 and 2). In FAS models, the temperature term was included in degrees Celsius. Four sub-models were considered under each model suite:

i) ‘linear intercept model’ where all fixed effects were added as intercept terms

ii) ‘linear interaction model’ where body weight and temperature effects were added in interaction

iii) ‘polynomial intercept model’ where temperature fixed effect was added as a second order polynomial intercept term

iv) ‘polynomial interaction model’ where body weight and second order temperature effects were added in interaction.

$$\mathrm{MR} = a*\mathrm{BM}^{b}\, e^{c(1000/\mathrm{K})} \qquad \text{(equation 1)}$$

$$ln\mathrm{MR} = ln(a) + b*ln\mathrm{BM} + c*1000/\mathrm{K} \qquad \text{(equation 2)}$$

$$MR_{1g} = MR_{observed} / BM^{b} \qquad \text{(equation 3)}$$

In these equations, MR = Metabolic Rate measure ($mgO_2\ g^{-1}$), and BM = body mass in grams. The coefficient, *c*, can be used to calculate Activation energy, *E* (eV), by using Boltzmann's constant (8.617×10^{-5} eV K^{-1}) and $c = -E/1000k$ (Downs et al., 2008; Gillooly et al., 2001). The slope of activation energy indicates mass-independent thermal sensitivity of a given performance (MMR, RMR, and AS).

To explore MMR and RMR scaling relationships for each species and each ecology and morphology group, we used simple linear regression models (glm, Gaussian error distribution). The number of species and trials within each subgroup were limited, which led to singularity issues and thus prevented the use of random-effects models. Ecological group metabolic scaling models included *ln*BM and temperature as explanatory variables. Species-level scaling models included *ln*BM as a single explanatory variable because of insufficient temperature coverage for each species.

<table>
<tr><th colspan="2"><i>Optimal conditions</i></th></tr>
<tr><td><i>ln</i>RMR</td><td>~ <i>ln</i>BM + T_K + (1|sp) + (0 + <i>ln</i>BM|sp:tr) + (1|sp:tr)
RMR is explained independently by body mass and temperature (independent explanatory variables: <i>ln</i>BM, T_K). The intercepts of scaling relationships vary at <i>i)</i> species level (random scaling intercept term; 1|sp) and further at <i>ii)</i> specific trial level, which is linked with species-specific variation (nested random intercept term: 1|sp:tr). The metabolic scaling slopes vary between trials nested within species (nested random slope term: 0 + <i>ln</i>BM|sp:tr). Correlation between slopes and intercepts across the same random effect level is not estimated.</td></tr>
<tr><td><i>ln</i>MMR</td><td>~ <i>ln</i>BM * T_K + (1|sp) + (0 + <i>ln</i>BM|sp) + (1|sp:tr)
MMR is explained by body mass and temperature in interaction (independent explanatory variable group: <i>ln</i>BM * T_K). If temperature changes, the body mass scaling relationship also changes. The intercepts of scaling relationships vary at <i>i)</i> species level (random scaling intercept term; 1|sp) and further at <i>ii)</i> specific trial level, which is linked with species-specific variation (nested random intercept term: 1|sp:tr). The metabolic scaling slopes vary at species level (random slope term: 0 + <i>ln</i>BM|sp). Correlation between slopes and intercepts across the same random effect level is not estimated.</td></tr>
</table>

***ln*FAS**	**~ *ln*BM + T_C + (1|sp) + (0 + *ln*BM|sp) + (1|sp:tr)** FAS, metric for metabolic capacity, is explained independently by body mass and temperature (independent explanatory variables: ***ln*BM**, **T_C**). The intercepts and scaling slopes are affected by of non-independent explanatory variables (random effects) in the same way as outlined above for *ln*MMR model.
***ln*AS**	**~ *ln*BM + T_K + (1|sp) + (0 + *ln*BM|sp) + (1|sp:tr)** (Same as *ln*FAS model above)
Warm conditions	
***ln*RMR**	**~ *ln*BM + T_K + (1|sp) + (1|sp:tr)** RMR is explained independently by body mass and temperature (independent explanatory variables: ***ln*BM**, **T_K**). The intercepts of scaling relationships vary at *i)* species level (random scaling intercept term; **1|sp**) and further at *ii)* specific trial level, which is linked with species-specific variation (nested random intercept term: **1|sp:tr**). The metabolic scaling slopes do not vary across species or trials.
***ln*AS**	**~ *ln*BM + T_K + (1|sp) + (1|sp:tr)** (Same as outlined above for *ln*RMR model in warm exposed fish)
***ln*MMR**	**~ *ln*BM + T_K + (1|sp) + (0 + *ln*BM|sp) + (1|sp:tr)** MMR is explained independently by body mass and temperature (independent explanatory variables: ***ln*BM**, **T_K**). The intercepts and scaling slopes are affected by of non-independent explanatory variables (random effects) in the same way as outlined above for *ln*MMR model in fish under optimal conditions.
***ln*FAS**	**~ *ln*BM + poly(T_C, 2) + (1|sp) + (0 + T_C|sp) + (1|sp:tr)** FAS is explained independently and linearly by body mass and independently but non-linearly by temperature (***ln*BM**, **poly($T_{K,2}$)**). The intercepts of scaling relationships vary at *i)* species level (random scaling intercept term; **1|sp**) and further at *ii)* specific trial level, which is linked with species-specific variation (nested random intercept term: **1|sp:tr**). The metabolic scaling slopes do not vary across species or trials, but the non-linear temperature effect varies across species (random slope term: **0 + T_C|sp**)

Table 1: Structure and description of scaling models.
Best models for each metabolic rate performance and thermal condition. Models are provided in the syntax used with the ‘lmer’ function from the R package ‘lme4’. The hypothesis and biological interpretation are outlined for each model structure. Abbreviations: sp = species, tr = trial, T_K = inverse temperature in Kelvin (1000/ºK), T_C = temperature in ºC, *ln*BM = natural log body mass in grams.

2.2.3. Multi-model inference, metabolic scaling parameters, and confidence estimates

All scaling relationship parameter estimates were estimated using maximum likelihood, and the best models were selected using SIC (also called BIC) (Jerde et al., 2019). We used SIC over the commonly used AIC for a more robust model selection (Dennis et al., 2019; Taper et al., 2021). The model with the lowest SIC score was accepted as the best model (Table 1). The ΔSIC between the best model and all other considered models is used as a statistic to report the strength of evidence for any given model to be the "true" model explaining the data while considering the constraints that only a set of models are provided (Jerde et al., 2019). To estimate the error and reliability of each parameter estimate (scaling slope, scaling intercept, temperature term), we used 90 % confidence intervals. Residual distribution was visually assessed for each model.

2.2.4. Mass independent effects on metabolic performance

Mass independent measures of metabolic performance were used in the Arrhenius plots for temperature sensitivity estimates (RMR and MMR), for metabolic scope comparison between species sharing similar ecologies and morphologies (FAS and AS), and for broad-scale comparison to compare directly how thermal history affect metabolic capacity. Metabolic rate measurements were mass normalized to a 1-gram fish to obtain mass-independent metabolic rate measurements using equation 3 (Glazier, 2022). We used performance specific mass scaling exponents that were obtained from best fit mixed-effects models ($b_{\text{MMR-warm}} = 0.84$, $b_{\text{MMR-optimal}} = 0.81$, $b_{\text{RMR-warm}} = 0.82$, $b_{\text{MMR-optimal}} = 0.81$, $b_{\text{AS-warm}} = 0.78$, $b_{\text{AS-optimal}} = 0.81$).

We tested for the difference in FAS and mass-independent AS between fish from different Climate, Morphology, Salinity, and Lifestyle subgroups and for significant differences between thermal histories (optimal and warm). Both FAS and mass-independent

AS were normally distributed within each subgroup and thermal history category, thus allowing for the use of mixed models with normal gaussian error distribution. Since metabolic scopes are always positive and often skewed, we also used log-normal models with a normal error distribution. Three structurally different models were constructed for AS and FAS and each ecological subgroup (Climate, Morphology, Salinity, and Lifestyle): *i*) with temperature (ºC) as the only fixed effect (null model), and *ii)* with temperature and ecological subgroups as two fixed factors, and *iii*) with temperature, ecological subgroup, and thermal history group (optimal, and warm) as three fixed factors. All mass-independent models contained random intercept effects of trial nested within species. Grouped models with increasing complexity were compared using ΔSIC. The best-fitting model was used to determine the significance of thermal history and the ecological group as explanatory factors predicting mass-independent AS and FAS. Lastly, to directly examine if metabolic capacity, the FAS, mass-independent MMR, and RMR differ in fish tested under optimal conditions and warm-exposed fish, we used a simple t-test.

2.3. RESULTS

The metabolic rate database compiles 94 species, 87 studies, 267 trials, and 10287 individual metabolic rate measurement data points (MMR and RMR combined), providing 3155 estimates of aerobic scope measurements from 73 species, 48 studies, 156 trials (warm and optimal conditions combined). Temperature ranges between 0ºC and 31ºC in the optimal temperature group and 1ºC and 39ºC in the warm-exposed fish group. A more descriptive breakdown of the dataset focusing on optimal temperature and warm temperature subsets is provided in Table 2.

	Optimal conditions			***Warm conditions***		
	MMR	**RMR**	**Metabolic scopes***	**MMR**	**RMR**	**Metabolic scopes***
Species (n)	71	82	56	24	23	17
Individuals (n)	3105	5367	2470	891	924	686
Trials (n)	149	222	105	38	42	27
Studies (n)	46	76	35	23	23	17
Temperature avg. (range) ºC:	19.6 (0, 31)	20.11 (0, 31)	19.84 (0, 31)	27.27 (8, 39)	27.08 (1, 36.73)	28.83 (8, 35)
Body size avg. (range) g:	240.58 (0.04, 155000)	139.95 (0.04, 126000)	166.54 (0.04, 126000)	390.94 (0.2, 6795.93)	301.6 (0.33, 6350.99)	209.32 (0.33, 3190)

**Metabolic scope measurements shown are for factorial aerobic scope FAS; aerobic scope (AS) had one less measurement in Warm conditions; this exclusion does not change reported ranges.*

Table 2: Summary metrics of meta-analysis dataset.

2.3.1. Metabolic scaling relationships in fishes

Metabolic scaling slopes of MMR, RMR, and AS are all allometric, with the highest observed values falling below $b = 0.90$ (Figure 3; Table 3). Increasing temperature tended to elevate MMR and RMR metabolic scaling slopes. Under optimal conditions, MMR scaling slope increases with increasing test temperature and captures low $b_{\text{MMR-optimal}} = 0.72$ at 0 ºC and $b_{\text{MMR-optimal}} = 0.86$ at 30 ºC (the temperature range of MMR measure database; Figure 3A). RMR scaling slope was $b_{\text{RMR-optimal}} = 0.81$ under optimal conditions, and temperature elevates the metabolic rate as expected but does not change scaling slopes (Figure 3B). Under warm exposure, metabolic scaling relationships increased by a small margin in MMR ($b_{\text{MMR-warm}} = 0.82$ {0.75, 0.89}), and by a larger margin in RMR ($b_{\text{MMR-warm}} = 0.84$ {0.81, 0.87}) (Figure 3AB, Table 3).

We found a slight but noticeable greater increase in RMR scaling slope than MMR scaling slope in warm exposed fish, suggesting a decreasing aerobic scope with body mass in fish with warming. This is directly observed by comparing metabolic scaling of AS in fish under optimal conditions and warm conditions $b_{\text{AS-optimal}}$ = 0.825 {0.78, 0.87} > $b_{\text{AS-warm}}$ 0.78 {0.73, 0.84} (Figure 3C, Table 2). Also, decreasing factorial aerobic scope suggests a metabolic constraint developing in larger fish, particularly when warm exposed. FAS in warm exposed fish scales negatively with $b_{\text{FAS-warm}}$ = -0.065 compared to nearly mass unaffected FAS under optimal conditions $b_{\text{FAS-optimal}}$ = -0.012 (Figure 3D).

	Optimal conditions			
	MMR	**RMR**	**AS**	**FAS**
*Slope, **b**,* *SE {$CI_{90\%}$}:*	*NA (temperature dependent)*	**0.81** 0.02 {0.79, 0.84}	**0.82** 0.03 {0.78, 0.87}	**-0.01** 0.02 {-0.04, 0.02}
*Intercept, **ln(a),*** *SE {$CI_{90\%}$}:*	4.14, 1.21 {2.14, 6.14}	15.9, 0.48 {15.11, 16.68}	7.54, 0.99 {5.91, 9.17}	2.06, 0.09 {1.92, 2.21}
*Body mass * T* *SE {$CI_{90\%}$}:*	-0.37, 0.09 {-0.51, -0.23}	*NA*	*NA*	*NA*
Activation energy (E) eV; *SE {$CI_{90\%}$}:*	*NA*	-5.15, 0.14 {-5.38, -4.92}	-2.36, 0.29 {-2.84, -1.87}	-0.03, 0.02 {-0.03, -0.02}
	Warm conditions			
	MMR	**RMR**	**AS**	**FAS**
*Slope, **b**,* *SE {$CI_{90\%}$}:*	**0.82** 0.04 {0.75, 0.89}	**0.84** 0.02 {0.81, 0.87}	**0.78** 0.03 {0.73, 0.84}	**-0.07** 0.02 {-0.1, -0.03}
*Intercept, **ln(a)**,* *SE {$CI_{90\%}$}:*	6.89, 1.01 {5.23, 8.56}	20.26, 1.07 {18.48, 22.05}	-4.12, 1.9 {-7.28, -0.98}	*NA*
*Body mass * T* *SE {$CI_{90\%}$}:*	*NA*	*NA*	*NA*	*NA*
Activation energy (E) eV; *SE {$C_{90\%}I$}:*	-2.04, 0.3 {-2.54, -1.54}	-6.39, 0.32 {-6.91, -5.86}	1.12, 0.57 {0.18, 2.07}	*NA*

Table 3: Metabolic scaling relationships in fishes.
Presented are maximum likelihood estimates from ‘lmer’ summary output and corresponding error estimates. The scaling slope of MMR increases with increasing temperature, which is defined by the negative interaction term (as the temperature increases, the lower is the effect of body mass on MMR, thus raising the slope). Abbreviations: SE = standard error, CI = confidence interval, T = temperature. Original model outputs with additional detail are available in Appendix 1, Table 4.

2.3.2. Variability in metabolic scaling relationships: species and their ecologies

Ecological and morphological attributes are strong explanatory factors of metabolic performance and thus scaling relationships in fish. The scaling relationships between species as we all as species groups with common ecologies and morphologies vary remarkably (Figure 4). At the species level, scaling relationship intercepts ($ln(a)$) negatively correlate with scaling slopes (b) in all metrics, MMR, RMR, and FAS (Pearson's correlations: MMR-warm: $r = -0.586$, $df = 22$; MMR-optimal: $r = -0.716$, $df = 69$; RMR-warm: $r = -0.847$, $df = 21$; RMR-optimal: $r = -0.769$, $df = 80$; FAS-warm: $r = -0.902$, $df = 15$; FAS-optimal: $r = -0.655$, $df = 54$; all $p < 0.01$). These correlations were not significant within ecological subgroups.

Conventional approaches for estimating the mean slope from a histogram are presented in Figure 4. Diverging outcomes between results from mixed models and species-specific histogram means emerge for FAS. Species-specific mean scaling slope is positive ($b = 0.22$ SE 0.76) but negative using mixed models ($b = -0.07$ SE 0.02). It is not surprising to find a discrepancy between these results and those from mixed models as this approach discounts any variability that is attributed to species and to trial-specific conditions, some of which are powerful contributors to estimating allometry (i.e., giving more explanatory power, a larger sample size, a larger range of fish mass). Nevertheless, these differences present the importance of variation in metabolic scaling.

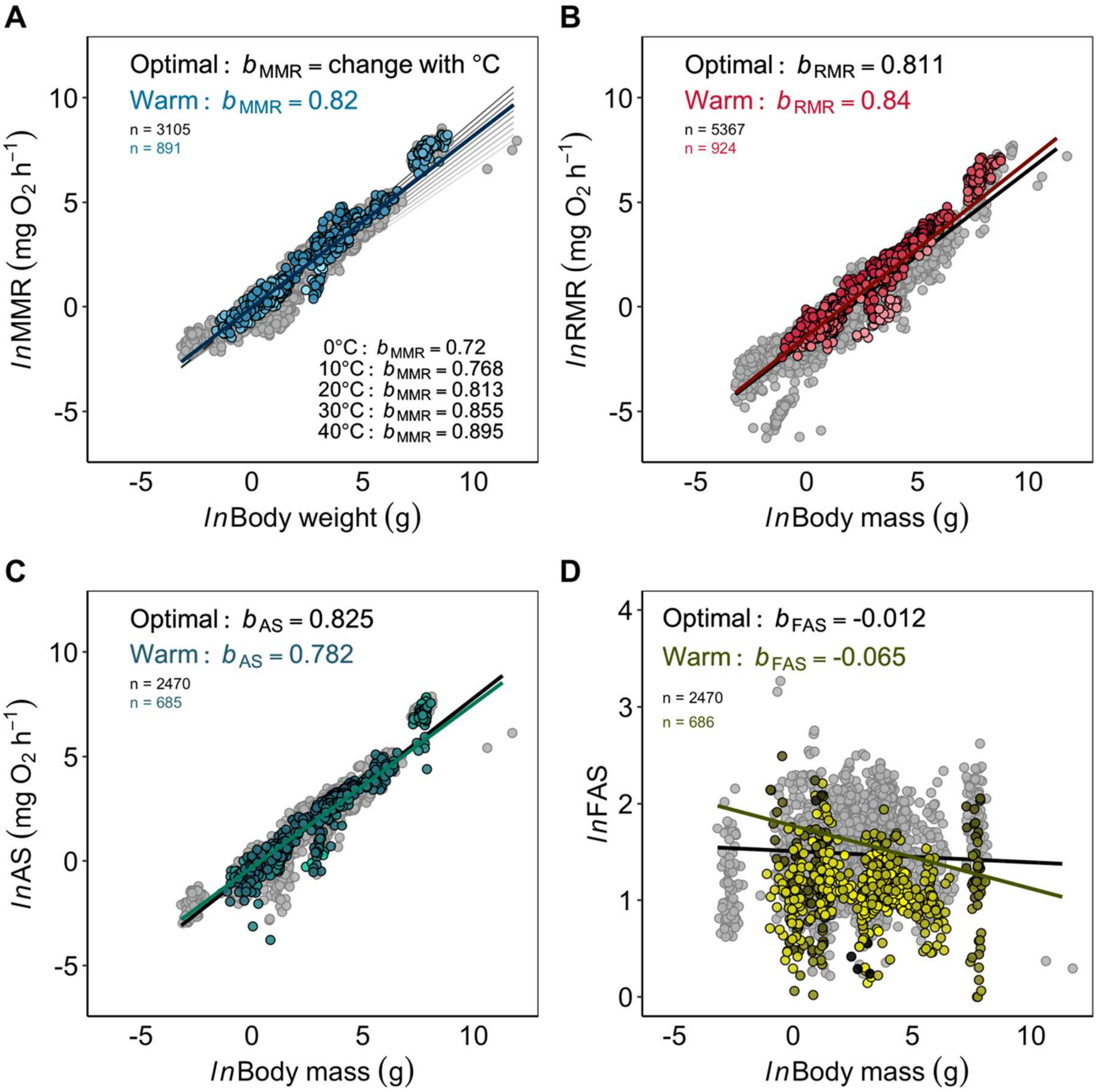

Figure 3: Metabolic scaling relationships across thermal conditions.
Maximum metabolic rates (MMR; A), resting metabolic rates (RMR; B), aerobic scope (AS = MMR – RMR; C), and the relationship between factorial aerobic scope (FAS = MMR/RMR) and body mass (g) (D). In all body size scaling relationships, the grey dots are individual fish metabolic rates in ecologically relevant temperatures and the black lines are scaling slopes (b_{MMR}), accordingly. MMR was best explained by the interaction between temperature and body mass in fish under ecologically relevant conditions; these results are indicated by multiple grey-scale scaling slopes (A, the darker the color tone the higher the temperature). In all panels the colored dots belong to fish exposed to warm conditions (the darker the color tone the higher the temperature), the colored line is the respective scaling relationship (B: b_{RMR}; C: b_{FAS}).

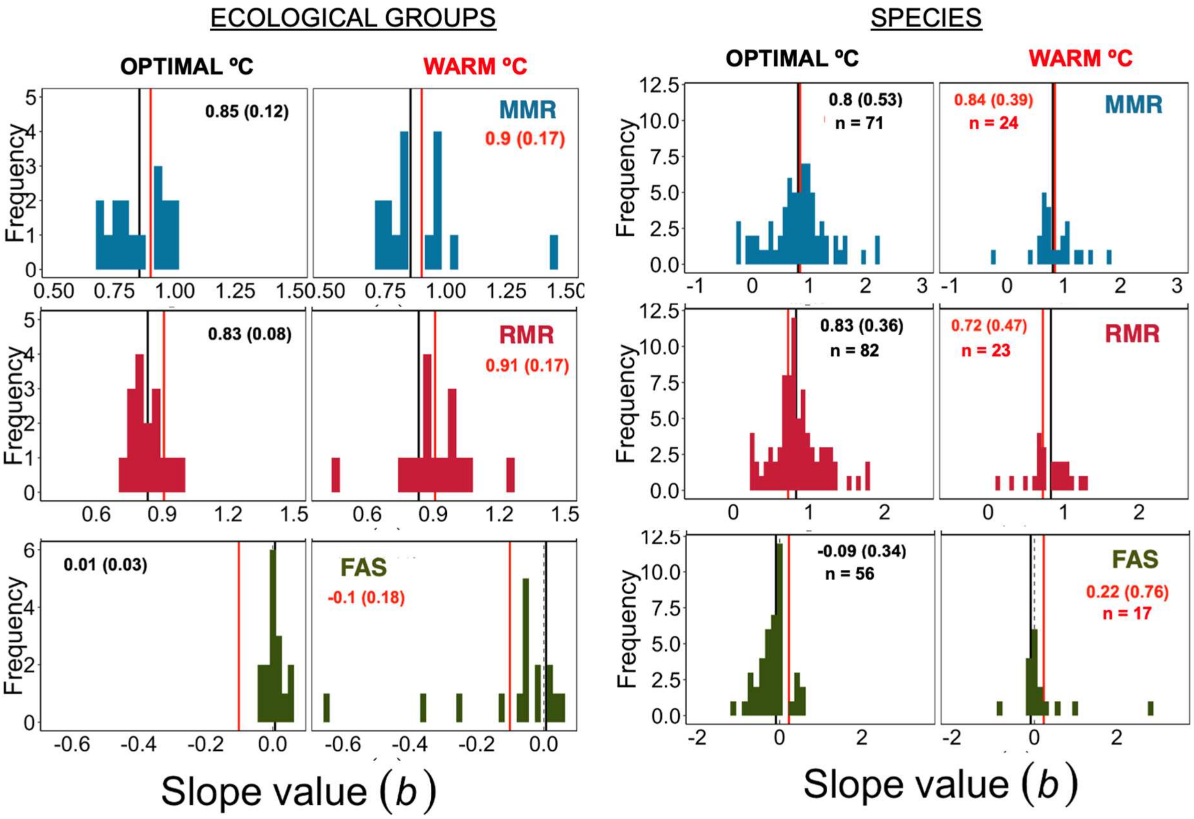

Figure 4: Histograms of metabolic scaling slopes.
Distribution of metabolic scaling slopes (MMR = blue/top, RMR = red/middle, FAS = green/bottom) observed between fish with shared ecologies (left panels), and between species (right panels), both under ecologically relevant and warm conditions. The lines indicate the mean scaling slope in warm exposed fish (red), and ecologically relevant condition (black). The slope values (and standard deviation) are plotted in each panel. Sample size of each species-specific panel are denoted on the plot. The sample size of all ecological subgroup histograms is consistent (n=16).

Metabolic scaling relationships constructed on ecological subgroups well suited for scaling suggest various degrees of vulnerability across diverse fishes. Generally, MMR and RMR scaling slopes are elevated when fish are exposed to warm ºC ($b_{\mathrm{optimal}} < b_{\mathrm{warm}}$, both MMR and RMR), which suggests a loss of body size advantage with warming (i.e., mass-specific metabolic rates go up in larger fish under warming) (Figure 5). Irrespective of thermal history (optimal and warm ºC), the interrelationship $b_{\mathrm{MMR}} < b_{\mathrm{RMR}}$ suggests decreasing estimated AS with body size, thus also constraining larger individuals' metabolic capacity. Marine fish (optimal conditions: b_{MMR} 0.78 < b_{RMR} 0.80, warm conditions: b_{MMR}

0.84 < b_{RMR} 0.88) and benthopelagic fish (optimal conditions: b_{MMR} 0.88 < b_{RMR} 0.9, warm conditions: b_{MMR} 0.97 < b_{RMR} 1) have decreasing estimated AS with body size under both optimal and warm conditions and scaling slopes elevate under warming. However, there is no evidence of increased loss of AS in marine and benthopelagic large fish with warming (Figure 5) (approximately equal elevation of both b_{MMR} and b_{RMR}).

Groups where $b_{\text{MMR}} < b_{\text{RMR}}$ emerges only under warm ºC conditions and not under optimal conditions may indicate increased vulnerability with warming. This trend ($b_{\text{MMR-warm}} < b_{\text{RMR-warm}}$; $b_{\text{MMR-optimal}} > b_{\text{RMR-optimal}}$) is shared by demersal fishes (optimal: b_{MMR} 0.77 > b_{RMR} 0.75, warm: b_{MMR} 0.71 < b_{RMR} 0.78), subtropical fishes (optimal: b_{MMR} 0.94 > b_{RMR} 0.86, warm: b_{MMR} 0.97 < b_{RMR} 0.99), and temperate fishes (optimal conditions: b_{MMR} 0.93 > b_{RMR} 0.89, warm: b_{MMR} 1.02 < b_{RMR} 1.06). Moreover, a decreasing AS with warming also emerges through a different mechanism when the MMR scaling slope drops significantly from optimal to warm conditions. This was found in fusiform fish, reef-associated fish, and demersal fish (Figure 5).

Lastly, there were no groups of species where AS would increase with body mass with warming. All scaling relationships in warm fish were $b_{\text{MMR-warm}} < b_{\text{RMR-warm}}$ or $b_{\text{MMR-warm}} \sim b_{\text{RMR-warm}}$ (Figure 5).

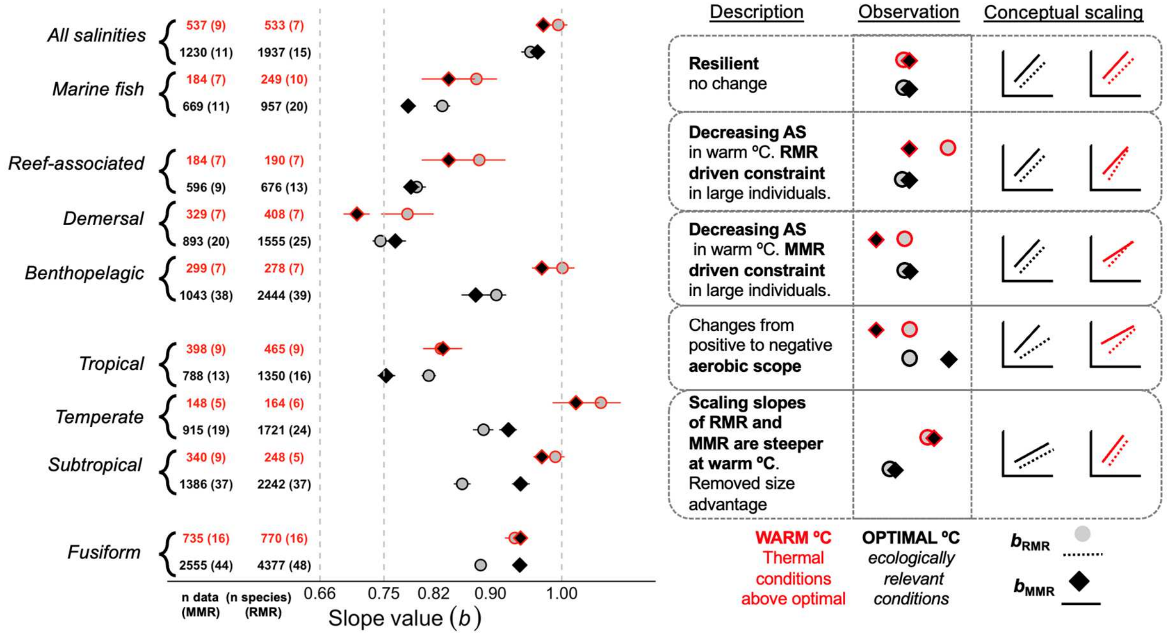

Figure 5: Variation in scaling slopes and aerobic constraints.
Variation in MMR and RMR scaling relationships between species sharing similar ecologies and morphologies. The symbols are scaling slope values (b), the error is confidence interval. Sample sizes (n datapoints (n species)) are provided on the panel (left = MMR, right = RMR). The dashed lines are marked at biologically relevant values $b = 0.66$, $b = 0.75$, $b = 1$. On the right side are described interpretations of various general patterns of MMR and RMR scaling, and a conceptual presentation of corresponding scaling patterns. Color and fill donation is explained in the legend. Plotted are only groups where data subsets were sufficient for scaling in both temperature groups, the optimal and warm.

FAS scaling slope values decreased under warming conditions compared to those under optimal conditions for every ecological and morphological group (Figure 6). Furthermore, six out of nine $b_{\text{FAS-warm}}$ were negative (all except fish in group 'all salinities' $b_{\text{FAS-warm}} = 0.02$, subtropical $b_{\text{FAS-warm}} = 0.05$, and fusiform $b_{\text{FAS-warm}} = 0.01$), compared to only two out of nine slightly negative FAS scaling relationships in fish under optimal conditions (Figure 6). Only fusiform and subtropical fish had positive b_{FAS} under both warming and optimal conditions. Maximum likelihood estimates and C.I.$_{90\%}$ {low; high} for MMR, RMR, and FAS are provided in Appendix 1, Table 5.

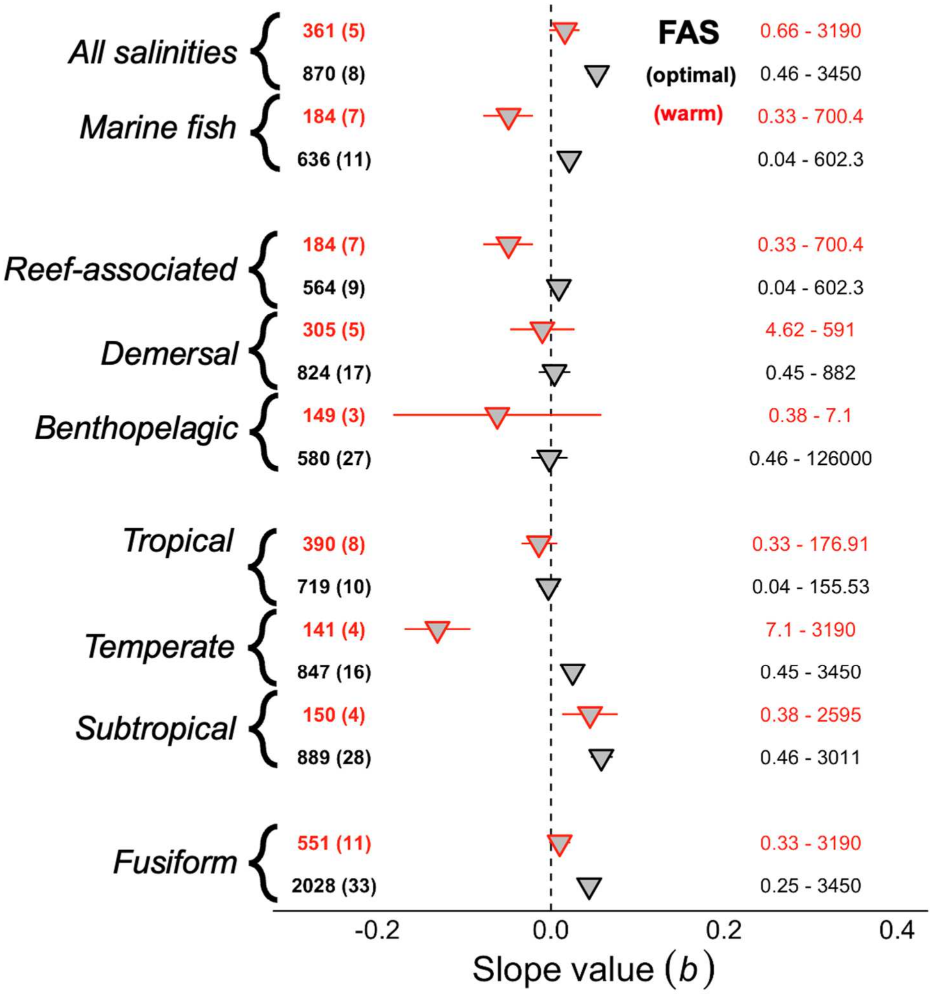

Figure 6: Scaling of factorial aerobic scopes.
Changes in factorial aerobic scope (MMR/RMR, unitless) with body mass in fish grouped by different ecologies and morphologies. Fish under optimal conditions are in black and those in warm conditions are in red. The numbers indicate: (left) n individual fish data (n species), and the range of body sizes in each subgroup (g). Grey dashed line marks scaling slope value of zero indicating no change in FAS with body size. Plotted are only groups where data subsets were sufficient for scaling in both temperature groups, the optimal and warm.

2.3.3. Mass independent measures: temperature sensitivity

The steepness of the Arrhenius slope reflects temperature sensitivity, which is expressed in activation energy (E, eV). RMR is more sensitive to temperature than MMR in fishes. Under optimal temperature conditions, the activation energy for RMR is $E_{\text{RMR-optimal}}$ =

0.444 eV, and it increased to $E_{\text{RMR-warm}} = 0.551$ eV. The temperature sensitivity of MMR changes in fish across body size but is predicted $E_{\text{MMR-optimal}} < 0.3$ eV for fish that at the time of measurement were below 1kg (95 % (5092/5362) in our database). The thermal sensitivity of MMR in warm-exposed fish is comparatively low at $E_{\text{MMR-warm}} = 0.112$ eV (Figure 7). Figure 7 describes the Arrhenius plots and conceptually presents the hypothesis and relevance of the approach.

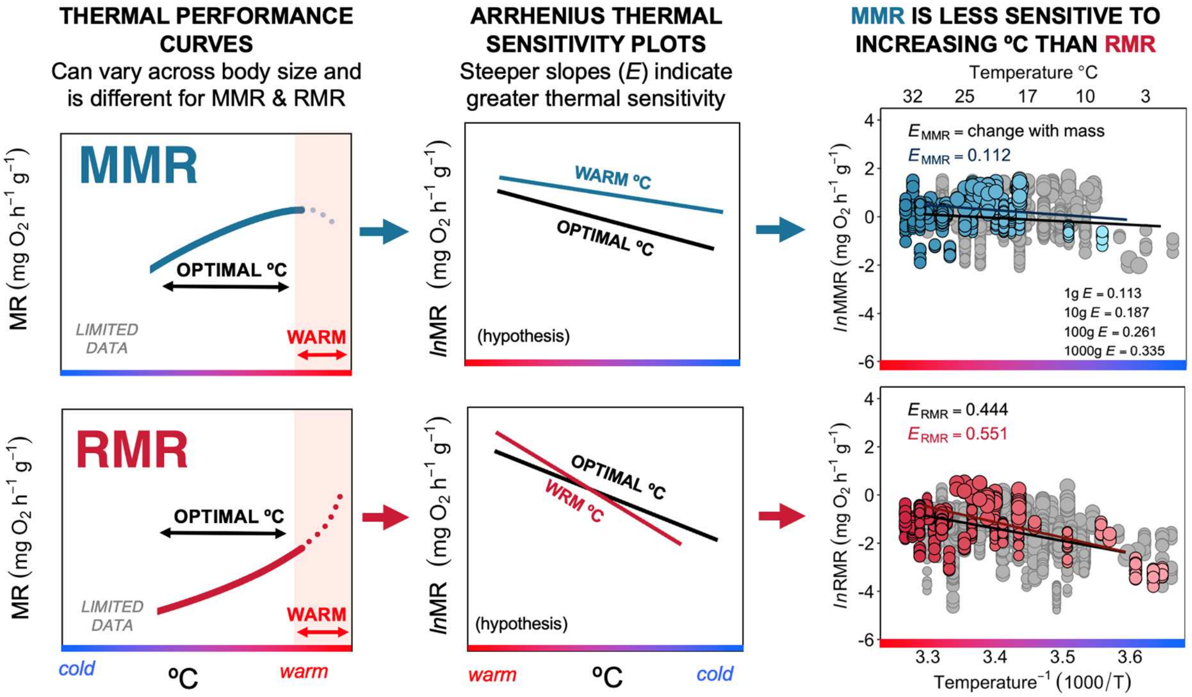

Figure 7: Conceptual view and results of thermal sensitivity of maximum and resting metabolic rates.

A presentation of our analyzed datasets and a conceptual view for an individual or species - specific thermal performance curves (left), the conceptual presentation of expected Arrhenius plot (middle), and synthesis results (right). All metabolic rate data presented are mass normalized using our estimated metabolic scaling slopes for optimal temperature group ($b_{\text{MMR}} = 0.81$, and $b_{\text{RMR}} = 0.81$) and for warm temperature group ($b_{\text{MMR}} = 0.82$, and $b_{\text{RMR}} = 0.84$), the color-stroked symbols are warm-exposed fish, and grey stroke symbols are fish from the optimal condition group.

Fishes across body mass maintain high FAS at optimal temperatures (mean = 4.74 (0.039 SE), n = 2470), but decreases were observed when exposed to warming (mean = 3.31

(0.048 SE), n = 686) (t = -23.135, df = 1670.2, p-value < 0.001) (Figure 8C). The mass normalized MMR and RMR were significantly greater in warm fish compared to fish under thermally optimal conditions (MMR: t = 11.842, df = 1261.9, p < 0.001; RMR: t = 16.694, df = 1087.5, p < 0.001). This further supports the finding that a metabolic constraint develops with body size in fish under warming.

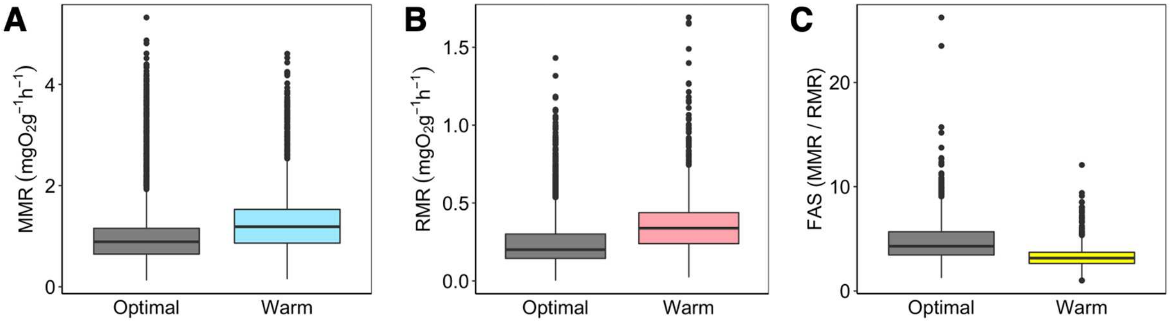

Figure 8: Mass-independent metabolic performance across temperatures.
Higher mass independent MMR and RMR, and lower FAS in fish under warm conditions compared to performance under ecologically relevant (optimal) conditions. MMR was scaled using *b* = 0.81 (optimal ºC) and *b* = 0.82 (warm ºC), and RMR was scaled using *b* = 0.81 (optimal ºC) and *b* = 0.84 (warm ºC); the maximum likelihood estimates from main mixed models. Boxes and whiskers capture the interquartile ranges, solid line is the median and points outside the whiskers are outliers (> 1.5 beyond interquartile range). All mass-corrected metabolic capacity metrics were significantly different between optimal and warm groups (t.test, p < 0.001).

2.3.4. Mass independent measures: metabolic scopes across fish with similar ecologies

Mass-independent AS differs between subgroups of fish with different Lifestyles (Figure 9A), but there is no difference between fish under warm or optimal temperatures (ΔSIC = 0, best model with ecological subgroup as independent predictor; ANOVA: χ^2 = 83.976, df = 3, p < 0.001). Specifically, mass-independent AS is different between pelagic fish and other groups of fishes: benthopelagic fish (post hoc: df = 107, p < 0.001), demersal fish (post hoc: df = 107, p < 0.001), and reef-associated (post hoc: df = 105, p < 0.001). Pelagic fish have more than double the estimated mean mass-independent AS compared to any other Lifestyle subgroup of fish (pelagic est. mean: 1.612 (0.097 SE) $mgO_2\ g^{-1}\ h^{-1}$) (Figure 9). FAS differs between fish from various Climate subcategories ($\chi^2 = 66.913$, 3, $p < 0.0001$), and their FAS is significantly lower in fish when warm exposed ($\chi^2 = 23.941$, df = 1, $p < 0.0001$) (Figure 10C). Polar fish had significantly lower FAS than any other Climate subgroup: subtropical fish (post hoc: df = 142, $p < 0.001$), temperate fish (post hoc: df = 142, $p < 0.001$), and tropical (post hoc: df = 148, $p < 0.001$). A mild difference emerges between FAS of subtropical and temperate fish (post hoc: df = 107, $p = 0.071$). FAS and mass specific AS do not significantly differ within any other ecological and morphological category (Figures 9, 10).

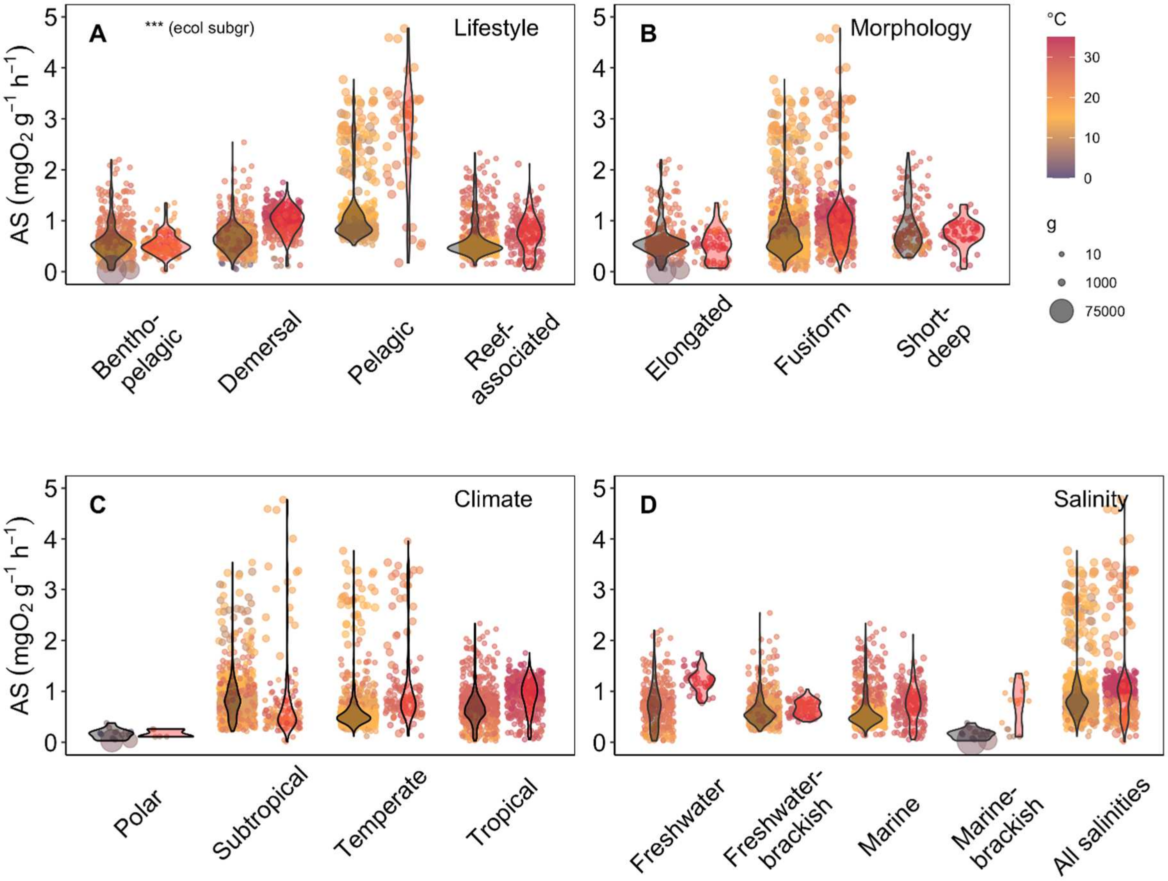

Figure 9: Variation in aerobic scope in fish with different ecologies.

The variation in mass-independent individual fish aerobic scopes (AS = MMR - RMR) across different ecologies and morphologies, and in fish exposed to different thermal conditions (ecologically relevant and warm ºC). Individual AS were scaled using *b* = 0.82 (optimal ºC) and *b* = 0.78 (warm ºC). Aerobic scopes of individual fish are grouped in one of the sub-categories under each panel (black violin = optimal conditions, red violin = warm conditions). The color of the dot shows the temperature at which metabolic rate measurements were taken (MMR and RMR to derive AS); the size of each symbol represents the relative body mass of the individual. *** indicates significant effect of subgroups.

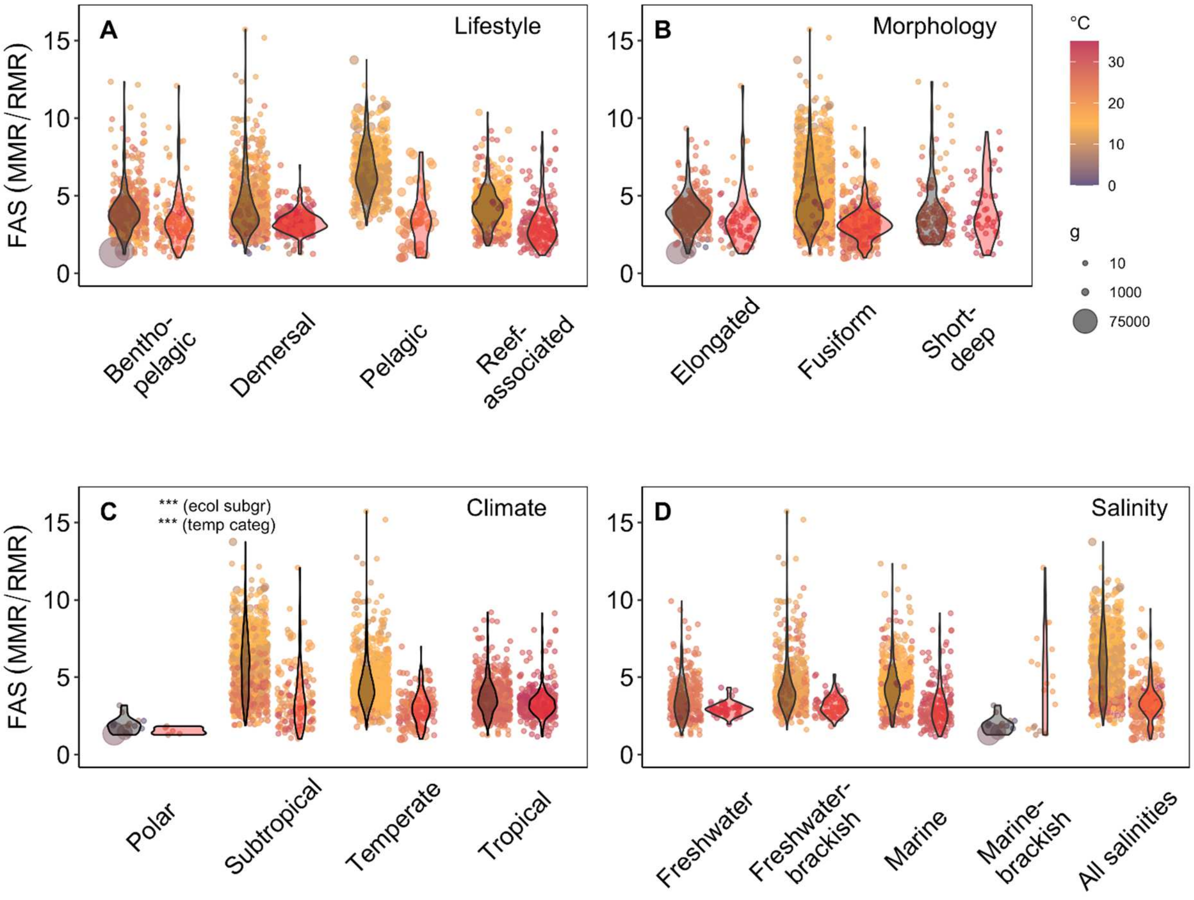

Figure 10: Variation in factorial aerobic scope in fish with different ecologies.
The variation in individual fish factorial aerobic scopes (FAS = MMR / RMR) across different ecologies and morphologies, and in fish exposed to different thermal conditions (ecologically relevant and warm ºC). Factorial aerobic scopes of individual fish are grouped in one of the sub-categories under each panel (black violin = optimal conditions, red violin = warm conditions). The color of the dot shows the temperature at which metabolic rate measurements taken (MMR and RMR to derive AS); the size of each symbol represents the relative body mass of the individual. *** indicates significant effect.

2.4. DISCUSSION

We estimated the metabolic scaling relationships using individual fish maximum and resting metabolic rates to present allometric scaling of MMR, RMR, and aerobic scope in fish under ecologically and physiologically optimal conditions as well as warming. We show temperature-dependent allometric scaling of metabolic rates, which are different for MMR and RMR and are different under optimal and warm thermal conditions (Figure 11). Under optimal temperature conditions, scaling slopes of MMR change with temperature, where slope elevates with increasing temperature ($b_{\text{MMR-optimal}} < 0.9$ within ecologically relevant range; $b_{\text{MMR-optimal}} = 0.72$ at 0ºC and $b_{\text{MMR-optimal}} = 0.86$ at 30ºC). RMR scales with $b_{\text{RMR-optimal}} = 0.81$ under optimal conditions. Exposure to a warm temperature (acute and acclimation) elevates scaling slopes of both MMR and RMR and removes the interactive effect between MMR scaling and temperature ($b_{\text{MMR-warm}}\ 0.82 < b_{\text{RMR-warm}}\ 0.84$). These results are against the common hypothesis that $b_{\text{MMR}} > b_{\text{RMR}}$ (Darveau et al., 2002; Glazier, 2005). The lower scaling slopes of MMR than RMR and the estimated allometric scaling of aerobic scope ($b_{\text{AS-optimal}} = 0.82$) suggest that larger individuals have a lower mass-specific metabolic capacity to invest in vital activities (e.g., locomotion, foraging, digestion, reproduction). This effect is stronger under warm conditions ($b_{\text{AS-optimal}}\ 0.82 > b_{\text{AS-warm}} = 0.78$). However, these metabolic scaling relationships describing fish taxa embrace substantial variability associated with species, their ecologies, morphologies, and lifestyles. We begin untangling fish metabolic scaling to identify vulnerable and understudied groups of species, populations, or communities and discuss potential concerns to fisheries given our findings.

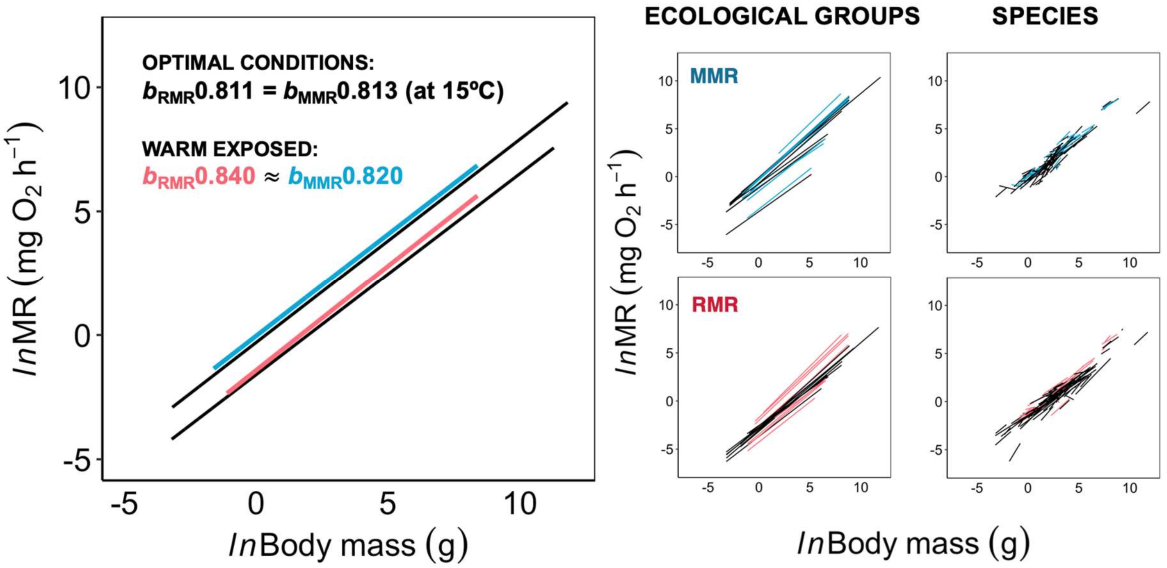

Figure 11: Temperature effects on metabolic scaling in all fishes together, across ecologies, and species.
Metabolic scaling relationships of MMR and RMR under optimal and warm conditions across different levels of biological categorization. Large panel show scaling in fish taxa (all fish together), the right-side panels show scaling of MMR and RMR in ecological subgroups (Climate: polar, temperate, tropical, subtropical; Salinity conditions throughout an animal's lifespan: marine, all salinities; Lifestyle: demersal, benthopelagic, pelagic, reef-associated; Morphology: fusiform), and species. Scaling relationships for ecological subgroups and species were established separately for each group. Black lines are scaling relationships for ecologically relevant, optimal conditions, and colored lines indicate warm-exposed fish.

2.4.1. Metabolic scaling theories, hypotheses, and empirical evidence

Multiple theories and empirical frameworks have conceptualized the metabolic scaling relationship with body mass. Metabolic Theory of Ecology (MTE) advocates for a common metabolic rate scaling slope of $b = 0.75$ shared by all taxa (Brown et al., 2004). However, MTE does not explicitly differentiate MMR and RMR within the framework. The Metabolic Level Boundary hypothesis (MLB) suggests that b varies between two extremes of $b = 0.66$ and 1 and depends on a species-specific general metabolic level. According to MLB, when metabolic rate is limited by surface area, the b will be closer to 0.66 (resting and sedentary animals), and when metabolic rate is limited by energy-demanding tissue mass, the *b* will approach 1 (during activity and species with highly active lifestyles) (Glazier, 2005). MLB hypothesis incorporates metabolism scaling of active individuals, but it becomes difficult to disentangle the overlap between activity as it relates to routine lifestyles of different species (intra-specific level) and activity describing MMR of a particular individual (inter-specific level). We overcome this challenge by having MMR and RMR of the same individual animals and by collating metabolic rates across diverse species. Alternatively, the mechanistically detailed allometric cascade model has conceptualized that MMR scales near $b \sim 1$, and this model supports variability in metabolic scaling relationships in animals at different physiological states, maximum activity, and while resting.

The common scaling frameworks, MTE, MLB, and the allometric cascade model, do not directly address how MMR and RMR shape aerobic scope (AS, FAS) changes with animal body size. Given that both MLB and the allometric cascade model predict $b_{\mathrm{MMR}} > b_{\mathrm{RMR}}$, we initially expected to observe an increase in AS and thus no growing constraint with increasing body mass. Concernig to fishes, the current evidence suggests that standard metabolic rate scales allometrically with $b = 0.89$ (Jerde et al., 2019) and that temperature and activity both decrease scaling slopes (Rubalcaba et al., 2020). Following these recent findings, we alternatively expected to observe $b_{\mathrm{MMR}} < b_{\mathrm{RMR}}$ and decreasing scaling of RMR and MMR with temperature in fish under optimal conditions and lower scaling slopes of RMR and MMR in warm exposed fish.

We found support as well as contrasting results for each prediction. Under optimal conditions, the b_{MMR} increased with temperature but did not exceed $b = 0.9$ within a biologically relevant temperature range (0 - 40ºC), while RMR scaled with relatively low

$b_{\text{RMR-optimal}} = 0.81$. Both scaling slopes, RMR and MMR, increased in warm exposed fish. Therefore, these findings do not follow the prediction and observations that $b_{\text{MMR}} > b_{\text{RMR}}$ with b_{MMR} approaching 1 (Darveau et al., 2002; Glazier, 2009, 2005) and also showed an opposite than expected pattern with temperature. Our metabolic scaling slopes describing different ecology and morphology categories ranged between 0.693 and 1.055 (specific ranges: RMR-optimal 0.738 and 1.001, RMR-warm, 0.783 and 1.055; MMR-optimal 0.693 and 1.017, MMR-warm 0.712 and 1.020), which are within the bounds of predictions by MLB (*b* range between 0.66 and 1.0). Our RMR and MMR scaling relationships merged with $b_{\text{SMR}} = 0.89$ or scaling of standard metabolic rates in fish (Jerde et al., 2019): $b_{\text{SMR}} > b_{\text{RMR}} \geq b_{\text{MMR}}$. This trend likely emerged because *i)* our dataset is a further expansion of that used by Jerde et al. (2019), *ii)* SMR is measured in non-reproductively active, resting, post-digestive fish, but by alleviating the rigor of data inclusion criteria from SMR to RMR, some greater than SMR level metabolic rate measurements are included, *iii*) if MMR scales < SMR than RMR would be expected to be between b_{MMR} and b_{SMR}. Between all scaling relationships that we established (MMR and RMR), the MTE predicted $b = 0.75$ was the most common slope value falling within the 90% confidence interval limits of our slope parameters. *Common* scaling relationships describing physiology in a given taxon, or even all animals together, are useful, and they have been successfully applied in theoretical and applied ecology (Brown et al., 2004). However, generalizations could have negative consequences (e.g., skewed estimates of fisheries productivity; Barneche et al., 2018). Therefore the intra-specific variation in metabolic scaling should not be overlooked.

2.4.2. Variation in metabolic rates and mass scaling: optimal thermal conditions

Fish with different ecologies can have distinct metabolic scaling relationships that are not always apparent unless directly tested. The inter- and intra-specific variation of MMR and RMR scaling slopes ($b_{\mathrm{MMR}} = b_{\mathrm{RMR}}$, $b_{\mathrm{MMR}} < b_{\mathrm{RMR}}$, and $b_{\mathrm{MMR}} > b_{\mathrm{RMR}}$) and relationships between FAS and size allowed us to begin identifying fish species with specific ecologies in which larger body mass may come with a potential metabolic constraint (e.g., $b_{\mathrm{MMR}} < b_{\mathrm{RMR}}$, a lower predicted AS with increasing mass). Demersal and reef-associated fish had comparatively lower scaling slopes of MMR and RMR with no change in aerobic scopes (demersal: b_{MMR} 0.77 ≈ b_{RMR} 0.75; $b_{\mathrm{FAS}} = 0$; reef-associated: b_{MMR} 0.79 ≈ b_{RMR} 0.80; $b_{\mathrm{FAS}} = 0.01$). Statistically indistinguishable scaling slopes of MMR and RMR were also found in fish that can encounter all salinity conditions within their lifetime (All salinities: b_{MMR} 0.97 ≈ b_{RMR} 0.96; $b_{\mathrm{FAS}} = 0.05$), but these were one of the steepest slopes observed. These tight scaling relationships between MMR and RMR and the significant positive relationship between RMR and MMR may indicate a direct physiological link between these performances and the co-evolution of both traits (Auer et al., 2017). If RMR sets the limit for scaling of MMR at ecologically relevant conditions, this may become a concern under warming when RMR elevates.

Alternatively, a possible constraint where aerobic scope decreases with increasing body mass was observed in tropical fish (b_{MMR} 0.75 < b_{RMR} 0.81; non-overlapping $\mathrm{CI}_{90\%}$), in short-deep fishes (b_{MMR} 0.71 < b_{RMR} 0.75), marine fish (b_{MMR} 0.78 < b_{RMR} 0.83, non-overlapping $\mathrm{CI}_{90\%}$), and benthopelagic species (b_{MMR} 0.88 < b_{RMR} 0.91). When AS decreases with body mass because of $b_{\mathrm{MMR}} < b_{\mathrm{RMR}}$, larger fish may be metabolically limited by MMR, not RMR (e.g., Sandblom et al., 2016). However, $b_{\mathrm{MMR}} < b_{\mathrm{RMR}}$ may also indicate a size-associated constraint, particularly in resource-limiting environments (Auer et al., 2020). For example, larger individuals still require more food than smaller ones, and if larger fish lose mass-specific AS, their growth capacity could suffer (Jutfelt et al., 2021). In the latter case, it would be likely to observe a decrease in body size in fish.

Alternative to absolute AS, the factorial aerobic scope (FAS = MMR/RMR) can reveal metabolic constraints because it indicates an individual's metabolic capacity with respect to its RMR (Halsey et al., 2018). FAS varied from 1.24 to 26.2 (mean = 4.74, SE = 0.039, n = 2470) and was maintained across body sizes (all fish, optimal conditions) or even showed positive trends with increasing size (ecological groups). How much FAS a fish needs to thrive likely varies across species. For example, juvenile salmonids double their RMR to digest a meal (Adams et al., 2022; Eliason and Farrell, 2014), thus a FAS ~ 3 is a physiologically relevant threshold for that group and life history stage (Anlauf-Dunn et al., 2022; Eliason et al., 2022). Pelagic species with active lifestyles had relatively higher FAS (mean (min, max) = 6.68 (3.09, 13.7), n = 502). Climate was the strongest ecological subgroup correlate factor (Figure 8), and in this group, fish with relatively low FAS < 3 even in optimal conditions were from tropical systems (24.3 %, n = 175/719) and polar (FAS < 3.17 in all, n = 15) ecological groups, compared to subtropical species (7.2 %, n = 64/889) and temperate species (8.9 %, n = 75/847). This hints at possible vulnerabilities of specialist species from stable ecosystems. The causes of context-dependent metabolic constraints are complex and likely embedded in diverse life-history strategies (Kozłowski et al., 2020).

Other species and species groups do not appear to have a metabolic constraint with increasing body size when considering only optimal conditions. These include some of the most commonly studied species, often with active lifestyles and fusiform bodies that come from the most studied climates -the temperate and subtropical zones (fusiform fish: b_{MMR} 0.94 > b_{RMR} 0.89, temperate fish: b_{MMR} 0.93 > b_{RMR} 0.89, and subtropical fish: b_{MMR} 0.94 > b_{RMR} 0.86). For example, the well-studied salmonids (*Oncorhynchus* spp., *Salmo* spp., Salmonidae) dominate the pelagic species and species that inhabit all salinities within their lifetime (i.e., anadromy). In these groups, AS increased or had no proportional change with body mass ($b_{\mathrm{MMR}} \geq b_{\mathrm{RMR}}$) (pelagic: b_{MMR} 1.02 ≈ b_{RMR} 1.00, 'all salinity' group: b_{MMR} 0.97 ≈ b_{RMR} 0.96). In salmonids, this may be expected because both high AS and larger body size can bring a direct fitness advantage to migrating adults. For example, larger salmon can faster swim speeds (Brett, 1965b), store more energy for migration (Lennox et al., 2018a), and increase their reproductive output in their once-in-lifetime spawning opportunity (Beacham and Murray, 1985). Therefore, scaling relationship patterns of $b_{\mathrm{MMR}} \geq b_{\mathrm{RMR}}$, especially in salmon, could be attributed to fish's athleticism, a phenomenon found in diverse taxa, including mammals (Darveau et al., 2002; Killen et al., 2010; Weibel and Hoppeler, 2005) and predicted by MLB.

Aerobic scope increased with body mass in freshwater fish species (b_{MMR} 1.00 > b_{RMR} 0.80) but not in marine species (b_{MMR} 0.78 < b_{RMR} 0.83), possibly suggesting that large freshwater fish may be less vulnerable to stressors compared to large marine fish (Comte and Olden, 2017). Further, an interesting trend emerged comparing fish that inhabit different salinity habitats. Aerobic scopes derived from b_{MMR} and b_{RMR} decrease in marine fish but not in fish from other salinity conditions (freshwater: b_{MMR} 1.00 > b_{RMR} 0.8, freshwater-brackish: b_{MMR} 0.83 > b_{RMR} 0.75). Fish can spend up to 30% of their RMR on osmo- and ion-regulation, and relative metabolic costs can differ with body size, salinity conditions, and activity (MMR versus RMR) (Rao 1968; Ern et al. 2014). These results may indicate that large marine fish spent proportionally less energy on osmo- and ion-regulations when active compared to when at rest. Whether there is a body size associated limitation of osmo-and ion-regulation in fish from diverse salinity conditions presents a fruitful venue for future work examining mechanisms responsible for metabolic scaling in aquatic animals.

The scaling relationships of temperate, fusiform, and freshwater species support the widespread prediction that $b_{\mathrm{MMR}} > b_{\mathrm{RMR}}$. These scaling relationships were the most robust with the largest sample sizes and were built on well-studied species commonly selected for scaling studies. Future studies may expand these boundaries by studying uncommon species with differing ecologies.

2.4.3. Sources of variation in metabolic scaling

Morphological and physiological features that are critical to support metabolic rate and scale with body mass could explain the allometric scaling of RMR and MMR. Many plausible mechanisms may partly explain the allometric scaling of metabolism, including the allometric scaling of respiratory organs and their capacity (Bigman et al., 2021; Lefevre et al., 2017; Pauly and Cheung, 2018; Weibel and Hoppeler, 2005), oxygen diffusion rates across a respiratory surface (Gillooly et al., 2016; Rubalcaba et al., 2020), hemoglobin content (Lv et al., 2018), function and morphology of red blood cells (Luo et al., 2015; Lv et al., 2018; Zhu et al., 2021), heart's capacity (Gillooly et al., 2017; Horrell et al., 2022; Weibel and Hoppeler, 2005), and the function of mitochondria (Horrell et al., 2022), Variation in scaling is likely driven by phylogenetic relatedness and is acquired through the evolution of diverse life histories and by a selection of performances that phenotypically change within a lifetime.

One of the prevailing mechanistic hypotheses for marine ectotherms is the Gill Oxygen Limitation Theory (Pauly and Cheung 2018), which postulates that hypo-allometric scaling of gill surface area (two-dimensional structure) limits a sufficient O_2 supply to support increasing O_2 demand as animals grow in size (three-dimensional bodies to support) (Pauly, 2021). The empirical support for GOLT is sparse in fish taxa, specifically for the hypothesis that the respiratory organ structure and function impose a metabolic constraint on metabolic rates, thus leading to allometric scaling of MMR or RMR (Lefevre et al., 2017; Scheuffele et al., 2021a; Seibel and Deutsch, 2020; Steinhausen et al., 2008). Supported by recent synthesis work (Scheuffele et al., 2021a), our results suggest that the dominant mechanisms of MMR and RMR scaling and any mismatches between oxygen demand and supply are species and context-dependent (Figure 11). The substantial variation in both b_{RMR} and b_{MMR} support that gill surface area is unlikely to be a limiting mechanism on lower mass-specific metabolism in larger fish.

Possibly, oxygen supply mechanisms evolved to meet maximum metabolic demands in animals across taxa irrespective of body mass (Seibel and Deutsch, 2020) or phylogeny (Hillman et al., 2013). The oxygen supply mechanism may include ventilation rates, gill morphology, diffusion rates across gills and into tissues, cardiac output, and oxygen and metabolic fuel transport capacity. In such cases, $b_{\mathrm{MMR}} < 1$ and $b_{\mathrm{RMR}} < 1$ would be associated with mechanisms that drive energy demand, at least in fish under ecologically relevant, physiologically optimal conditions, as discussed in this section. Nevertheless, the considerable variation in b_{MMR} and b_{RMR}, even in optimal conditions, warrants further work investigating the plausible mechanisms or physiological constraints that are behind diverse metabolic scaling relationships in particular groups of fish.\

2.4.4. Metabolic scaling and temperature

We found a consistent trend that the metabolic scaling slope increases with temperature. This was true for the MMR scaling relationship under optimal conditions and for MMR and RMR scaling relationships when comparing fish under optimal *versus* warm conditions. Both MMR and RMR scaling relationships increased from optimal to warm conditions in every ecological and morphological subgroup that was suited for reliable metabolic scaling (at least n = 100, and body mass range across at least one order of magnitude). Additionally, FAS scaling decreased in every ecological and morphological subgroup.

The [publicly available] data describing metabolic rates in fish that have been subjected to a temperature above their optimal ranges are not common. However, we collated a sufficient database for a first broad-scale study. The direct comparison of scaling between scaling in warm exposed versus fish under optimal conditions provides a unique opportunity to glimpse at how future warming may impact metabolic capacity in fish across size and intrinsically also life stages (Dahlke et al., 2020; Leiva et al., 2018; Twiname et al., 2020; Wootton et al., 2022). The decrease in mass-independent FAS with temperature was not surprising (e.g., Adams et al., 2022; Anlauf-Dunn et al., 2022), but the size-specific constraint in warm fish ($b_{\mathrm{FAS}} < 0$) and not those in the optimal temperature group brings, a novel contribution suggesting loss of metabolic capacity in larger fish under warming. Together, these trends agree with the large-scale observation of declining body size in fishes and the temperature-size rule that predicts a decrease in maximum body size under warming temperatures across a lifetime (Angilletta, 2004; Atkinson, 1994) and generations (Wootton et al., 2022).

We used the scaling relationships of MMR and RMR to compare their sensitivity to temperature change, acknowledging that this approach has limitations. MMR was less sensitive to increasing temperature than RMR ($E_{\mathrm{MMR}} < E_{\mathrm{RMR}}$, Activation energies in *e*V). This is opposite to recently reported findings in Rubalcaba et al. (2020) but agrees with other studies reporting less sensitive MMR than RMR in fish of the same size (Sandblom et al., 2016; Wootton et al., 2022). Activation energy is derived from the exponential thermal performance curve function (Dahlke et al., 2020), but not all performances increase exponentially across an animal's tolerance range (Sinclair et al., 2016). The continuous rise in performance is rare past an organism's optimal temperatures (Schulte, 2015; Sinclair et al., 2016). While the RMR thermal performance curves tend to follow the exponential form in ectotherms, it is uncommon in MMR and other metabolic rate performances (e.g., AS, FAS, digestion costs) (Eliason et al., 2022). Additionally, Arrhenius relationships assume that the considered physiological process is dependent on *one* rate-limiting step. Therefore, the Arrhenius plot best describes the performance of this *one* specific physiological or biochemical rate-limiting step process. This assumption does not apply to MMR, RMR, or aerobic scopes, that describe whole animal metabolic performance (Darveau et al., 2002). Alternative temperature sensitivity metrics, such as Q10 (Schulte et al., 2015) or Universal Temperature Dependence (UTD; Gillooly et al., 2001, Clarke and Fraser, 2004), also have drawbacks associated with the non-linear, context-specific thermal performance curves. The approaches to estimating temperature sensitivity of metabolic performances while incorporating mass-dependence of metabolism are not established (Glazier, 2022). This may be the next critical step in the field of ecological physiology.

2.4.5. Future directions

This study provides a robust dataset to evaluate scaling relationships. It includes diverse tropical to polar species, spans across a wide range of body sizes, and each datapoint was an individual specific metabolic rate allowing for robust inter- and intra-specific evaluation of metabolic scaling relationships. Still, 95% of fish in this dataset were < 1 kg at the time of measurement. Measured metabolic rates of large-sized Greenland sharks (Ste-Marie et al., 2020) not only fit well in our estimated scaling relationship of fish (both MMR and RMR), but their metabolic rates expectedly fell below the global scaling relationship representing their polar species ecology (Killen et al. 2010). Metabolic rates of the second-largest species, the adult salmon (*Oncorhynchus* spp.), fell above the global scaling relationships representing their high metabolic capacity and athleticism (salmon also had one of the highest mass corrected AS which they need to complete their strenuous migrations (Eliason and Farrell, 2016); pelagic species). The provided two examples reaffirm the reliability of our estimated scaling relationships and predictions of variation by species ecology.

We identified several areas for future research. The current database of MMR compiles less data than the RMR database and even fewer data for AS where both MMR and RMR are available (n = 3155, of which only 685 were in the warm condition category). A further expansion of the MMR database would decrease any ambiguity for the best MMR scaling model and its dependence on temperature and the form of FAS scaling relationship in warm conditions (is it a non-linear fit?). Lastly, we acknowledge that our models do not directly incorporate phylogenetic relatedness, which, when done, could have an influence on our scaling parameters (White and Kearney, 2014). However, a reliable phylogenetic model requires a well-informed phylogeny which is not available for all species and in fish taxa generally (Hughes et al., 2018). Extension of our work to add phylogeny is likely to remove some variation from species and nested unique test trials' random effect to account for phylogeny. Lastly, the majority of available individual data were on *i)* temperate and fusiform and *ii*) relatively small fish. We suggest that future work focuses on compiling metabolic rate measurements of large size individuals (> 300 g) across diverse species with diverse ecologies and morphologies.

The study of metabolic scaling is reinvigorated in the face of climate change because of its importance to energy flow through systems, especially systems dominated by ectotherms (Bernhardt et al., 2018; Bruno et al., 2015; Lindmark et al., 2018; Rall et al., 2012). Decreasing body size in aquatic animals in response to global warming is currently a popular research area (Audzijonyte et al., 2020, 2019; Daufresne et al., 2009; Forster et al., 2012; Gardner et al., 2011; Oke et al., 2020). This has particular importance in fish because several commercially valuable fisheries species appear to be "shrinking" in body size (Jeffrey et al., 2017; Oke et al., 2020; Tu et al., 2018). Notably, not all species and populations decrease in size, and what causes this variation remains unclear (Audzijonyte et al., 2020; Jeffrey et al., 2017). Our work suggests that temperature could change the metabolic scaling slope for MMR, but not RMR, thus implying that scaling of aerobic scope (AS) is also temperature-dependent in fish taxa (Figure 3 AB, Figure 7). At a finer scale, in diverse ecological subgroups of fishes, we found that most metabolic scaling changes are geared towards a temperature-induced constraint (Figure 5). Also, factorial aerobic scope (FAS) was generally lower in the cold (e.g., polar species) and warm temperatures (e.g., tropical species) but was higher in fish that were at ~15ºC (Figure 7C). Future work should consider temperatures outside the optimal species range to enable a more robust study of the potential links between shrinking individual body size with climate change.

It is a major challenge in synthesis work to develop broadly representative biological relationships while maintaining their relevance to lower-level biological groups, such as diverse species. This becomes particularly challenging for ectotherms across body size and temperature range because it merges two non-linear relationships that can be context-specific: the ubiquitous allometric metabolic scaling relationships (Brown et al., 2004) and the non-linear thermal performance curves (TPC) that describe how performance rates (e.g., MMR, RMR, AS, and others) change across temperature in an individual, populations, and species (Eliason et al., 2011; Kellermann et al., 2019; Scheuffele et al., 2021b). Furthermore, both the metabolic mass scaling relationships and TPC may differ between MMR and RMR and be specific to species (Figures 7, 11).

2.5. CONCLUDING REMARKS

We found that both maximum and resting metabolic rates scale allometrically in optimal thermal conditions (b_{MMR} 0.81 = b_{RMR} 0.81) and warm conditions (b_{MMR} 0.82 ≈ b_{RMR} 0.84). These common scaling relationships are ecologically and physiologically relevant and suitable for applied and mechanistic applications, including *i)* fisheries modeling (Cooke et al., 2012; Kearney et al., 2020), *ii)* fisheries management (Andersen and Beyer, 2015), *iii)* for single case studies to more robustly account for body size as a confounding factor (Glazier, 2022), *iv)* mechanistic modeling predicting ecosystem functions (trophic interactions, population densities, survival rates, food web stability (Bernhardt et al., 2018; DeLong et al., 2014), *v)* mechanistic modeling in physiology (growth rates, reproductive rates, fecundity (e.g.,(Barneche et al., 2018; Brown et al., 2004), and *vi)* ecosystem services (Barnes et al., 2018). In any of these situations, the biologically meaningful results and predictions can be influenced by the chosen metabolic scaling parameters.

We also presented convincing variability in scaling relationships of both MMR and RMR, which present a need for a context-specific scaling framework where all combinations $b_{\mathrm{MMR}} = b_{\mathrm{RMR}}$, $b_{\mathrm{MMR}} < b_{\mathrm{RMR}}$, and $b_{\mathrm{MMR}} > b_{\mathrm{RMR}}$ are plausible among diverse species, and a framework where warming may change the direction of these relationships. Body size allometry of metabolic performance does not appear to be a static biological phenomenon. This enriches the productive research avenue examining mechanisms underpinning variation in scaling across diverse taxa, temperatures, and critical physiological performances from metabolism to closely linked cardiorespiratory capacity.

CHAPTER 3: BODY SIZE AND TEMPERATURE AFFECT METABOLIC AND CARDIAC THERMAL TOLERANCE IN FISH.

3.1. INTRODUCTION

Declining body size in response to warming has been observed in many ectotherm species (Dahlke et al., 2020; Pörtner and Farrell, 2008; Pottier et al., 2022). The most vulnerable may be the smallest and largest counterparts – embryos, larvae, early juveniles, and mature, reproductively active adults (Kingsolver et al., 2011; Kingsolver and Buckley, 2020; Pörtner and Farrell, 2008) – as observed across species (Oke et al., 2020; Rubalcaba et al., 2020), and within species (Auer et al., 2021; Moyano et al., 2020). However, the physiological underpinning behind these trends remains unresolved. One hypothesis suggests that there is a temperature- and size-specific mismatch between an individual's rising metabolic demand (metabolic rate, MR) and cardiorespiratory physiology (e.g., diffusion of O_2 across the gills, heart rates f_H) responsible for supplying oxygen to the demanding tissues (Pörtner and Knust, 2007). The loss of cardiac function, specifically, is closely linked with the decline in metabolic capacity and thermal tolerance in many ectotherms (Casselman et al., 2012; Chen et al., 2019; Eliason and Anttila, 2017; Hofmann and Todgham, 2010; Somero, 2012; Stillman and Somero, 1996), thus presenting a target mechanism behind size-specific vulnerability. Furthermore, it is known that temperature and body mass can interactively affect MR (Lindmark et al., 2022; Rubalcaba et al., 2020), but the effects of body size effects on cardiac thermal tolerance are still not identified. Size-specific cardiac thermal tolerance can outline some physiological mechanisms behind size-specific vulnerability and survival.

Scaling relationships describe how body size affects a given morphological or physiological metric, such as MR and f_H (Brown et al., 2004; Schmidt-Nielsen, 1984). Metabolic rates scale positively with body mass following a non-linear power function ($MR = a BM^b$, BM = body mass, a = intercept coefficient, b = scaling exponent, scaling slope; Figure 12) (Brown et al., 2004; Clarke and Johnston, 1999; Gillooly et al., 2001; Killen et al., 2010) (Figure 12). Remarkably, all taxa could be united on a single metabolic rate scaling relationship with $b \approx 0.75$ (Brown et al., 2004), though, at a finer scale, inter-specific variation can be substantial and ecologically meaningful (Glazier, 2005; Killen et al., 2010). Scaling of f_H is less unified across taxa. However, it tends to scale negatively with body mass (cockroaches: Streicher et al., 2012; cetaceans: Blawas et al., 2021; review: Lillywhite et al., 1999) and following the reciprocal function to metabolism, $f_H = a BM^{-b}$ where $b \approx -0.25$ in mammals and birds (Dawson, 2014; Seymour and Blaylock, 2000). Although, in fishes scaling of f_H can follow a bell shape (Streicher et al., 2012) or does not scale strongly with body mass (Clark and Farrell, 2011; Farrell, 1991). These discrepancies in scaling of MR and f_H may change further when evaluated under changing temperatures and thus could explain the temperature-dependent scaling of metabolic capacity (e.g., Rubalcaba et al., 2020) and provide mechanisms of size-specific vulnerability to warming.

Besides body size, temperature is the most prominent factor governing physiological rates in ectotherms (Fry, 1971; Gillooly et al., 2001; Patricia M. Schulte, 2015). The temperature dependence of a given performance is described by thermal performance curves, TPC (Farrell, 1997; Schulte et al., 2011), which are performance-specific (Hardison et al., 2021; Kellermann et al., 2019) and typically non-linear (Figure 12). The minimum metabolic rate (RMR) representing the minimum energy required to sustain life rises exponentially with temperature; the maximum metabolic rate (MMR) rises continuously with temperature, or MMR may peak and plateau, or peak and decline. The absolute aerobic scope (AAS = MMR - RMR) that represents an individual's aerobic capacity to thrive (e.g., move, digest, reproduce) peaks at optimal temperatures (T_{opt}) and typically plummets towards both warmer and colder temperatures (Figure 12). The factorial aerobic scope (FAS = MMR / RMR) indicating a metabolic constraint often decreases linearly with temperature (Eliason et al., 2022). Similarly, the maximum f_H (f_{Hmax}) increases with warming, then the rate of f_{Hmax} increase slows as it approaches the peak temperatures (T_{PEAK}). The temperature after T_{PEAK} when the heartbeat becomes irregular (arrhythmic) is T_{ARR} (ºC) (Figure 12) (Casselman et al., 2012). The key functional temperature tolerance indices derived from TPCs of AAS and f_{Hmax} are directly linked (Anttila et al., 2013; Casselman et al., 2012; Eliason et al., 2013a). Recent studies demonstrate that the TPC for metabolic rates can change across a lifetime within the same species (Sinclair et al., 2016; Twiname et al., 2020), suggesting that also the thermal dependence of f_{Hmax} could change with life stage and thus body size. Therefore, the scaling relationships of metabolic rates and cardiac thermal tolerance may be temperature-specific.

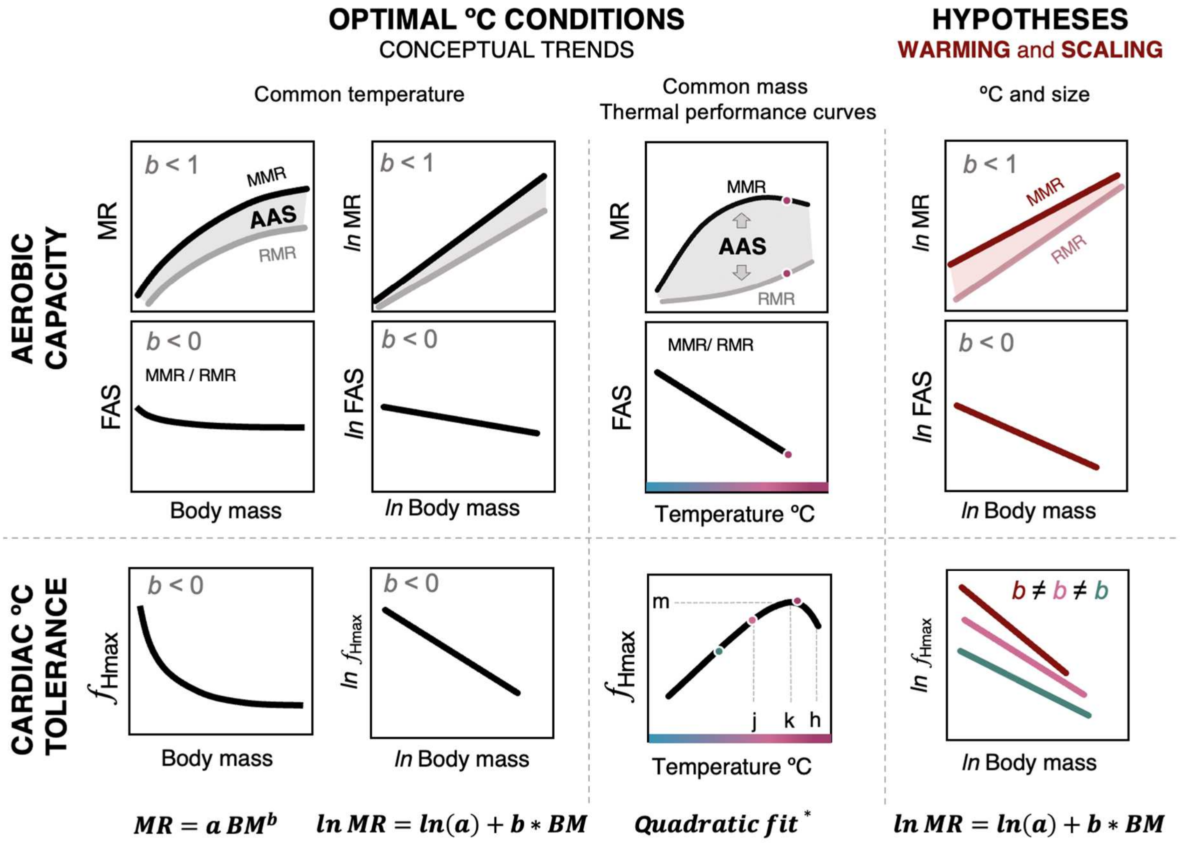

Figure 12: Conceptual presentation of body size and temperature effects on metabolic and cardiac thermal tolerance in ectotherms, and our hypotheses.

Conceptually presented the effects of body size (left panels) and temperature (middle panels) on metabolic and cardiac thermal tolerance in ectotherms. The right panel depicts our hypotheses about how temperature would modulate scaling relationships. All top plots represent maximum metabolic rates (MMR, dark lines) and minimum metabolic rates (RMR, light lines). The difference between them is the absolute aerobic scope (AAS; shaded). In the middle plots are the metabolic constraint metric and factorial aerobic scope (FAS = MMR / RMR). The bottom plots are maximum heart rates (f_{Hmax}). The equations for each panel are provided on the bottom; (*) the quadratic fits (or 2nd order polynomial fits) are commonly used to describe thermal performance curves, TPC, of physiological rates. The *b* is the scaling exponent or scaling slope and indicates the strength of the curvature in left side panels and the "tilt" of the slope in log-log plots (first panel and hypotheses). When $b = 1$ or $b = -1$, the fit is isometric (performance increases or decreases proportionally with increasing body mass); when $b = 0$, the body mass does not affect performance. The colored dot in the middle panels marks temperatures presented in the hypothesis panel. The letters on TPC of f_{Hmax} are cardiac thermal tolerance metrics: 'j' = T_{AB}, breakpoint temperature; 'k' = T_{PEAK}, the temperature at peak f_{Hmax}; 'm' = $\mathrm{PEAK}_{f\mathrm{Hmax}}$ corresponding to T_{PEAK}; 'h' = T_{ARR}, the temperature at cardiac arrhythmias. Units are not depicted; the figures are for conceptual representation only. BM = body mass, *a* = scaling intercept, *b* = scaling slope.

We studied metabolic rates and cardiac thermal tolerance in barred surfperch (*Amphistichus argenteus*), a subtropical viviparous marine fish species from thermally dynamic coastal habitats (surf-zone) (Figure 13). Barred surfperch are a good model for studying the size and life-stage specific ecological physiology because they give live birth to fully developed juvenile fish, their lifetime size range is < 3 g (laboratory-measured) up to a maximum of ~ 2.0 kg (Eschmeyer and Herald, 1999), and they remain in the same habitat throughout their lifetime. Thus, juveniles, subadults, and spawning adults experience the same thermal conditions. Metabolic rates were estimated across acute ecologically relevant temperatures (12, 16, 20, 22 ºC; Figure 13), and f_{Hmax} was measured during acute warming from 16ºC to the upper functional temperature limit, or where the heart became arrhythmic. We hypothesized that *i)* scaling of MMR will differ between temperatures, and specifically, we predicted that b_{MMR} would decrease with temperatures (Rubalcaba et al., 2020), *ii)* scaling of RMR will differ between temperatures, and specifically, we predicted that b_{RMR} would increase with temperatures, *iii)* scaling of RMR and MMR will differ, such that $b_{\mathrm{MMR}} > b_{\mathrm{RMR}}$, and specifically, we predicted that increasing temperatures would lead to more constrained AAS in larger fish (Rubalcaba et al., 2020; Verberk et al., 2021). Further, we hypothesized that *iv)* f_{Hmax} will scale negatively with body mass $b_{f\mathrm{Hmax}} < 0$ (Lillywhite et al., 1999) and that *v*) the $b_{f\mathrm{Hmax}}$ will decrease with temperature, the rationale being that PEAKf_{Hmax} is lower in larger fish. Hypotheses are conceptually presented in Figure 1. Our results provide mechanistic insight into temperature-dependent mass scaling relationships of aerobic capacity and cardiac thermal tolerance in fishes.

3.2. MATERIALS AND METHODS

All data and statistical analyses were done in R v. 4.0.4 (2021). All animal handling and holding procedures were approved under Protocol # 945 approved by the University of California, Santa Barbara Institutional Animal Care and Use Committee, and fish were collected under CDFW collection permits.

3.2.1. Animals

Barred surfperch, *Amphistichus argenteus* (N = 61) were caught in the beach zone in Santa Barbara County using a seine net (50 ft with catch bag, 30 ft no catch bag) or hook and line in April through May in 2021 (Spring experiments), and July 2021 (Summer experiments) (Appendix 2, Table 1). Fish were transported to the University of California, Santa Barbara, in aerated filtered ambient flow-through seawater (> 80 % air saturation). Wild-caught fish were kept in various size tanks (108-gal, 80-gal, 25-gal tanks; 2-13 fish per tank; Appendix 2, Table 1). Fish were grouped by size to avoid social stress between differently sized individuals. Barred surfperch are live barriers giving birth to fully developed juveniles in spring and early summer (Carlisle et al., 1960). Five females were collected gravid during spring experiments (confirmed during dissections), giving birth to 79 juveniles in the laboratory (parent females to each offspring could not be assured; > 1 gravid female per tank, Appendix 2, Table 1). Laboratory-born juveniles were transferred to 10-gal tanks at 16ºC (N = 6 to 12 fish per tank). Fish were kept at 16ºC (± 1.0ºC) using mixed chilled or heated filtered ambient seawater at > 90 % air saturation. Water quality was tested weekly using a test kit (API® saltwater master test kit) or test strips (Tetra 6-in1 EasyStrips) ($NO_2^- < 0.25$ ppm, $NO_3^- < 20$ ppm, $NH_3 < 0.25$ ppm (matching ambient water), pH = 7.7 – 8.0). The light cycle was 10D:14L throughout all experiments. Fish were fed daily to satiation with a diverse carnivorous diet (fresh or thawed mussels, thawed shrimp, squid, scallops, frozen brine shrimp, fresh sand crabs, *Emerita analoga*). Feeding was discontinued for at least 36 h before the respirometry trial. Fish were tagged with a visible fluorescent Elastomer tag (Northwest Marine Technology, Inc) to track individual-specific performance across repeat trials and provided at least a 3-day recovery between trials.

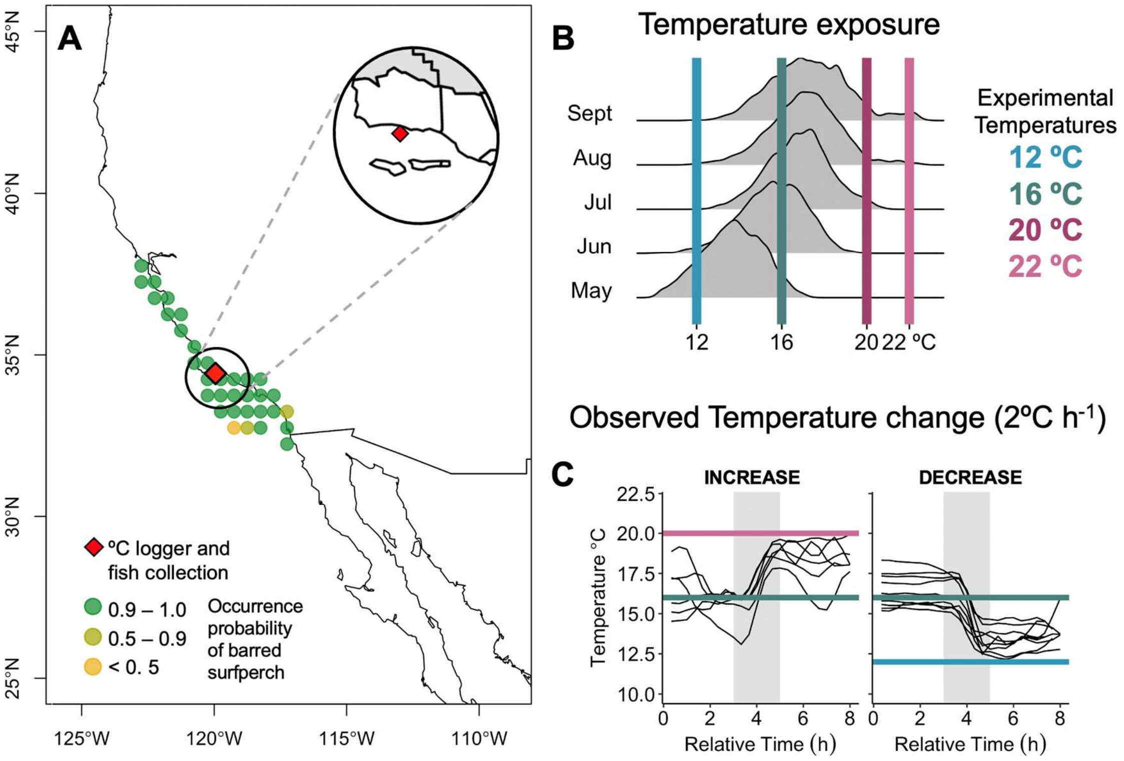

Figure 13: Habitat range and thermal conditions of barred surfperch.
The known native range of barred surfperch (**A**) and thermal conditions they experience (**B, C**). (**A**) Pacific coastline in North America with an inset that magnifies Santa Barbara and Ventura Counties (white) in California, US. (**B**) Density plots of recorded temperature at Naples Kelp Forest that describe the thermal conditions of wild barred surfperch. The data compiles five months (the total duration of this study) across years (2001 to 2021). (**C**) Continuous temperature trends across 8 hours that present ecologically relevant examples for selected acute temperature change treatments (shaded grey: decreasing temperatures from 16ºC to 20ºC (n = 9) and increasing temperatures (n = 9) at an average 2ºC h^{-1} rate). The presented native range is sourced from fishbase.org, referencing GBIF | Global Biodiversity Information Facility (GBIF, https://www.gbif.org/) and Ocean Biodiversity Information System (OBIS, https://obis.org/). Temperatures were monitored by the Santa Barbara Coastal Long Term Ecological Research program at Naples Kelp Forest (Coord. 34.42772, -119.95053). Haskell’s Beach (34.430767, -119.916717), the most common fish collection beach site, was approximately 2 km from the temperature logger.

3.2.2. Intermittent flow respirometry

Intermittent flow-through respirometry was used to measure oxygen consumption rates in individual fish. Respirometry chambers of various sizes (min 0.272 L, max 32.120 L) were custom-built to achieve a mean 42.9 (min 19.2, max 93.9) fish body mass (kg) to respirometer volume (L) ratio (Svendsen et al., 2016). Each chamber had one recirculating water loop and one flush loop, both connected to flow-controlled pumps (Ehaim compactON, Eheim universal; EHEIM GmbH & Co. KG. Deizisau, Germany) (Zhang et al., 2019). A robust fiberoptic oxygen sensor (PyroScience GmbH, Aachen, Germany) was placed in the recirculating loop. The temperature was controlled using submersible heaters and monitored using a Pt100 temperature probe (PyroScience GmbH, Aachen, Germany). Oxygen sensors and temperature probe were connected to FireSting Optical Oxygen Meter (PyroScience GmbH, Aachen, Germany). All respirometry trials were done in an environmental chamber, minimizing disturbance during the trial.

Maximum metabolic rates (MMR) were elicited following a standard chase and air exposure protocol (3-min chase, 1-min air exposure) (Little et al., 2020; Rummer et al., 2016). Chase tanks were selectively sized to allow bursting in all fish. Immediately after air exposure, fish was placed in the respirometry chamber, and their maximum metabolic rates were recorded ($\mathrm{MMR_{CHASE}}$). Fish were left in respirometers overnight on an automated 15-minute cycle of flush: measure (11:4, 10:5, 9:6, or 8:7 min, according to fish: chamber volumes and temperature), yielding > 60 $\mathrm{MO_2}$ measurements. During trials, oxygen levels were at > 70% air saturation and within ± 1ºC of experimental temperature. After the respirometry trial, fish were weighed to the nearest 0.01 g (fish > 60 g) or nearest 0.1 g (fish > 60 g), measured for length, depth, and circumference (cm), and returned to their housing tanks. Chases were performed between 0900 and 1300 h, and fish were removed from the chambers between 0700 and 0900 h. Background respiration by microorganisms was measured in empty respirometry chambers before and after each trial.

3.2.3. Acute temperature treatments

Metabolic rates were measured across four temperatures in a repeated measurement design. Fish were first tested at 16ºC (acclimation temperature), and then after an acute temperature change at 20ºC, 12ºC, and 22ºC (Appendix 2, Figure 2) (one round of trials was done in shuffled order to, confirming it did not affect results; Appendix 2, Figure 2). A higher, 24ºC acute temperature treatment was initially considered but led to 50% mortality (n = 4/8) in a group of laboratory-born juveniles. This treatment was discontinued. For the acute temperature treatments, the temperature was changed directly in housing tanks at a 2ºC h^{-1} rate by adjusting incoming flow rates of cold (10ºC) and warm (~ 20 to 22ºC) filtered seawater and by using submersible heaters. The ramp rate was selected to mimic ecologically relevant acute thermal events in kelp forests and nearshore environments along the Pacific coastline where barred surfperch live (Santa Barbara Costal Long Term Ecological Research, SBC LTER, data; Figure 13AC). Fish were kept at their treatment temperature for at least 30 minutes before chasing (± 1ºC). Because only two fish could be chased at the time, the time that fish spent in acutely changed temperature before the chase varied between ~ 30 to ~ 90 minutes. Once fish were returned to their housing tanks, the temperatures were brought back to 16ºC at the same rates (i.e., 2ºC h^{-1}).

3.2.4. Arrhenius breakpoint temperature

Arrhenius breakpoint temperature tests (ABT tests) were set up and carried out following established methods previously used on marine fish (Hardison et al., 2021;

Schwieterman et al., 2022) and described by (Casselman et al., 2012). We used a custom-built ABT test tank (33L x 20.5W x 22H cm, Igloo Playmate Elite Cooler 16 qt, filled to 12 L) that contained *i*) an elevated sling with silicone fish beds (n = 1 to 2; each with plastic straps to secure fish), *ii*) a circulation loop with flow control valve and soft plastic tubing to irrigate the gills of fish during the trial, *iii*) two air stones to keep oxygen levels at > 90% air saturation, and *iv*) heating coil connected to a Polystat recirculating heater/chiller unit (Cole-Palmer, Vernon Hills, IL, USA) to regulate the water temperature. The test tank was filled with seawater with a maintenance dose of anesthetic (65 mg MS-222 1g L^{-1} 1:1 buffered with $NaHCO_3^{-}$). Flow rates across the gills were kept between 25 ml s^{-1} and 55 ml s^{-1}, depending on fish size.

Individual fish selected for the ABT test were anesthetized in 80 mg MS-222 1g L^{-1} buffered with $NaHCO_3^{-}$, weighed to the nearest 0.01 g, and securely placed on the fish bed (laying on the side slightly tilted down and flow passing the gills). A stainless-steel Needle Tip Electrode (ADInstruments INC, Colorado Springs, CO, USA) was placed just under the skin on the ventral surface by the pericardium to detect an ECG signal. The ECG signal was amplified and filtered using Dual Bio Amp and Powerlab data acquisition system (ADInstruments INC, Colorado Springs, CO, USA) at the following settings: 60hz Notch filter; Mains filter; Low-Pass: 2Kz; High Pass: 10hz; Range: 2 mV. No more than four individuals were tested at the time.

Once all fish were positioned in the test tank, they were left undisturbed for a 30-minute equilibration period at 16 ºC. Atropine sulfate (1.2 mg kg^{-1} in 0.9% NaCl) was then injected intraperitoneally to block vagal tone, which was followed by a 15-minute equilibration period. Then, isoproterenol (4 µg kg^{-1} in 0.9% NaCl) was injected intraperitoneally to maximally stimulate β-adrenoreceptors (Hardison et al., 2021; Schwieterman et al., 2022), which was followed by the final 15-minute equilibration period. The temperature was then increased by 1ºC every 6 minutes (ramp rate 1ºC 5 min^{-1}) and held steady for 1 minute. Temperature and maximum heart rate (f_{Hmax}) for data analysis were recorded within the last 30 seconds of each 1ºC increment (i.e., minutes 5:30 to 6:00 of each temperature ramp interval). Incremental temperature ramp was continued until the heart became arrhythmic (T_{ARR}), defined by a clear transition from rhythmic to arrhythmic beating, or until missed QRS peak underlying a precipitous decrease in heart rate (Casselman et al., 2012) (Appendix 2, Table 7). This was an endpoint of the ABT test, and the fish was immediately removed from the anesthetic and euthanized for blood and organ collection.

3.2.5. Body morphology and organ analysis

The sample sizes of various morphological and organ (heart) measurements differ depending on the terminal test of the individual (Appendix 2, Table 2). Immediately, after ABT test, fish were individually euthanized, and their ventricle was excised and weighed. All euthanized fish were measured for body size metrics, including standard and fork lengths (cm), width (cm), and body mass (BM, g). Fish were sexed when possible. Barred surfperch are sexually dimorphic, but the sex-specific characteristics are not fully developed until fish reach approximately > 7 g in size.

3.2.6. Data analysis

The decreasing dissolved O_2 content (mg O_2 L^{-1}) collected during respirometry trials during each measurement cycle was plotted over time (min) and fitted with simple linear regression ('lm' in R). All linear regressions were visually assessed for quality and linearity. Only regressions with $R^2 > 0.96$ were used for analysis. The selected regression slopes were used to calculate individuals' oxygen uptake (MO_2, $mgO_2\ min^{-1}$), a proxy for metabolic rate following equation:

$$MO_2 = [(m_{\text{fish}}*V) - (m_{\text{background}}*V)] \qquad \text{(equation 4)}$$

where slope (m) is the decline of O_2 content (mg $O_2\ L^{-1}$) over time (min), and V is the volume of the respirometer (L). The background respiration levels were mean 10 % (median = 6.6 %) of individuals respiration.

Maximum metabolic rate (MMR) is often elicited after a strenuous swim, chase, or during digestion (Norin and Clark, 2016; Rummer et al., 2016; Steell et al., 2019), and standard metabolic rate or the minimum metabolic rate is measured in a post-absorptive, non-reproductively active, resting individuals (Chabot et al., 2016). Barred surfperch behaviorally respond to various stressors by laying down on their side (personal observation in field and laboratory). This was observed in the respirometers immediately after the chase, likely contributing to why 74 % MMR values were observed during spontaneous overnight activity; still, the values were comparable with those after the chase (Appendix 2, Figure 3). Additionally, five adult females from spring experiments were reproductively active. Males are reproductively active in fall, but mature gonads were not observed during dissections. Acknowledging these constraints, the AAS was calculated using RMR as a baseline of AAS, and MMR was the highest MO_2 observed at any time point during the trial. At least a 180-second slope was used to describe MMR (any steepest section for all post-chase measurements). RMR was calculated as the mean of the 10 lowest estimated MO_2 values after excluding the five lowest values from the entire trial (Chabot et al., 2016). We excluded the first 60 s of each measurement (mixing or wait period; (Rosewarne et al., 2016) but ensured that all measurements were at least 180 s long. The factorial aerobic scope (FAS) was calculated as FAS = MMR / RMR.

The electrocardiogram data from Arrhenius breakpoint temperature trials were analyzed directly in LabChart 8 (ADInstruments INC, Colorado Springs, CO, USA). Maximum heart rate (f_{Hmax}) was calculated for each 1ºC increment during 15 s (± 2 s) visually assessed measurement. The heart rate (beats min^{-1}) was calculated by automated ECG analysis tools available in LabChart 8, and each fit was confirmed visually. The f_{Hmax} values recorded before T_{ARR} were used to establish acute TPC of maximum heart rate for each fish, which was then used to calculate several cardiac performance metrics. The breakpoint at which the incremental increase in individual fish f_{Hmax} changed rates was estimated on regression $ln(f_{\text{Hmax}})$ ~ 1000/Temperature (in Kelvin) using the segmented function in R (package 'segmented'; Muggeo, 2003) and parametric bootstrap (n = 100 boot samples). The breakpoint estimate was not included when: *i*) the confidence interval of the estimated breakpoint exceeded ± 1.5ºC (n = 2), ii) the breakpoint was not statistically identified (n = 1). The temperature (ºC) corresponding to the breakpoint was calculated and is referred to as T_{AB}. The peak $\text{PEAK}_{f\text{Hmax}}$ refers to the highest f_{Hmax} recorded across all temperatures (i.e., the peak of the acute TPC of maximum heart rate), and the temperature at $\text{PEAK}_{f\text{Hmax}}$ is referred to as T_{PEAK}.

3.2.7. Statistical analysis

Mass scaling relationships were estimated for metabolic performance metrics (RMR, MMR, AAS, FAS), for cardiac physiology performances (f_{Hmax}, T_{AB}, T_{ARR}, T_{PEAK}, and $\text{PEAK}_{f\text{Hmax}}$), and between ventricle mass and body mass. All performance metrics and body mass (BM, kg) were natural log-transformed to comply with the linear form of the scaling law where b = scaling exponent defining scaling slope, and $\ln(a)$ = scaling coefficient, or the intercept (equation 5).

$$ln(\text{performance}) = ln(\text{a}) + b*ln(\text{BM}) \qquad \text{(equation 5)}$$

Consistency of scaling relationships across temperature treatments for RMR, MMR, AAS, FAS, and f_{Hmax} was tested using mixed-effect linear models ('lmer' in 'lme4' package; Bates et al., 2015). Repeated measures of individuals were accounted for by adding a random intercept effect. Cardiac physiology measures (T_{AB}, T_{ARR}, T_{PEAK}, and $\text{PEAK}_{f\text{Hmax}}$) and ventricle mass (VM) were independent and modeled using simple, generalized linear models ('lm', 'glm' functions). We also used simple linear regressions to develop temperature treatment specific (12, 16, 20, and 22ºC) scaling relationships for RMR, MMR, AAS, and FAS. In all cases, the independent explanatory variables were: body mass (*ln*BM), temperature (ºC, categorical variable), origin (laboratory-born fish, wild-collected fish, and sex (when available). The temperature was included as a categorical variable to test for differences in scaling relationships across temperature treatments, still allowing us to detect trends of thermal performance curves (we also consider that n = 4 temperatures are insufficient for robust curve analysis of TPC). We considered size class ("juvenile", < 50 g; "adult", > 50 g) as an explanatory variable. Since it had no significant effect, it was not further considered (data-deficient sets). Complementary models were compared using BIC, where the model with the lowest BIC score was accepted as the best fit (Jerde et al., 2019) (Appendix 2, Table 3). Model residuals were normally distributed, and fits were visually assessed. We acknowledge the redundancy of two statistical approaches, mixed-effect and simple temperature-specific models (e.g., Glazier, 2022; White and Kearney, 2014)). However, we chose this approach to best evaluate the consistency of the scaling relationships across temperatures and to test treatment-specific effects on scaling relationships.

The significance of body mass, temperature, sex, or origin was tested using Type II Anova ('car' package R (Fox and Weisberg, 2019)). The significance of performance between different temperatures was tested using the Tukey post hoc test ('emmeans' package in R (Lenth, 2019)). To evaluate only temperature effects on metabolic performances (RMR, MMR, AAS, and FAS) and f_{Hmax}, we obtained mass-corrected (removed allometric scaling effects, Glazier 2022) and mass-specific (units per 1 kg) performance estimates using scaling relationships from best mixed effect models. The mass-independent mean values were used to calculate the temperature sensitivity coefficient, Q_{10}, following equation 6, where R1 and R2 are the average performance values at their corresponding temperatures, T1 and T2.

$$Q_{10} = R2/R1^{(10/(T2-T1)} \qquad \text{(equation 6)}$$

We used a 95% confidence interval (CI) and standard error (SE) to report the error of mean estimates. All reported values are maximum likelihood estimates. The significance was accepted at $p < 0.05$.

3.3. RESULTS

3.3.1. Scaling relationships

Both MMR and RMR scaled allometrically with body size, and the acute temperature change only consistently impacted the scaling intercept but not slopes ($b_{\mathrm{MMR}} \approx b_{\mathrm{RMR}}$). This suggests that body size and temperature both separately affect aerobic capacity in barred surfperch, but not in an interactive manner (models with T * *ln*(BM) interaction term were all ΔBIC > 15). Specifically, MMR scaled with $b = 0.810$ {CI: 0.79, 0.83} with significantly different intercepts across temperature (Anova: *ln*(a): χ^2(df) = 463.88 (3), $p < 0.001$, Appendix 2, Table 4). The scaling slope of RMR was also consistent at $b_{\mathrm{RMR}} = 0.809$ {CI: 0.77, 0.85} with significantly different intercepts across temperatures (Anova: *ln*(a): χ^2(df) = 515.971 (3), $p < 0.001$).

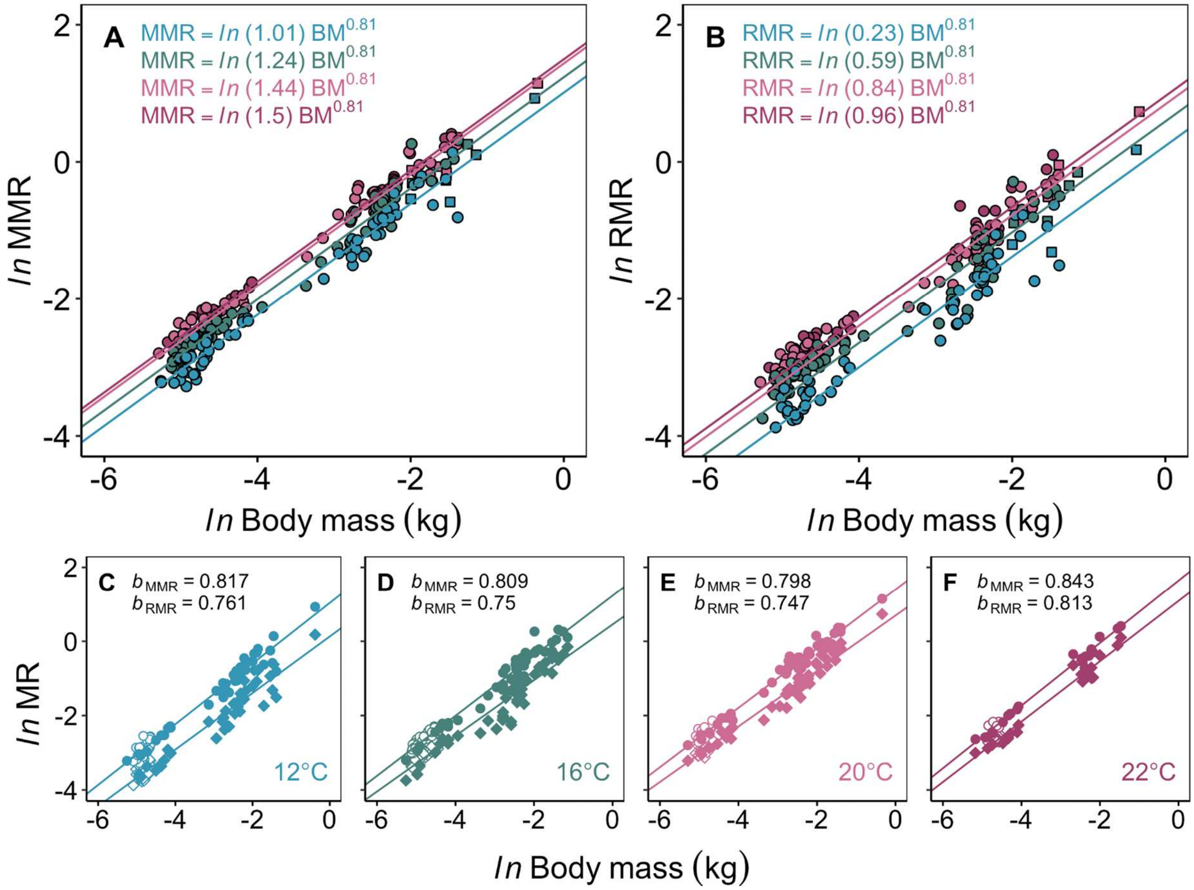

Figure 14: Scaling of metabolic rates across acute temperatures in barred surfperch.

Maximum metabolic rates (MMR, **A**) and minimum metabolic rates (RMR, **B**) scale allometrically with body mass ($b = 0.81$) and similarly across acute temperature changes (12, 16, 20, and 22ºC) in barred surfperch. Panels **A** and **B** show metabolic rates in all individuals and scaling relationships estimated using mixed models (temperature effects: intercept *ln*(a) MMR and RMR: $p < 0.001$; slope $p > 0.05$; Appendix 2, Table 4). Panels **C, D, E,** and **F** show MMR and RMR scaling relationships estimated on each temperature (color) (diamonds = RMR, circles = MMR). The difference between MMR and RMR is aerobic scope (AAS), which may be visualized as the "gap" between the plotted slopes (scaling of AAS: $b_{\mathrm{AAS}} = 0.88$, all temperatures, b_{AAS} (12ºC) = 0.878, b_{AAS} (16ºC) = 0.890, b_{AAS} (20ºC) = 0.883, b_{AAS} (22ºC) = 0.886). Fish were kept at 16ºC and were tested at each acutely changed temperature (repeat measures). The colors represent temperatures and are the same across all panels. The squares (**A, B**) mark data from reproductively active females, and the open symbols (**C, D, E,** and **F**) show data on laboratory-born juveniles.

Temperature-specific scaling relationships suggest that AAS increases slightly with body size $b_{\mathrm{MMR}} > b_{\mathrm{RMR}}$ in all temperatures, and AAS declines with temperatures (narrower "gap" between b_{MMR} and b_{RMR}) (Figure 14CDEF). This suggests that aerobic capacity does not decrease with body mass in barred surfperch. Scaling slopes of MMR ranged between $b_{\mathrm{MMR}} = 0.80$ at 20ºC and $b_{\mathrm{MMR}} = 0.84$ at 24ºC (CI for all temps 12, 16, 20, and 22 ºC ranged between $\mathrm{CI}_{2.5\%}$ 0.77 and $\mathrm{CI}_{97.5\%}$ 0.87) (Figure 14CDEF, Table 4). However, the scaling slopes of RMR were lower, with the lowest $b_{\mathrm{RMR}} = 0.747$ at 20 ºC and the highest $b_{\mathrm{RMR}} = 0.813$ at 22ºC (CI ranged between $\mathrm{CI}_{2.5\%}$ 0.71 and $\mathrm{CI}_{97.5\%}$ 0.87; Table 4). As a result, higher scaling of AAS was remarkably consistent across all temperature-specific subsets (b_{AAS} (12ºC) = 0.883, b_{AAS} (16ºC) = 0.890, b_{AAS} (20ºC) = 0.878, b_{AAS} (22ºC) = 0.886, Table 4). In addition, this consistency in AAS scaling was captured by $b_{\mathrm{AAS}} = 0.883$ {CI: 0.85, 0.92} estimated using mixed models. Opposite to our prediction, FAS did not scale negatively with body mass, which was consistent across all temperatures (b_{FAS} ranged between 0.02 and 0.056, Table 4). These results imply that larger barred surfperch do not have lower aerobic metabolic performance. Perhaps, their aerobic capacity may even slightly increase with body mass because $b_{\mathrm{AAS}} > b_{\mathrm{RMR}}$ and $b_{\mathrm{AAS}} > b_{\mathrm{MMR}}$, and FAS scaled slightly positively with body mass.

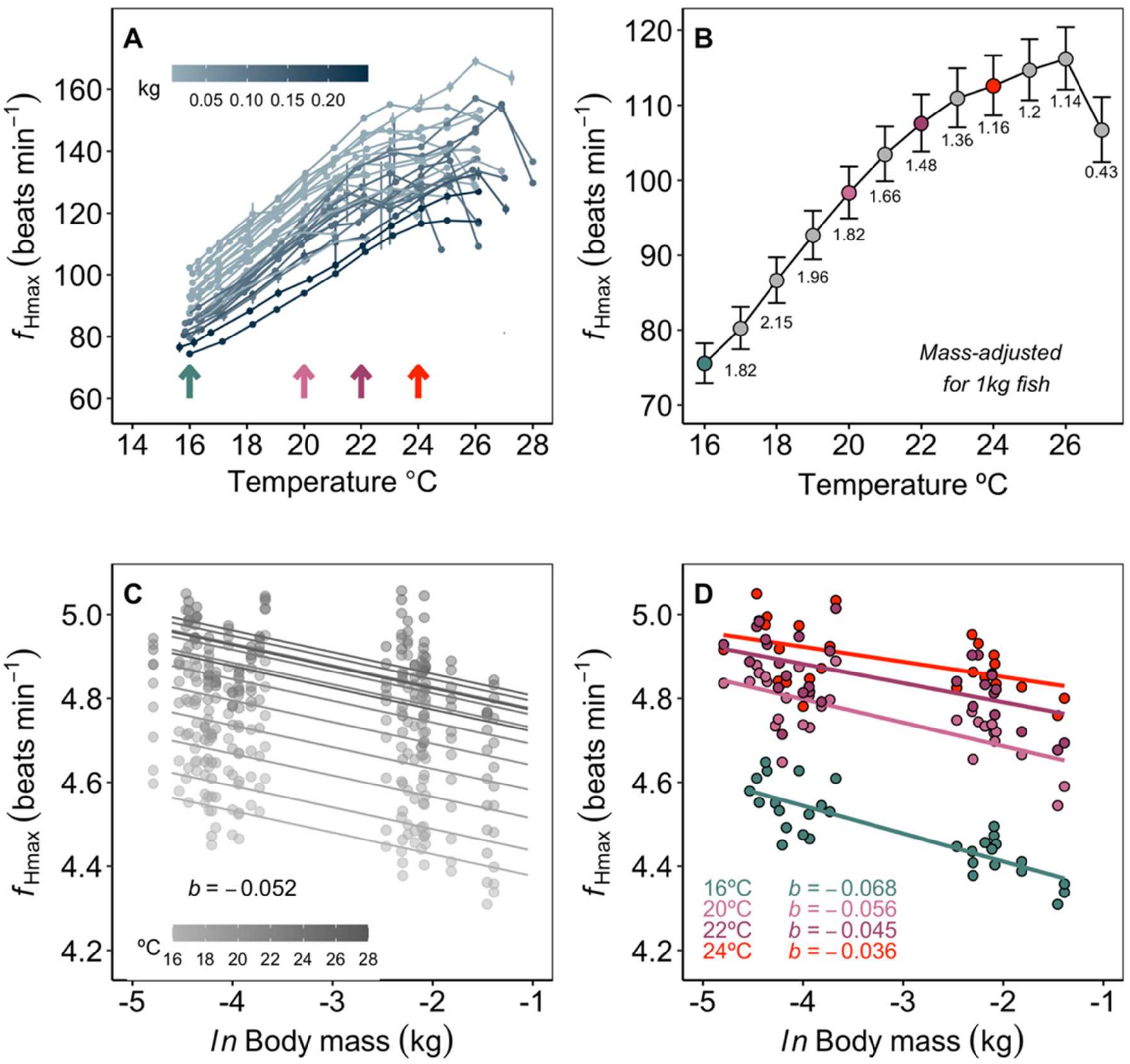

Figure 15: Negative scaling of Maximum heart rate (fHmax) in barred surfperch across temperature.

Panel **A**: Individual's f_{Hmax} across temperatures, the error is the SD of the heart rates at the given temperature, and color darkness indicates the body size (darker = larger fish, lighter = smaller fish). The temperatures at which metabolic rates were measured in the same cohort of fish are indicated by arrows. Panle **B**: Mass-independent mean f_{Hmax} across temperatures for 1kg barred surfperch. The numbers are Q_{10} for each temperature increment. Colored symbols are at temperatures at which metabolic rates were measured in the same fish. Panel **C**: Mass scaling relationships of f_{Hmax} estimated using mixed effect models, darker the color, higher the test ºC. Panel **D**: Mass scaling relationships of f_{Hmax} are estimated at 16, 20, 22, and 24 ºC separately.

The f_{Hmax} scaled consistently negatively with body mass with $b_{f\mathrm{Hmax}} = -0.052$ {CI: -0.07, -0.03} in barred surfperch. Therefore, f_{Hmax} is also significantly impacted by body size and temperature independently but without interactive effects (models with T * *ln*(BM) = ΔBIC > 45). At their acclimation temperature (16 ºC), the individual with the lowest recorded f_{Hmax} (74.399 beats min^{-1}) was 233 g, and the individual with the highest recorded f_{Hmax} (104.375 beats min^{-1}) was 12.59 g (Figure 15A). Scaling relationships on temperature-specific subsets suggested that the $b_{f\mathrm{Hmax}}$ increases, approaching zero, with increasing temperatures (b = -0.068 at 16ºC to b = - 0.036 at 24ºC; Figure 15D, Table 4).

Cardiac thermal tolerance metrics, T_{ARR}, T_{AB}, and T_{PEAK}, all similarly and positively scaled with body mass (b = 0.03 to 0.034; Figure 16ABC, and Appendix 2, Figure 4). Thus, larger fish had slightly higher cardiac thermal tolerance. The $\mathrm{PEAK}_{f\mathrm{Hmax}}$ was not significantly associated with body mass (Null model: ΔBIC = 0; Appendix 2, Table 3). Ventricle mass scaled with body mass with b = 0.854 {$\mathrm{CI}_{2.5\%}$: 0.796, $\mathrm{CI}_{97.5\%}$: 0.913} (Table 4, Appendix 2, Figure 5).

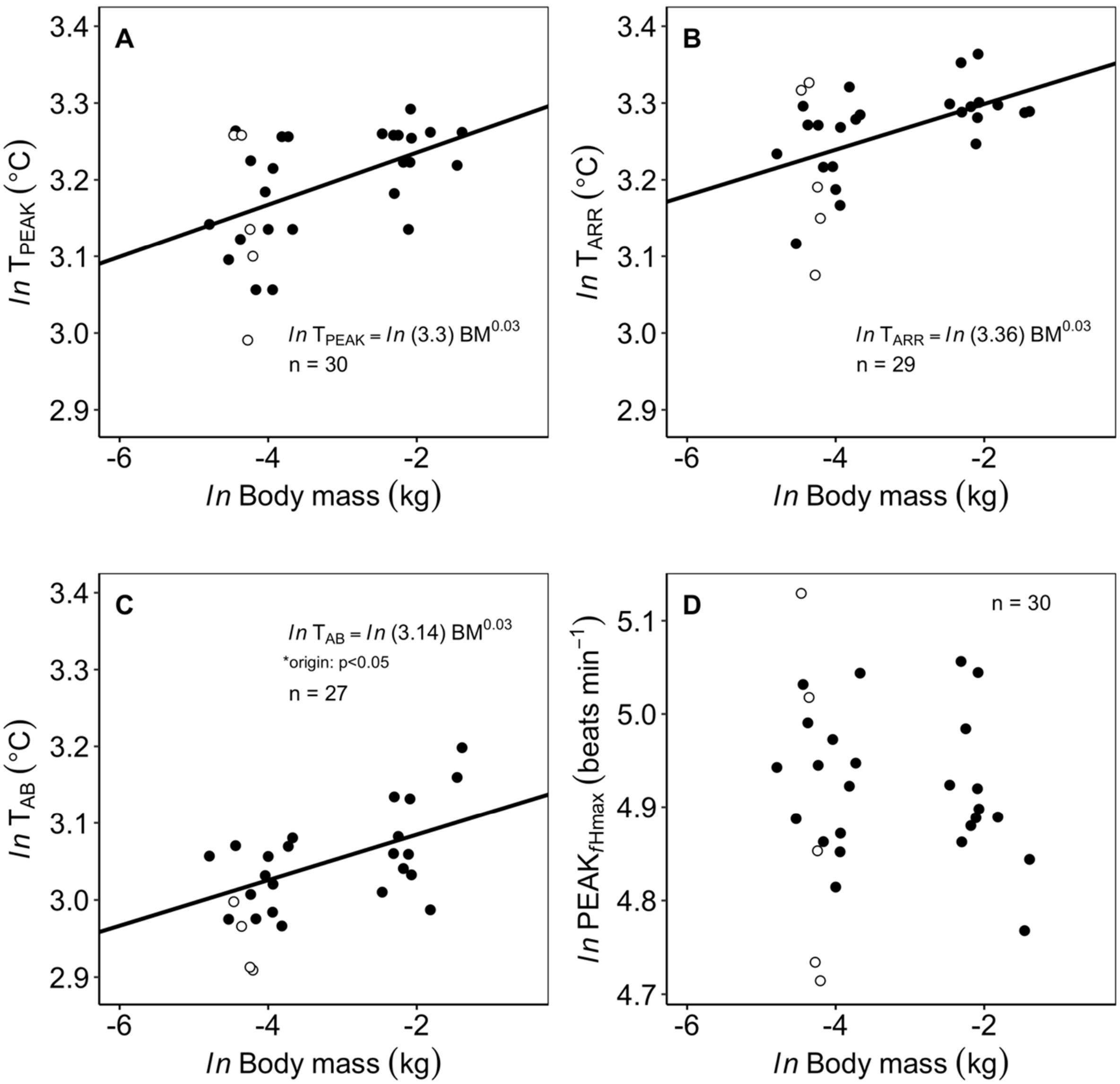

Figure 16: Mass scaling of cardiac thermal performance indices.
Plotted are T_{PEAK} (**A**), T_{ARR} (**B**), T_{AB} (**C**), f_{Hmax} (**D**). In T_{AB} (**C**), the origin of an individual – laboratory-born (open symbols) and wild-collected fish (closed symbols) – was a significant explanatory variable. The peak maximum heart rate at any temperature ($PEAK_{fHmax}$) (**D**) was not significantly explained by body mass.

3.3.2. Mass-independent temperature effects

Both MMR and RMR increased with acute temperatures between 12 to 20 ºC. The MMR was low (mean at 12ºC: 2.75 mgO_2 min^{-1} kg^{-1}, at 22ºC: 4.47 mgO_2 min^{-1} kg^{-1})

increasing significantly up to 20 ºC (post-hoc, 12 *vs.*16 ºC and 16 *vs.* 20 ºC: $p < 0.05$, Figure 17A). The mean MMR continued to increase from 20 to 22ºC, but this increase was not significant ($p = 0.180$, Appendix 2, Table 4). The RMR increased steadily across all temperatures following an expected exponential trend (mean at 12ºC: 1.26 $mgO_2\ min^{-1}\ kg^{-1}$, at 22ºC: 2.64 $mgO_2\ min^{-1}\ kg^{-1}$; post-hoc, $p < 0.05$ all temperature comparisons; Figure 17B, Appendix 2, Table 4). Additionally, laboratory-born juveniles had significantly higher RMR (origin: χ^2 (df) = 11.035 (1), $p = 0.001$). The non-significant increase of MMR above 20ºC in combination with the steady, significant increase of RMR with warming may suggest a limitation of aerobic capacity in barred surfperch above 20ºC.

The AAS changed minimally with acute temperature change (Figure 17C), while the FAS declined with increasing temperature (Figure 17D). Specifically, AAS was the highest at 20ºC and slightly non-significantly decreased at 22ºC (post hoc: 16 *vs.* 20ºC, $p = 0.008$; 20 *vs.* 22ºC, $p = 0.963$; Figure 17CD, Appendix 2, Tables 4 and 5). The mass-specific AAS estimated means were low, not exceeding 2.1 $mgO_2\ min^{-1}\ kg^{-1}$ at 20ºC, $T_{opt\text{-}AAS}$ (Appendix 2, Table 5). The FAS the highest at 12ºC (mean = 2.08; range = 1.27 min, 3.60 max), and it dropped further with every increase in temperature to its lowest at 22ºC (mean = 1.57; range = 1.29 min, 2.17 max) (Figure 17C, Appendix 2, Table 5). FAS was also lower in laboratory-born juveniles (χ^2(df) = 8.013 (1), $p = 0.005$; Appendix 2, Tables 4 and 5). Together, these results suggest that at temperatures beyond 20ºC, the aerobic capacity in barred surfperch is declining.

The shape of the TPC for f_{Hmax} followed the expected pattern, with a steady rise, peak, and fall at the thermal tolerance limit (Figures 12 and 15AB). Across all fish, the mean observed T_{PEAK} was at 24.37ºC (min = 19.90ºC, max = 26.90ºC), but the hearts became arrhythmic (T_{ARR}) soon after at mean 26.06ºC (min = 21.66ºC, max = 28.90ºC) (Appendix 2, Table 6). The observed values of these two upper thermal tolerance metrics, T_{PEAK} and T_{ARR}, varied substantially between individuals and were only apart by a mean of 1.746ºC (min = 0.47ºC, max = 3.70ºC; T_{ARR} *minus* T_{PEAK}). The observed mean $T_{AB,}$ indicating the optimal temperature for aerobic activity, was at 20.87ºC (min = 18.34 ºC, max = 24.49ºC; Figure 15B and Appendix, Table 6). Additionally, laboratory-born juveniles had lower T_{AB} (F(df) = 5.28 (1), p = 0.0306) (Appendix 2, Table 5). Notably, the cardiac thermal tolerance indices (T_{AB}) suggest that ~ 20ºC is optimal for aerobic performance, and further that the upper thermal tolerance in barred surfperch is ~ 24 to ~ 26 ºC as indicated by T_{PEAK}, and T_{ARR}, respectively.

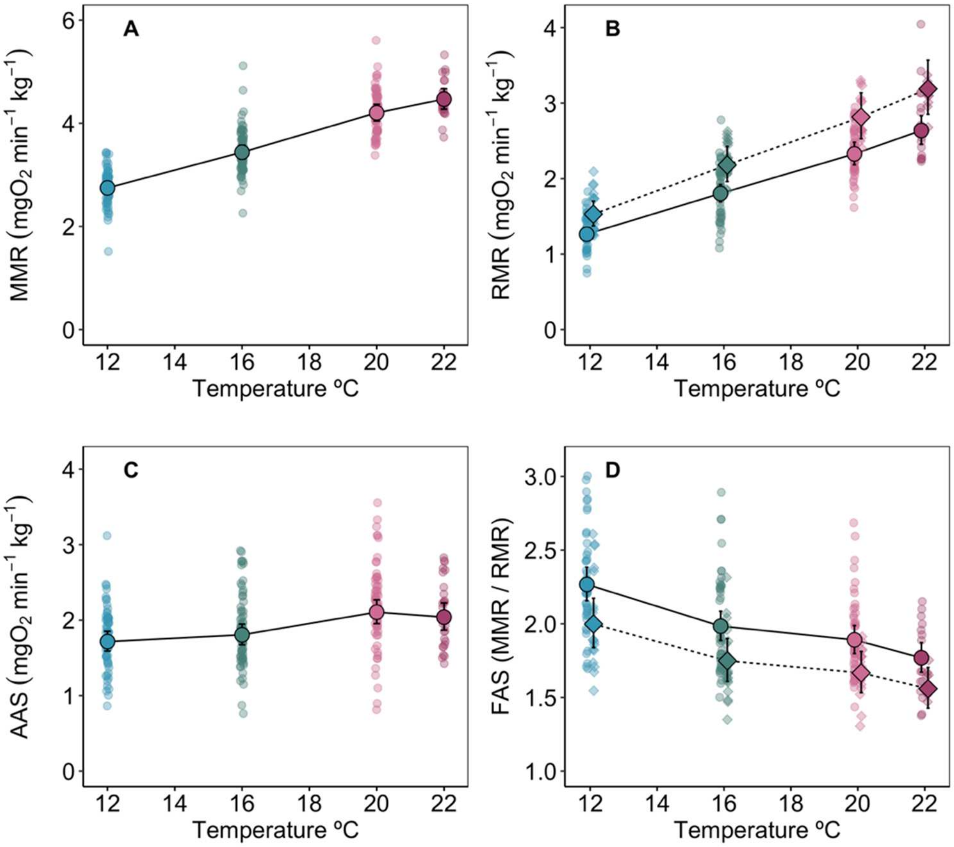

Figure 17: Mass-independent metabolic performance across temperatures (12, 16, 20, 22 ºC) in barred surfperch.

Panel **A**: Maximum metabolic rates (MMR), Panel **B**: Minimum metabolic rates (RMR), Panel **C**: Absolute aerobic scope (AAS = MMR - RMR), and Panel **D**: Factorial aerobic scope (FAS = MMR /RMR, unitless). Plotted are estimated individual (shaded symbols) fish performance and estimated means (large, solid symbols). All values are mass-adjusted to a common 1 kg body mass using parameters from the best fit mixed model for each performance. RMR was significantly higher in laboratory-born juveniles (Anova: p = 0.0009), and FAS was significantly lower in laboratory-born juveniles (Anova: p = 0.0046), which are visually depicted by diamonds and dashed lines (**B**, **C**).

The temperature sensitivity of aerobic and cardiac performances was generally low (Q_{10} ~ 2 and lower) and decreased with increasing temperatures. The RMR was the most temperature-sensitive performance, followed by f_{Hmax}, and MMR (Figure 18). The aerobic scopes (AAS and FAS) were the least temperature-sensitive metrics, with Q_{10} dipping below 1 (Figure 18D). Both MMR and RMR increased with temperature within the tested range, but after 20ºC, the rate of increase slowed (Figure 17AB and 18D). For RMR, the rate of increase was the most rapid, from 12ºC to 16º ($Q_{10\,(12\text{-}16^{\circ}C)} = 2.43$, $Q_{10\,(16\text{-}20^{\circ}C)} = 1.89$, and $Q_{10\,(20\text{-}22^{\circ}C)} = 1.87$, Figure 18D). The MMR also increased steadily and significantly across temperatures, except between 20 and 22ºC ($Q_{10} < 1.75$ all temperature comparisons, Figure 18D). The Q_{10} values for AAS were below 1.46. The f_{Hmax} peaked around 24ºC (Figure 15C and 18CD). The Q_{10} of f_{Hmax} decreased steadily across temperatures from ~ 2.0 to 1.35 and plateaued after ~ 23ºC (Q_{10} ~ 1.20) until a precipitous drop at 27ºC (Figure 15B and 18D). Lastly, considerable interindividual variation was common across all performances and temperatures.

Physiological performance	**n indiv. (n obs)**	**T, ºC**	**Scaling slope, *b* (SE)** {$CI_{2.5\%}$, $CI_{97.5\%}$}	**Intercept, *ln*(a) (SE)**
MMR (mgO$_2$ min^{-1})	83 (238)	*MM*	**0.81 (0.01) {0.79, 0.83}**	1.011 (0.039)
	66	12	0.817 (0.017) {0.78, 0.85}	1.036 (0.064)
	76	16	0.809 (0.014) {0.78, 0.84}	1.231 (0.054)
	68	20	0.798 (0.012) {0.77, 0.82}	1.401 (0.043)
	28	22	0.843 (0.016) {0.81, 0.87}	1.641 (0.062)
RMR	81 (233)	*MM*	**0.809 (0.02) {0.77, 0.85}**	0.235 (0.063)

(mgO$_2$ min^{-1})	66	12	0.761 (0.024) {0.71, 0.79}	0.13 (0.087)
	74	16	0.75 (0.022) {0.71, 0.79}	0.454 (0.084)
	66	20	0.747 (0.015) {0.72, 0.78}	0.696 (0.053)
	27	22	0.813 (0.027) {0.76, 0.87}	1.089 (0.103)
Absolute aerobic scope (mgO$_2$ min^{-1}) (MMR - RMR)	81 (233)	*MM*	**0.883 (0.019) {0.85, 0.92}**	0.541 (0.075)
	66	12	0.878 (0.027) {0.83, 0.93}	0.534 (0.098)
	74	16	0.89 (0.029) {0.83, 0.95}	0.618 (0.108)
	66	20	0.883 (0.033) {0.82, 0.95}	0.754 (0.117)
	27	22	0.886 (0.038) {0.81, 0.96}	0.736 (0.144)
Factorial aerobic scope (MMR / RMR)	81 (233)	*MM*	**0.02 (0.016) {-0.01, 0.05}**	0.819 (0.049)
	66	12	0.056 (0.018) {0.02, 0.09}	0.906 (0.065)
	74	16	0.06 (0.017) {0.03, 0.09}	0.78 (0.063)
	66	20	0.052 (0.015) {0.02, 0.08}	0.713 (0.055)
	27	22	0.028 (0.02) {-0.01, 0.07}	0.546 (0.076)
f_{Hmax} (beats min^{-1})	30 (317)	*MM*	**-0.052 (0.009) {-0.07, -0.03}**	4.325 (0.034)
	27	16	-0.068 (0.009) {-0.09, -0.05}	4.27 (0.032)
	30	20	-0.056 (0.01) {-0.08, -0.04}	4.575 (0.035)
	29	22	-0.045 (0.012) {-0.07, -0.02}	4.7 (0.043)
	26	24	-0.036 (0.012) {-0.06, -0.01}	4.78 (0.04)
T_{ARR} (ºC)	na	na	0.03 (0.01) {0.01, 0.05}	3.359 (0.037)
T_{PEAK} (ºC)	na	na	0.034 (0.012) {0.01, 0.06}	3.304 (0.041)
PEAK$_{f\mathrm{Hmax}}$ (beats min^{-1})	na	na	na	4.916 (0.018)
T_{AB} (ºC)	na	na	0.03 (0.01) {0.01, 0.05}	3.144 (0.033)
Ventricle Mass (kg)	na	na	0.855 (0.029) {0.8, 0.91}	-7.639 (0.097)

Table 4: Estimated mass scaling relationships of all measured physiological performances. All temperatures are included as a categorical explanatory variable. T = Temperature, SE = standard error, MM = mixed model, ns = not significant.

3.4. DISCUSSION

3.4.1. Aerobic metabolism scales with mass allometrically and does not consistently change with temperature.

Many ectotherms, including some species of fish, are declining in body mass with warming (Audzijonyte et al., 2020; Gardner et al., 2011). Scaling relationships of MMR and RMR together can provide mechanisms for this trend, specifically declining MMR and increasing RMR scaling slopes with temperature (Lindmark et al., 2022; Rubalcaba et al., 2020; Tan et al., 2019). When scaling relationships across temperatures are established at intra-specific levels, like barred surfperch, it can help identify how vulnerability changes in this species as individuals grow in size. Consistent b_{MMR} and b_{RMR} across a 10ºC acute temperature range (12, 16, 20, and 22ºC) and the similarity between them ($b = 0.81$) suggest that aerobic constraints do not develop with growing size under warming in barred surfperch. Further, when taking interindividual variability into account and considering temperature-specific scaling relationships, our study suggests increasing AAS with body size ($b_{\mathrm{AAS}} \approx 0.89$). The temperature sensitivity of metabolic scaling seems to be species-specific. For example, decreasing scaling slopes with temperature in round stingray (b_{RMR}, (Silva-Garay and Lowe, 2021), no change in carp species (b_{RMR}, (Li et al., 2020; Xiong et al., 2022), and variable change in Atlantic cod (b_{MMR} and b_{RMR}, (Tirsgaard et al., 2015), European perch (b_{MMR} and b_{RMR}, (Christensen et al., 2020), and yellow perch (b_{RMR}, (Enders et al., 2006). At inter-specific scales, evidence points to decreasing scaling slopes with temperature (Rubalcaba et al., 2020), which differs significantly between species (Lindmark et al., 2022). Further, previous meta-analyses demonstrated that scaling differs with an ontogenic stage (Killen et al., 2016; Norin and Gamperl, 2018) and varies based on species-specific ecologies and athleticism (a spectrum where the most non-athletic species have $b \approx 0.66$ and most athletic fusiform are at $b \approx 1$; (Glazier, 2005; Killen et al., 2010; Killen et al., 2016). In our system, the $b_{\mathrm{MMR}} \approx b_{\mathrm{RMR}}$ may be underlined by the ecology and morphology of barred surfperch. Barred surfperch of all sizes and life stages live in the surf zone (Carlisle et al., 1960), where they can excel at maneuvering with their compressed oval shape bodies (Webb, 1984). They also routinely come to the swash zone to feed on hard-shelled sand crabs forage (i.e., high routine costs, moderate digestion costs). Based on their lifestyle, barred surfperch can be considered non-athletic and be predicted to possess lower absolute aerobic scopes (high RMR, lower MMR) (Clark et al., 2013; Killen et al., 2016); together, it would explain the lower b_{RMR}, as well as and b_{MMR}. Furthermore, it would be interesting to study scaling of alternate aerobically demanding activities like digestion (Clark et al., 2013; Steell et al., 2019) to further understand how metabolic demand changes with size and temperature (Jutfelt et al., 2021). Nevertheless, at odds with our original hypothesis, the temperature insensitive $b_{\mathrm{MMR}} \approx b_{\mathrm{RMR}}$ does not suggest that larger barred surfperch have reduced aerobic capacity under acute warming.

The similarity of b between MMR and RMR was quite surprising because MMR and RMR rates are different physiological states (Darveau et al., 2002). During rest, tissue oxygen demand is lower, thus, cardiac output is decreased, and blood is distributed to visceral organs and minimally to muscle tissue (Thorarensen and Farrell, 2006), leading to lower cardiorespiratory costs (Farrell et al., 2001). In contrast, after exhaustive exercise (e.g., MMR state), the muscle is perfused near maximally, and the cardiovascular system works hard to recover physiological balance (Eliason et al., 2013b). The partitioning of these processes at each metabolic state could further change with temperature and provide mechanisms for size-specific constraints if any exist. The size-specific constraint may be shown via negative scaling of FAS (Eliason et al., 2022), which also was not present in our study. In contrast, we found a slightly positive scaling of FAS across acute temperatures. FAS scaled negatively ($b_{\mathrm{FAS}} = -0.033$) in European perch acclimated to static optimal temperatures (15ºC) for 3 weeks, and FAS dropped further to $b_{\mathrm{FAS}} = -0.067$ at warm 28ºC (Christensen et al., 2020). On the other hand, FAS did not change with warming in coral reef species (leopard coral grouper: Messmer et al., 2017). This discrepancy between studies might be due to acclimation *versus* the acute nature of temperature change or indicate species-specific responses to temperature change.

As hypothesized, we observed allometric scaling relationships ($b < 0$) for all metabolic metrics MMR, RMR, and AAS. However, our scaling relationships do not directly fit within any *universal* theories. For example, our scaling slopes were greater than $b = 0.75$ as the Metabolic Theory of Ecology (MTE) predicts (Brown et al., 2004) and were not following the predicted trend of the allometric cascade model, $b_{\mathrm{MMR}} > b_{\mathrm{RMR}}$ (Darveau et al., 2002). MTE and the allometric cascade model both consolidate many species, and so the discrepancies between these theories and our findings may emerge due to differences in scaling between endotherms and ectotherms (Gillooly et al., 2017), as well as the scales (one *vs.* many species). Recently, Rubalcaba et al. 2020 outlined another framework specific to ectotherms, where scaling slopes decrease with temperature and activity (Rubalcaba et al., 2020). Additionally, Gill Oxygen Limitation Theory (GOLT) predicts that relative gill surface decreases with increasing body size, thus, limiting sufficient O_2 supply as fish grow larger (Pauly, 2021); in the context of scaling, GOLT suggests that strong allometric scaling of gill surface area underscores allometric scaling of aerobic metabolic demands. Therefore, according to both GOLT and Rubalcaba et al. (2020), metabolic scaling slopes would decline with warming because of limited oxygen supply with growing size. In our study system, the oxygen supply was unlikely the limiting factor because neither b_{MMR} and b_{RMR} consistently changed with temperature, the $b_{\mathrm{AAS}} > b_{\mathrm{MMR}} \approx b_{\mathrm{RMR}}$, and FAS scaled positively, indicating that aerobic capacity was not limited in larger barred surfperch (Lefevre et al., 2017). Lastly, the heart function is not explicitly incorporated in Rubalcaba et al., 2020 and

GOLT, while MTE suggests a reciprocal $b = -0.25$ scaling of f_H (Brown et al. 2004). The allometric cascade model conceptualized the importance of cardiac function, predicting that $b_{MMR} > b_{RMR}$ (Darveau et al., 2002). Further study of cardiac thermal performance across body size may provide additional mechanisms behind temperature related changes in body size.

3.4.2. Maximum heart rates scale with mass allometrically and do not consistently change with temperature.

The heart is the central organ in the cardiovascular system that pumps blood across the body, providing adequate delivery of oxygen, nutrients, and hormones to the tissues and supporting the removal of metabolic waste products. The function of the heart is the key factor determining upper thermal tolerance in fishes (Eliason and Anttila, 2017). We chose to measure f_{Hmax} because the temperatures at which f_{Hmax} plateaus and the heartbeat becomes arrhythmic indicate the functional thermal limits where cardiac capacity collapses and, consequently, the aerobic capacity falls in fishes (Eliason and Anttila, 2017). Additionally, f_{Hmax} is an established tool to test T_{opt} of aerobic performance, i.e., AAS (Casselman et al., 2012), and provides ecologically relevant indices that can be used for species conservation and management (Eliason and Anttila, 2017; Moyano et al., 2020). Our study found that larger barred surfperch have lower f_{Hmax} compared to smaller individuals (negative scaling $b_{fHmax} = -0.05$, consistent across acute temperatures; $CI_{2.5\%} = -0.070$, $CI_{97.5\%} = -0.033$). The scaling of f_{Hmax} ($b = -0.05$) was weaker compared to scaling of oxygen demand, MMR, and RMR ($b = 0.81$), and all were consistent across acute temperatures. Together this finding suggests that larger size barred surfperch under an acute thermal change are not aerobically disadvantaged.

We expected to see a stronger scaling effect of f_{Hmax}. The MTE predicts $b_{f\mathrm{H}} = -0.25$, in mammals the f_{H} is reported to scale with $b_{f\mathrm{H}} \approx -0.25$ (Stahl, 1967; White and Kearney, 2014) or lower $b_{f\mathrm{H}} = -\ 0.187$ during exercise (Bishop, 1997), in flying birds $b_{f\mathrm{H}} = -0.163$ (Bishop, 1997), in lizards at 30ºC $b_{f\mathrm{H}} = -0.15$ (Bartholomew and Tucker, 1964), in terrestrial snakes at 25ºC $b_{f\mathrm{H}} = -0.229$ (Seymour, 1987), and between $b_{f\mathrm{H}} = -0.16$ and -0.34 in cetaceans (Blawas et al., 2021). However, our results align with the previous finding in fishes (Chen et al., 2018; Clark and Farrell, 2011; Lillywhite et al., 1999). A study using the same experimental protocol found $b_{f\mathrm{Hmax}} = -0.1$ in redband trout (Chen et al., 2018). Additionally, a significant body size effect on heart rates has been detected before from multivariate statistics, but the scaling exponent was not reported (f_{Hmax} in adult Arctic char and brown trout: (Mottola et al., 2020), and field f_{H} in adult Chinook salmon (Twardek et al., 2021)), and in Baltic herring embryos (f_{Hmax} (Moyano et al., 2020). In Atlantic salmon parr (~ 11 g) and post-smolts (~ 300 g) at 20ºC, the f_{Hmax} was 157 beats min^{-1} and 130 beats min^{-1}, respectively (Anttila et al., 2014). Assuming these mean values represent and comply with the f_{Hmax} mass scaling relationship, it would result in $b_{f\mathrm{Hmax}} \sim -0.06$, a very similar scaling to ours ($b_{f\mathrm{Hmax}} = -0.05$). In comparison to Atlantic salmon, we measured lower f_{Hmax} at 20ºC, specifically ~ 123 beats min^{-1} in fish < 15 g and ~ 96 beats min^{-1} in > 200 g fish. However, our $\mathrm{PEAK}_{f\mathrm{Hmax}}$ values for ~ 200 g fish (~ 122 beats min^{-1}) compare well to 115 beats min^{-1} in ~ 450 g European perch (Ekström et al., 2016); note the difference in methods). Worth noting that in our study $\mathrm{PEAK}_{f\mathrm{Hmax}}$ did not significantly relate to body mass, but it could be explained by the fact that $\mathrm{PEAK}_{f\mathrm{Hmax}}$ was achieved at different temperatures across individuals. The biological significance of the negative scaling of f_{H} and its temperature dependence is not clear yet, but certainly important to consider within and across species (Eliason and Anttila, 2017).

3.4.3. Positive scaling of cardiac performance metrics.

Surprisingly, larger barred surfperch (~ 250 g) had higher cardiac thermal tolerance than their smaller counterparts (~ 10 to 15 g, young-of-the-year). This was evidenced by positive relationships between body size and cardiac thermal tolerance indices, T_{AB}, T_{ARR}, and T_{PEAK}. Similarly, body size-related differences in T_{AB} and T_{PEAK} were found in Atlantic salmon between parr (~ 11 g) and post-smolts (~ 300 g) (Anttila et al., 2014). In their study, the smaller parr had lower T_{AB} by ~ 2.5 to 5ºC, and higher T_{PEAK} by ~ 2.5 to 3ºC, with no differences in T_{ARR} (Anttila et al., 2014). In comparison, in our study, T_{AB}, T_{PEAK}, and T_{ARR} were all lower in smaller juvenile fish by average of 1.62ºC, 1.79ºC, and 1.72ºC, respectively (juveniles considered at < 50 g; Carlisle et al., 1960). Therefore, both studies suggest that intra-specifically, the T_{opt} for cardiac performance is lower in smaller fish. In contrast, a study on cardiorespiratory capacity in Chinook salmon tested within 13 to 25ºC found cardiac arrhythmias only in the largest individuals (Clark et al., 2008; note the different methods). Together, the discussed findings across studies reaffirm that the acute thermal performance curves of f_{Hmax} are species-specific (Eliason and Anttila, 2017) and possibly also size and life-stage-specific (e.g., Pörtner and Farrell, 2008). These hypotheses need a more refined study as in this study, as we did not specifically aim to test differences in cardiac thermal tolerance across life stages and were unable to test cardiac thermal tolerance in spawning females that may be the most vulnerable (Auer et al., 2021; Dahlke et al., 2020; Eliason et al., 2020).

Heart rates are one of the two cardiac performances contributing to cardiac output ($\dot{Q} = f_{\mathrm{H}} * V\mathrm{s}$; mL min^{-1}; Vs = cardiac stroke volume). Cardiac output increases with temperature, which is predominantly controlled by increasing heart rates in fishes (Eliason and Anttila, 2017). Even still, to ensure sufficient oxygen supply with growing body size, the scaling of f_{H} could be compensated by the corresponding scaling of Vs. White and Kearney 2014 outlined that the discrepancy between the scaling of MR and f_{H} can be explained by the scaling of Vs, because increased MR can be achieved by increasing either (or both) f_{H} and V_{S} (White and Kearney, 2014); i.e., expecting reciprocal $b_{\mathrm{MR}} = 0.75$, $b_{f\mathrm{H}} = -0.25$, $b_{\mathrm{Vs}} \approx 1$, see also MTE (Brown et al., 2004). More, direct links between oxygen uptake rates (measured MR) and cardiac output (Vs and f_{H}) can be explained by Fick's equation: MR = $f_{\mathrm{H}} * V\mathrm{s}\ (\mathrm{C_aO_2} - \mathrm{C_vO_2})$; where $\mathrm{C_aO_2}$ and $\mathrm{C_vO_2}$ are oxygen content (ml dl^{-1}) in arterial and venous blood, respectively; scaling of these is not established in fishes (but see Clark et al 2008). Fick's equation states that oxygen uptake by the tissues is a product of cardiac output (thus $f_{\mathrm{H}} * V\mathrm{s}$) and the differential between the $\mathrm{O_2}$ content in arterial and venous blood (Eliason and Anttila, 2017; Farrell et al., 2009). To our knowledge, no studies directly have report scaling of V_{S}, while one study that directly estimated (and reported) mass effects on $\dot{Q}$ in fish species (rainbow trout, *O. mykiss*) found isometric scaling ($b_{Q} = 1$; $\dot{Q}_{\mathrm{max}}$ increase by 48.53 mL min^{-1} kg^{-1}, and $\dot{Q}_{\mathrm{min}}$ by 20.39 mL min^{-1} kg^{-1}, but both proportionally with mass (Thorarensen et al., 1996)). In our study, the $b_{\mathrm{MR}} = 0.81$ and $b_{f\mathrm{H}} = -0.05$, that may suggest that cardiac stroke volume scales with body mass with ~ 0.85 [$b_{V\mathrm{s}}\,(0.85) + bf_{\mathrm{Hmax}}\,(-0.05) = b_{\mathrm{MR}}\,(0.80)$] (White and Kearney, 2014). Whether this would lead to corresponding scaling of $\dot{Q} \approx 0.81$ partly provide support for $b_{\mathrm{MMR}} \approx 0.81$ in barred surfperch may be examined next. Additionally, higher Vs is supported by larger relative ventricular mass, VM (Franklin and

Davie, 1992), which in barred surfperch scaled with $b_{\mathrm{VM}} = 0.854$; matching if assuming $b_{V\mathrm{s}} = 0.85$). Therefore, allometric scaling of Vs would not be entirely surprising in our fish. Importantly, these are only cautiously outlined ideas that should be examined empirically as the Vs and the contributions of f_{H} to $\dot{Q}$ in this species is unknown. Similarly, the scaling of $\dot{Q}$, Vs, C_aO_2, or C_vO_2 in our species is not known (e.g., Clark et al., 2008). Nevertheless, this discrepancy between the scaling of MR and f_{Hmax} is intriguing and may be studied further.

Other cardiac physiological and morphological metrics could help identify the limitations or trade-offs associated with body mass and temperature. For example, animals with larger ventricles relative to their body mass have higher aerobic scopes (Gillooly et al., 2017)(Farrell, 1991), greater V_{s} (Franklin and Davie, 1992), and thus greater aerobic capacity. In comparison, our $b_{\mathrm{VM}} = 0.85$ was lower than found in freshwater fishes, including freshwater perches ($b = 0.939$ (Edmunds et al., 2018), salmonids ($b \sim 1$ (Farrell et al., 1990), or more broadly across endotherms and ectotherms (mammals, birds, fishes, amphibians, and reptiles; $b_{\mathrm{VM}} \sim 0.9$, (Gillooly et al., 2017). Isometric and weaker scaling would support $b_{\mathrm{MMR}} > b_{\mathrm{RMR}}$ because larger relative ventricular mass allows for greater cardiac power output that can support high metabolic rates during activity (Darveau et al., 2002; Hochachka et al., 2003). Additionally, it is interesting that the ventricle size had a stronger scaling exponent than any other physiological performance measured in our study (Figure 12) because we observed higher cardiac thermal tolerance in larger fish (*see next section*). The differences among mass scaling of cardiac performances, aerobic metabolism, and ventricle mass warrant further study.

3.4.4. Mass-independent temperature affects aerobic and cardiac performances.

The acute thermal performances of MMR, RMR, AAS, FAS, and f_{Hmax} together indicate a decline in functional thermal tolerance beyond ~ 20ºC, an emerging T_{opt} for this species (Figures 14A, 16, and 17C). There was no clear T_{opt} for MR metrics, which is characteristic in eurythermal species (common killifish: (Healy and Schulte, 2012), brook trout (Durhack et al., 2021), cutthroat trout (Anlauf-Dunn et al., 2022), and European perch (Jensen et al., 2017). However, somewhat surprising were the low RMR and MMR (mean 2.33 and 4.20 $mgO_2 \, min^{-1} \, kg^{-1}$ at 20ºC, respectively), resulting in low aerobic scopes (mean AAS = 2.11 $mgO_2 \, min^{-1} \, kg^{-1}$ at 20ºC), and FAS (2.27 and lower). Still, they are comparable with its close relative, striped surfperch (*Embiotoca lateralis*, family Embiotocidae), in which MO_2 varied from low ~ 1.3 mgO_2 $min^{-1} \, kg^{-1}$ swimming at 0.5 body lengths s^{-1} to ~ 3 $mgO_2 \, min^{-1} \, kg^{-1}$ swimming maximally in 11ºC (Cannas et al., 2006). The maintained aerobic performance across temperatures was also reflected in relatively low Q_{10} values in all performance metrics ($Q_{10} < 2$, MMR, FAS, AAS; Fig 7D), except for RMR (Q_{10} = 2.0 to 2.5). The Q_{10} of f_{Hmax} dropped from $Q_{10\,(17\text{-}18ºC)} = 2.15$ (n = 30) to $Q_{10\,(25\text{-}26ºC)} = 1.14$ (n = 20) within the temperature tolerance range but agreed with values observed in fishes (Eliason and Anttila, 2017) and closely resembled those found in the similarly sized Atlantic salmon (Q_{10} ~ 2.3 to 1.3) (Anttila et al., 2014). Therefore, the aerobic metabolism performance was generally less temperature-sensitive than f_{Hmax}, signifying the importance of cardiac thermal tolerance that supports aerobic capacity.

Both MMR and RMR increased with temperature, with only MMR slightly declining at acute 22ºC, so oxygen supply to demanding tissues is unlikely to limit the thermal tolerance in barred surfperch (Patricia M. Schulte, 2015). The decline in MMR was still sufficient to suggest declining AAS beyond 20ºC. Also, T_{AB} (the ºC where the f_{Hmax} first stops increasing at the same rate with warming) was ~ 20ºC (mean < 21ºC). Therefore, results agree with the commonly found overlap of T_{AB} and optimal temperature for aerobic scope, $T_{opt\text{-}AAS}$ (Anttila et al., 2013; Casselman et al., 2012; Ferreira et al., 2014). The aerobic and cardiac performances fell above 20ºC – the AAS began to decline at 22ºC, FAS was < 2 at 22ºC, the peak f_{Hmax} was reached at ~ 24ºC and cardiac arrhythmias were observed at ~ 26ºC. Additionally, at 24ºC, we observed mortality in juveniles during a discontinued respirometry trial. Together, the upper thermal tolerance in barred surfperch was ~ 24 to ~ 26 ºC as indicated by T_{PEAK} and T_{ARR} and mortality, while aerobic capacity suffered > acute 20ºC in our species (Eliason and Anttila, 2017).

Several mechanisms could explain the declining performances beyond 20ºC. In most fishes, the heart relies on oxygen supply delivered by venous blood returning from systemic circulation (Davie and Farrell, 1991). During warming and activity, the systemic oxygen demand and tissue O_2 extraction increase, leaving less O_2 for the ventricle (Ekström et al., 2016; Eliason et al., 2013b; Eliason and Anttila, 2017). Therefore, one reason for cardiac failure in fishes can be insufficient venous O_2 (partial pressure and content) to support the production of ATP in the heart tissue (Eliason et al., 2013b). For example, in European perch, cardiac failure, particularly the plateau and consecutive fall of f_H with warming, was directly associated with a low partial pressure of venous O_2 (Ekström et al., 2017). Furthermore, in their study, the absolute thermal tolerance (CTmax) and the temperatures at which f_H peaked overlapped (Ekström et al., 2017). That aligns with our results, where $PEAK_{fHmax}$ and mortality were both observed at ~ 24ºC. Furthermore, the temperatures at which f_{Hmax} plateau and begin to fall indicate where the scope for heart rate (maximum – resting f_H) is essentially zero in fishes (Eliason et al., 2013b; Eliason and Anttila, 2017) triggering a decline in maximum aerobic capacity. Notably, also in barred surfperch, the mean T_{PEAK} was ~ 22ºC suggesting that declining aerobic capacity with warming is triggered by a limitation in maximum heart rate. It would be interesting to study mechanisms behind cardiac failure with temperature, especially in the context of scaling, because we found positive correlations between mass and T_{AB}, T_{ARR}, and T_{PEAK} (e.g., Clark et al., 2008).

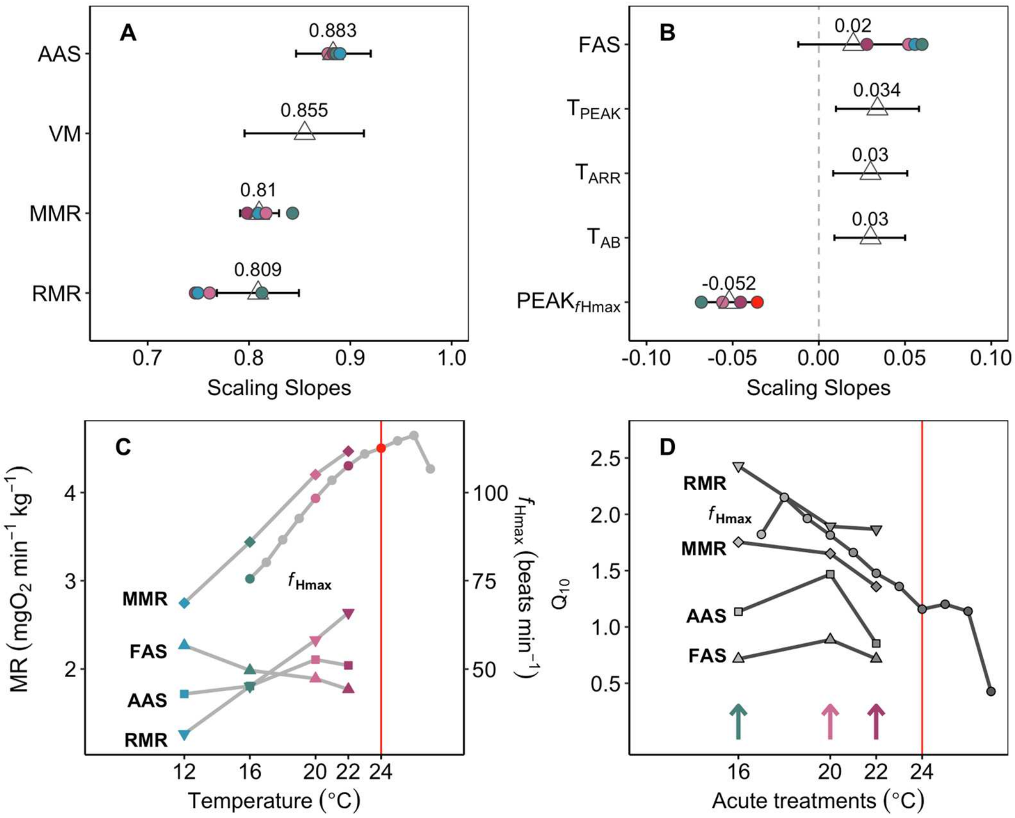

Figure 18: Variation in temperature-specific scaling and thermal performance curves across physiological performances in barred surfperch.
Mass scaling slopes of metabolic performance and cardiac performance were not significantly different across temperatures (mixed effect model results) but varied between performances (A, B). Triangles are scaling slope estimates with corresponding values denoted above, and the error is a 95% confidence interval (mixed models estimates). The colored circles show scaling relationships estimated on temperature-specific subsets of data. Panels C and D present thermal sensitivities of different mass-corrected (to 1 kg fish) physiological performances. Red symbol (C) and red line (D) mark 24ºC, a temperature at which 50% mortality was observed during a respirometry trial; this treatment was discontinued. Abbreviations: AAS = absolute aerobic scope (MMR - RMR), FAS = factorial aerobic scope (MMR / RMR), T_{ARR} = temperature at which the heart becomes arrhythmic, T_{AB} = the breakpoint temperature of maximum heart rate, T_{PEAK} = temperature at which fish had the highest recorded maximum heart rate, $PEAK_{fHmax}$ = maximum heart rate in any temperature, and VM = ventricular mass.

3.4.5. Sources of inter-individual variation.

We observed a considerable variation between individual performances that can be ecologically meaningful (Bennett et al., 2019; Burton et al., 2011; S. S. Killen et al., 2016). RMR was more variable than MMR, and AAS varied the most among individuals (percent coefficients of variation, CV, across temperatures; CV_{RMR}: 15 – 19 %; CV_{MMR}: 7.77 – 12.6 %, CV_{AAS}: 21.4 – 24.8 %; Appendix 2, Table 5). The variation decreased with temperature in MMR and FAS (Appendix 2, Table 5). There are several possible explanations we can provide – *i*) the time from when the acute temperature was achieved and the time the fish was chased varied up to 1 h between individuals (due to the limitations of the experimental setup), *ii*) we used different size respirometry chambers across trials (Svendsen et al., 2016), but the same fish were repeat-tested in the same size chambers, and *iii*) once sufficiently recovered from the chase protocol, fish were spontaneously active throughout the overnight trial. Barred surfperch tend to lay on their side after the chase and air exposure (general behavior also observed in the wild, *personal communication*), and their higher activity overnight could likely resemble their active lifestyles living in the surf zone. MMR from spontaneous activity overnight, but not elicited by the chase protocol, has been observed in other fish species (e.g., Kraskura and Hardison 2021). Lastly, females tested in the Spring term were pregnant, and on two occasions, the female gave birth to 2 juveniles each time (< 3 g). The born juveniles were removed from the respirometry chamber as soon as the occurrence was identified. These factors should not affect any of the biologically meaning and interpretations as all data were carefully visually assessed for quality.

3.4.6. Ecological context and relevance.

Barred surfperch are eurythermal viviparous species historically abundant within the temperatures selected in our study (12 ºC to 23ºC) (Carlisle et al., 1960). Therefore, our acute 24ºC treatment represents the near future climate change levels (Intergovernmental Panel on Climate Change, 2022). Also, the acute timescales of the temperature change of 2ºC h^{-1} are ecologically relevant and currently observed (Figure 13). The thermal extremes at both acute to chronic timescales are becoming more frequent and more severe (Frölicher et al., 2018; Guo et al., 2022) threatening coastal marine species. Barred surfperch of all sizes and across all life stages (newly born juveniles (< 3 g), spawning adults ~ 2 kg) live in nearshore surf zone habitats that are thermally dynamic systems with distinct seasonal, diurnal, and anomalous (heatwaves and upwelling) changes. Additionally, they are increasing in popularity as recreational fisheries species ("California Department of Fish and Wildlife", Enhanced Status Report, 2019), and play ecologically important roles in connecting aquatic nearshore and terrestrial communities (*personal communication*, Jessica Madden, Jennifer Dugan, UCSB). Despite this, nearly nothing is known about their physiological thermal tolerance at any life stage.

Our results suggest that smaller barred surfperch (young-of-the-year) may be the most vulnerable under acute thermal conditions surpassing 20ºC, as indicated by their lower cardiac thermal tolerance, T_{ARR}, T_{AB}, and T_{PEAK} (Eliason and Anttila, 2017). Irrespective of body size, the aerobic performances, AAS, RMR, and MMR, were maintained relatively stable from 12 to 20ºC, but > 20ºC was aerobically limiting. This is a temperature threshold that barred surfperch currently encounter in the wild (Figure 13), and suggests that they do not have much additional warming tolerance (e.g., Anlauf-Dunn et al., 2022; Sunday et al., 2014). Their current range spans from Bodega Bay, central California, to Santa Rosalia Bay in central Baja California (Carlisle et al., 1960) (Figure 12). The southern populations of barred surfperch in Baja California can experience heat waves that bring 24ºC for up to 16 h in the surf zone (Fernández-Aldecoa et al., 2019). In the laboratory, we experience 50% mortality of juveniles at 24ºC. Therefore, northward range shifts in this species are likely. Alternatively, perch from northern or southern populations may possess different functional and absolute thermal limits, that could also be size (or life-stage) specific. If barred populations are genetically different is not known. The observed inter-individual variability across performances, if repeatable at an individual-specific level, may be beneficial in ensuring that successful traits can be selected across diverse suboptimal conditions (Bennett et al., 2019).

We acknowledge that the lack of temperature-sensitive scaling in our study may be because fish were exposed to an acute temperature exposure treatment, as opposed to a full, multi-week acclimation period. For example, the mechanisms that alter the scaling slopes with temperature for both MR and f_{Hmax} may be gained through thermal acclimation of each performance (Jayasundara and Somero, 2013; Porter et al., 2022; Safi et al., 2019; Sandblom et al., 2016). In fishes, metabolic rates can take from 72 h to ~ 5 days to stabilize at a new temperature (Hanson and Stanley, 1970; Klicka, 1965); interestingly, juveniles had shorter acclimation times than adults in freshwater South American fish species (Barrionuevo and Fernandes, 1998). Likewise, the f_{Hmax} can acclimate to new temperatures within the first 48 to 72 hours (Gilbert et al., 2022, Hardison et al., *in prep*). Upwelling (cold) and heatwaves can onset rapidly and last from days to weeks, so acclimation and acute responses are both ecologically relevant and important to understand (Schulte et al., 2011). Curiously, the next step may be to explore scaling in thermally acclimated fish and evaluate the scaling of acclimation capacity (e.g., are larger individuals able to increase their thermal tolerance by a greater % than smaller counterparts).

3.5. CONCLUDING REMARKS

Within and across ectotherm species, including fish, larger animals appear to be more vulnerable to climate change, particularly to warming, compared to smaller ones (Dahlke et al., 2020; Dulvy and Reynolds, 2002; Lindmark et al., 2022; Messmer et al., 2017). A mechanistic underpinning of this trend may be a disproportionally faster increase of metabolic demands with increasing mass than an individual's ability to supply adequate oxygen to support the high demands under warming (Dahlke et al., 2020; Pauly, 2021; Rubalcaba et al., 2020). Our case study, at intra-specific level on live-bearing barred surfperch, did not support this hypothesis. We tested mechanisms that may underline size-specific vulnerability by establishing scaling relationships and found that larger barred surfperch may cope better with warming compared to their smaller counterparts. Specifically, in barred surfperch, the scaling of MMR and RMR were largely insensitive to acute temperature change within 10ºC range (12ºC, 16ºC, 20ºC, 22ºC), and slopes were parallel ($b = 0.81$) indicating no size-specific change in aerobic scopes (AAS, and FAS). We also found less strong scaling of maximum heart rates ($b_{f\mathrm{Hamx}} = -0.052$; O_2 supply mechanism) compared to the scaling of metabolic rates (O_2 demand) suggesting that oxygen supply is an unlikely constraint giving rise to allometric scaling of aerobic capacity in barred surfperch. Furthermore, larger perch outperformed smaller ones in their cardiac thermal tolerance as all indices, T_{AB}, $T_{PEAK,}$ and $T_{ARR,}$ were positively correlated with body mass. Although, the discrepancy between scaling of metabolic rates and maximum heart rates was interesting and warrants further study, the scaling of our measured physiological performances does not mechanistically suggest that larger barred surfperch are more vulnerable to acute warming.

However, aerobic metabolism (AAS, FAS, MMR, RMR) and cardiac thermal tolerance all pointed to declining aerobic capacity above 20ºC (Anttila et al., 2014; Eliason et al., 2013b; Eliason et al., 2011). This temperature is within a range that barred surfperch of all sizes, and life stages currently experience in their habitat, the shallow surf zone. A relatively low functional thermal tolerance may constrict their suitable habitat northward (Sunday et al., 2014). Barred surfperch are indicator species for ecosystem function connecting resource flow from sandy beaches to coastal waters. The declining physiological performance of this species with near future warming (Intergovernmental Panel on Climate Change, 2022) could contribute to changing ecosystem functions and functions of size-structured communities (Audzijonyte et al., 2013; Daufresne et al., 2009). Mechanistically, the limits of functional thermal tolerance above ~20ºC were triggered by a limitation in maximum heart rate in barred surfperch.

CHAPTER 4: A REVIEW OF ADULT SALMON SWIM PERFORMANCE

4.1. INTRODUCTION

Fish locomotion has strong implications for conservation and management, motivating countless studies across biological and physical science disciplines. For most fish, swimming is inherent to nearly all activities – fish swim to forage, avoid predation, catch prey, engage in social interactions, defend their territories, mate and reproduce, and migrate. All of these activities require some combination of bursting, burst-and-coasting, leaping, hovering, and steady, sustained swimming. Swimming capacity is thus a vital performance in fishes and is paramount to their ecological and evolutionary success (Langerhans and Reznick, 2010). In some fishes, such as salmonids, adults complete remarkably challenging migrations back to their natal rivers to spawn (Brett, 1965b; Tamario et al., 2019). Furthermore, in Pacific salmon with one lifetime opportunity to spawn, successful spawning migration depends on an individual's capacity for sustained and burst swimming (Brett, 1965b).

The challenges for survival and thus fitness in fishes across the globe are compounding at rapid rates due to natural and anthropogenic factors such as temperature rise, drought, changes in river flows, habitat degradation, and fragmentation (Cooke et al., 2012; Tamario et al., 2019). As a result, many salmon populations are increasingly vulnerable, threatened, or endangered (*Endangered Species Act of 1973, As Amended through the 108th Congress* 1973; Irvine et al., 2005; Crozier et al., 2019). These environmental stressors can have profound effects on the salmon spawning migration. A recent extreme example of an acute ecological change is the 2018 Big Bar Landslide on the Fraser River, the largest salmon-producing River in British Columbia, Canada. This landslide was unpassable to adult salmon for several months of the year and entirely prevented many salmon populations from completing their spawning migration (Government of Canada, 2019b). Emerging from this acute conservation disaster was a pressing need to understand the maximum swimming (bursting) capacity of adult migrating Pacific salmon across species, and populations, in the presence of secondary intrinsic stressors (e.g., sex and body size) and across environmental conditions (e.g., temperature, disease). Intra- and inter-specific maximum swimming capacity data are essential to predict passage success in any freshwater system and to inform necessary mitigation plans to facilitate individual movement across barriers (Birnie-Gauvin et al., 2019).

Ecological physiologists and conservation biologists have extensively studied swim performance and swimming energetics for decades producing a wealth of knowledge previously summarized in various comprehensive reviews (e.g., Kieffer, 2000; Plaut, 2001; Kieffer, 2010). This review was motivated by raised questions regarding swimming capacity and passage probability of adult Pacific salmon after the Big Bar Landslide. Our primary objective was to review the literature and collate the maximum swim performance of adult salmonid species (Pacific salmon, *Oncorhynchus* spp., steelhead or rainbow trout *O. mykiss*, or Atlantic salmon, *Salmo salar*). We present the current known maximum swim performance in adult salmon, focusing on inter-and intra-specific variation. We also identify major knowledge gaps in adult salmon swim performance and outline a diverse range of research topics addressing them. Further, these results may be used to develop management and mitigation plans to overcome conservation challenges, including habitat fragmentation, drought, fish passage design, and landslides. At a broader scope, this review contextualizes fish swim performance and discusses the implications of swimming studies in applied fisheries management.

4.1.1. Evaluating fish swim performance

Fish swimming is measured in the context of exercise physiology (Eliason et al., 2013a; Eliason and Farrell, 2016), locomotion kinematics (Lea et al., 2016), hydrodynamics and robotics (Lauder, 2015), and conservation and management (Rodgers et al., 2019; Cooke et al., 2020; Bett et al., 2022). Fishes display diverse body forms and fin shapes that produce a spectrum of locomotion types (e.g., body-caudal swimming, paired fin swimming (Webb, 1984). Similarly, fish engage in various swimming modes, including steady swimming, burst-and-glide, fast start acceleration, and maneuvering, which can be used strategically to maximize swimming efficiency (Beamish, 1978; Fish, 2010). This flexibility in swimming allows fish to be effective at predator avoidance (Ghalambor et al., 2004), jumping across waterfalls (Lennox et al., 2018b), or traversing several thousand-kilometer migrations (Crossin et al., 2004). We discuss fish swimming in the context of exercise physiology and fisheries management and conservation.

4.1.2. Modes and energetics of fish swimming

Salmon migrations vary in their difficulty (Crossin et al., 2004; Abe et al., 2019; Crozier et al., 2019), but to reach the spawning grounds, it takes a combination of sustained swimming, unsteady burst and coast, and maximum burst swimming (Hinch and Rand, 2000; Lauritzen et al., 2010; Miyoshi et al., 2014; Bett et al., 2022) (Figure 19). Sustained swimming is common for daily behaviors, foraging, exploring new environments, hovering, and steady swimming against low flows, and it does not lead to fatigue (Brett et al., 1958).

The unsteady swimming mode consists of sustained swimming interspersed with rapid bursts, turns, and consecutive burst-and-coast episodes (Dutil et al., 2007), eventually leading to fatigue. Sprinting, bursting, jumping, and predator escape responses are unsustainable, physiologically exhausting swimming modes that quickly lead to fatigue (Black, 1958; Kieffer, 2000).

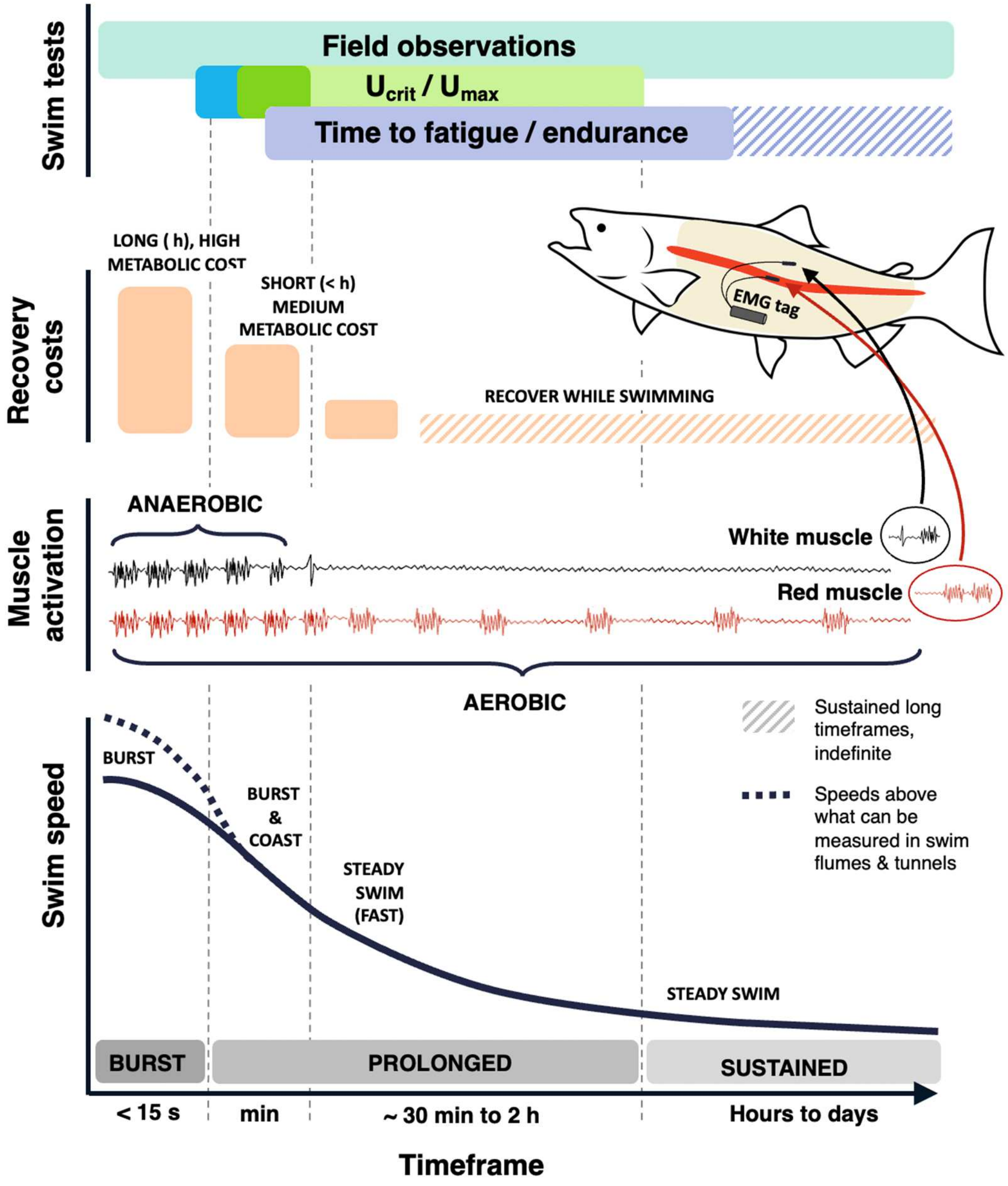

Figure 19: Conceptual presentation of applied physiology of swim performance and recovery.

Conceptual timeframe representation of various processes during swimming in the field and well-established swim tests (U_{crit}, U_{max}, and endurance swimming tests). All sections – swim speed, muscle activation, recovery costs, and swim tests – are shown on the same conceptual timescale. The dashed lines that link all sections connect the processes with relative time based on swimming mode (burst, burst and coast, fast-steady swim, and stead sustained swimming). These modes are broadly grouped in bursting, mixed aerobic and anaerobic swimming with burst and coast (i.e., prolonged), and sustained swimming modes (bottom panel) (Beamish 1978). These modes alternatively can be identified by the amount of aerobic and anaerobic swimming, which describes the amount of white (anaerobic) and red (aerobic) muscle activation. In an experimental setting, this can be measured by electromyogram (EMG) tags. Anaerobic swimming leads to fatigue and requires recovery; the greater the anaerobic swimming effort, the higher post-swimming recovery costs a fish will incur. Fully aerobic swimming does not lead to fatigue, allowing fish to restore energy and clear metabolic waste products as it continues to swim aerobically. Therefore, the fastest swimming within the shortest timeframes necessitates the highest recovery costs. Most knowledge on fish swimming in salmon comes from field studies, laboratory studies using swim flumes (U_{crit} and U_{max}), or time to fatigue or endurance swim test using raceways, swim flumes, or similar apparatuses (top panel). In the wild, fish are required to swim at a broad spectrum of speeds. The U_{crit} and U_{max} swim tests are ramp-speed tests where the endpoint is when the fish can no longer continue to swim (reached fatigue). These tests can effectively measure steady swimming (aerobic; green), fast-steady swimming (aerobic and anaerobic; green), and burst-cost swimming capacities (highly anaerobic and aerobic, dark green = burst and coast, blue = sprint). However, fish cannot burst maximally (limited distance) or engage in any type of anaerobically powered leaping activity in swim flumes. The endurance swim tests measure sustained aerobic swimming, where fish occasionally may engage in unsteady swimming, but the chosen (constant) water velocity would not consistently require it. Endurance tests may or may not lead to fatigue.

Sustained swimming is predominantly powered by aerobic metabolism (in red muscle), keeping the energy supply and demand balanced (Nelson and Chabot, 2011). During aerobic swimming, the cardiovascular system can supply sufficient oxygen and substrates to the working muscle tissue, where energy (ATP) is generated via oxidative phosphorylation yielding ~ 36-38 ATP per one glucose molecule (Nelson and Chabot, 2011). Likewise, the cardiovascular system can support the removal of by-products (mainly CO_2) generated by aerobic metabolism. Under optimal conditions across a range of lower velocities, sustained swimming activity can be maintained nearly indefinitely (Brett et al., 1958; Brett, 1973) (Figure 19) and is therefore optimal for long migrations.

Fish begin bursting or combined burst-and-coasting when aerobic metabolism is insufficient to support swimming requirements (Weihs, 1974; Marras et al., 2010). Burst swimming is powered by anaerobic metabolism (in white muscle) (Geist et al., 2003; McKenzie, 2011; Hachim et al., 2021) but can only be maintained for < 30 s (~ 15 s) (Bainbridge, 1962; Beamish, 1978; Nelson and Claireaux, 2005; Lauritzen et al., 2005; Castro-Santos et al., 2012; Bell, 1991) (Figure 19). During anaerobic metabolism, ATP is produced rapidly without oxygen through glycolysis or phosphocreatine metabolic pathway. However, glycolysis is inefficient and yields only 2 ATP per glucose molecule, leading to a buildup of metabolic by-products that must be cleared to avoid muscle fatigue (Moyes and West 1995) and thus exhaustion. After bursting, fish must recover their endogenous reserves of muscle ATP, glycogen, and high-energy phosphates, remove built-up lactate, and re-establish ion and osmotic balance (Scarabello et al., 1991; Zhang et al., 2018). Although streamlined fishes like salmonids are efficient at bursting and burst-and-coast swimming (Fish, 2010), these swimming modes still typically lead to fatigue within the next ~ 3 hours depending on how vigorously the fish is burst swimming (Beamish 1978; Marras et al., 2010; Hvas and Oppedal, 2017). Anaerobic swimming and mixed aerobic and anaerobic swimming are not energetically optimal for long migrations.

Recovery required after *an*aerobic swimming is energetically costly and can be long-lasting depending on the intensity of the anaerobic effort (Lee et al., 2003a; Zhang et al., 2018). For salmon, long-lasting recovery can have ecological consequences such as delayed migration (Caudill et al., 2007; Babin et al., 2021), increased susceptibility to predation, increased susceptibility to infection and disease, and a reduction in already finite energy stores (Rand et al., 2006). Anaerobic swimming is essential for salmon to migrate through river main stems and tributaries (e.g., Fraser River Canyon, Hell's Gate: Hinch and Bratty, 2000) to pass dams (Keefer et al., 2004, 2021; Caudill et al., 2007; Crozier et al., 2020), to climb fishways (e.g., Burnett et al., 2017, 2014a, 2014b), to pass culverts (Mueller et al., 2008), and to jump across waterfalls (Kondratieff and Myrick, 2006; Lennox et al., 2018b).

Swim performance in fish is often expressed in speeds relative to an individual's body length (BL/s) instead of in absolute swim velocity units (cm/s). When salmon approach rapids, each individual must swim upstream against the same current (cm/s) irrespective of their body size or length. Therefore, the absolute swim speed (cm/s) is a necessary measure to understand the maximum swim performance of an individual fish. In contrast, relative swim performance (BL/s) facilitates easy comparison of swimming capacity across species and contexts. Generally, larger fish can achieve greater absolute swim speeds, but smaller fish can swim faster relative to their length (Bainbridge, 1958; Katopodis et al., 2019) (e.g., Appendix 3, Figure 4). Despite the species- and context-specificity, fish tend to maintain steady aerobic swimming up to speeds of ~ 1.5 BL/s and then transition to anaerobic swimming modes at speeds of ~ 2 BL/s (Geist et al., 2003; Eliason et al., 2013a; Hachim et al., 2021) (Figure 20). Consequently, the absolute velocity (cm/s) at which a fish transitions to anaerobic swimming varies depending on its body size. For example, at a velocity of 80 cm/s, an 80 cm fish could swim aerobically at ~1 BL/s. However, at the same velocity, a 30 cm fish would likely need to swim anaerobically at ~ 2.6 BL/s speed (Figure 20). Absolute velocity (cm/s) is directly comparable across observations, species, and environmental conditions. It is, therefore, arguably the most relevant metric of swim performance in the context of natural conditions (e.g., the river flows).

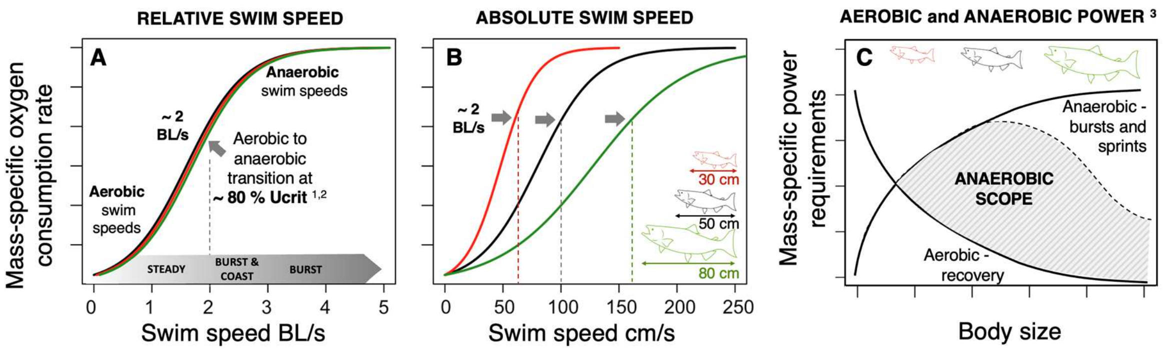

Figure 20: Conceptual presentation of swimming physiology across size fish.

The conceptual representation of metabolic requirements of different size fish (colors) swimming at increasing velocities, and aerobic and anaerobic metabolic power output of fish at different body sizes. In panels, **A** and **B** and oxygen consumption rate is plotted as a function of swim speeds, which is a proxy for the aerobic metabolism of fish. The dashed lines represent 2 BL/s swim speed for all individuals (color) in **A** and **B** panels. Oxygen consumption increases rapidly in fish of any body size until they reach ~ 1.5 BL/s speed (the grey band); then, the oxygen consumption begins plateauing slowly while the swim speed continues to increase. Individuals begin to swim anaerobically, burst-and-coast swimming around 1.5 to 2 BL/s (**A**). Eventually, oxygen consumption tends to plateau, which indicates that the individual increasingly relies more on anaerobic swimming while reaching the maximum burst-and-coast or full burst swim speeds. The same relationships and physiological states are represented in panel (**B**) but in absolute swim speed (cm/s). Panel (**C**) depicts conceptual relationships from Goolish, 1991, presenting body size-specific anaerobic scopes (or capacities). Larger fish have higher mass-specific requirements to power burst swimming (top line, positive power function) but lower mass-specific aerobic requirements necessary during recovery from bursting activity (bottom line, negative power function) and limited capacity for glycogen storage (dashed line). The anaerobic scope (shaded area) is constrained in larger individuals by allometric scaling of aerobic metabolism, thus limiting recovery capacity and glycogen storage. References literature: [1] Geist et al., 2003, [2] Hachim et al., 2021, [3] Goolish, 1991.

4.1.3. How is swim performance measured?

Various types of swimming tests to measure the aerobic and anaerobic swimming capacity of fish have been designed, broadly implemented, cross-compared, and reviewed (Steffensen et al., 1984; McDonald et al., 1998; Kern et al., 2018; Videler and Wardle, 1991; Reidy et al., 1995; Hammer, 1995; Nelson et al., 2002; Farrell, 2008; Kieffer, 2010; Little et al., 2020; Plaut, 2001; Kieffer, 2010). Below, we describe approaches used in the laboratory and field to measure swimming ability in salmonids and many other species.

Most swim performance studies, especially on salmonids, have been conducted in a controlled setting (field stations and laboratories) using swim tunnels and following popular standardized swim performance tests: critical speed test (U_{crit}; Brett, 1965a) and maximum swim speed test (U_{max}, Farrell, 2008; Tierney, 2011; also called constant acceleration test U_{cat}, Oufiero et al., 2021; sprint test U_{sprint}, Starrs et al., 2011; or burst test U_{burst}, Reidy et al., 1995). During both U_{crit} and U_{max} tests, individual fish is swum against incrementally greater velocities until the fish stops swimming because it can no longer maintain an upright position against the flow. U_{crit} is a step-test where the velocity is increased and held at that speed for a pre-determined time (often 20 min; Brett, 1964; Plaut, 2001; Kern et al., 2018). During U_{max}, the velocity is continuously accelerated at a rate typically between 1 and 10 cm s^{-1} min^{-1} (Nelson et al., 2002; Farrell, 2008; Starrs et al., 2011). These tests examine aerobic swimming capacity with a combination of transitional burst-and-coast swimming, but they are not designed to capture maximum anaerobic swimming capacity (e.g., Farrell et al., 2003). U_{crit} and U_{max} tests allow investigators to closely examine exercise physiology to understand mechanisms of swimming capacity, fatigue, exhaustion, and recovery (e.g., cardiorespiratory physiology, Eliason et al., 2011, 2013b, 2013c; Clark et al., 2011; recovery: Lee et al., 2003a; Eliason et al., 2013b; Hvas et al., 2021).

At field stations and laboratories, the target performances – burst swimming, fatigue, and recovery – can be examined using alternative approaches. One approach is using custom-built one-way sprint drag strips (e.g., Nelson et al., 2002). To date, this technique has been used for smaller fish species (Oufiero et al., 2021; Hardison et al., 2021) or juveniles (Martínez et al., 2002; Nelson and Claireaux, 2005; Kraskura and Nelson, 2018). Although not a swim performance test specifically, another commonly adopted approach in exercise physiology is a standard chase to exhaustion test often combined with short (~ 1 minute) air exposure (Rummer et al., 2016; Little et al., 2020). During this test, continuous bursting is elicited by chasing the fish using a net or hand while ensuring minimal physical contact. This test is designed to simulate angling, catch and release events (Donaldson et al., 2010). It exhausts the anaerobic and aerobic capacity of fish in a short timeframe (typically in 3 min; < 5 minutes) and is commonly used to measure recovery performance (e.g., Zhang et al., 2018). However, bursting speeds are not quantified during this test, taking away the opportunity to directly link bursting performance with the recovery performance.

In the field, swim performance is measured using different types of tags (e.g., acoustic tags: Burnett et al., 2017; accelerometer tags: Wilson et al., 2013; Burnett et al., 2014a; electromyogram (EMG) tags: Geist et al., 2000; Hinch et al., 2002; and radio tags: Colavecchia et al., 1998). Tagging studies provide important information about salmon migration patterns and their behavior which has a proven value for fisheries management (Cooke et al., 2013; Bett et al., 2022; Matley et al., 2022). However, these tags must be calibrated in a laboratory setting to yield interpretable data (e.g., EMG tags, Rand and Hinch, 1998, Thorstad et al., 2000, Geist et al., 2003; acoustic accelerometers: Wilson et al., 2013). Calibrations are often done using swim tunnels (e.g., U_{crit} and U_{max} tests), and therefore any constraints estimating true maximum burst capacity using tunnels may apply to the calibration (Cooke et al., 2016). Development, validation, and use of other types of tags, such as heart rate bio-loggers, can help advance the understanding of swim performance, recovery, and behavior of migrating and spawning fish in the wild (Prystay et al., 2017; Bjarnason et al., 2019; Meese and Lowe, 2020; Zrini and Gamperl, 2021; Twardek et al., 2021; Doherty et al., 2022).

Lastly, swimming can be evaluated on coarser time scales which is relevant for migrating species (km/d, km/h, e.g., Hanson et al., 2008a), or at very fine time scales during fast-start or startle responses (Domenici and Blake, 1997). However, these performances are beyond the scope of this review.

4.1.4. Collating adult salmon swimming data

To consolidate and summarize the maximum swimming capacity of adult salmon, we performed a comprehensive and systematic literature review and curated a dataset that compiles maximum swimming speeds, biological information on tested fish, and biotic and abiotic conditions when available. Extended methods are available in Appendix 3, Section 1.

Briefly, a total of 91 studies were included in the review as they met the following criteria: i) quantitative swimming speed of fish (groups or individuals) must be reported either in text, table, or be plotted; plotted values were extracted using tracking software ImageJ v 1.52 (Schneider et al., 2012), ii) swim speed must belong to Pacific salmon, (*Oncorhynchus* sp.), rainbow or steelhead trout (*Oncorhynchus mykiss*), or Atlantic salmon (*Salmo salar*), and iii) fish must have reached an adult life stage. Studies that met these criteria were individually reviewed to extract species, swim speed (absolute or relative; ft/s, cm/s, m/s, BL/s), fish size (g, kg, length), temperature, and sample size of the swum fish when noted. Whenever possible, we extracted additional variables that can impact swim performance: type of swim test used, intrinsic physiological conditions of the fish, extrinsic environmental conditions, sex, surgery or tagging procedures, salinity, maturity levels, gonad size, water flow, and discharge, reported mortality occurrence, the origin of the fish (e.g., population, collection site, farmed), and the type of recovery evaluated in the original study if any.

To obtain the most comprehensive outlook of the swimming capacity of salmon applicable to ecologically applied settings, we aimed to evaluate and standardize swim performance between absolute and relative swim speeds. We estimated absolute swim speeds (cm/s) from reported BL/s and length measures of fish where possible, but it must be noted that these estimates contain uncertainty (Appendix 3, Section 1). Lastly, throughout this review, we mark two reference speed thresholds. First, a 2 BL/s because fish may be required to rely on anaerobic swimming at this speed (Geist et al., 2003; Hachim et al., 2021). Second, a 200 cm/s equivalent to 4 BL/s for a conservative estimate of the mean size (50 cm BL) of migrating adult salmon represents the flow speed at which salmon will need to burst and are likely to avoid (Li et al., 2021; Bett et al., 2022).

4.2. TRENDS IN FISH SWIMMING RESEARCH

4.2.1. Trends through time

The earliest studies on swim performance of adult salmon date back to the 1950s and 1960s (Paulik and DeLacy 1957; Brett, 1964). The peak time in salmon swimming work was during the early 2000s, but studies continue to be conducted both in the field and in laboratories (Figure 21). An increase in studies conducted on adult salmon can be partly attributed to the development of mobile field swim tunnel respirometers (Farrell et al., 2003) and advancements in tagging technology (e.g., use and calibration of EMG tags) (Geist et al., 2000; Hinch et al., 2002). Telemetry continues to advance, providing promising opportunities to measure fine-scale field swimming speeds in migrating fish (Matley et al., 2022).

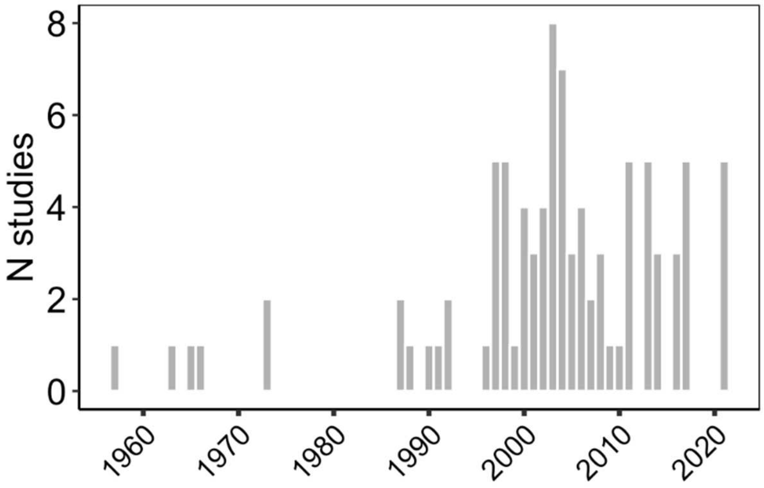

Figure 21: Histogram of published studies reporting swim speeds in adult salmonids. The number of published studies measuring swim speeds in adult pacific salmon (Data queried between 1950 - 2022).

4.2.2. How fast can adult salmon swim?

The vast majority of adult salmon swimming research has focused on aerobic swimming, measuring swim speeds in adult salmon below 200 cm/s (Figure 22 presenting all collated data). However, there is a clear indication that adult salmon can achieve burst swim speeds up to 600-800 cm/s and likely even higher speeds (Figure 22; *O. nerka, O. tshawytscha, O. keta, O. mykiss).* The quantitative measures of high-speed burst swimming are sparse. The duration and distance covered at these highest reported speeds are unknown. The swim speeds reported in relative speeds (BL/s) are generally below 4 BL/s, but 53.4 % (490/917) of all reported values are 2 BL or greater (Figure 23 presenting all collated data). Only two species have records of > 5 BL/s (*O. nerka* and *S. salar*) (Figure 23, summary in Tables 5 and 6).

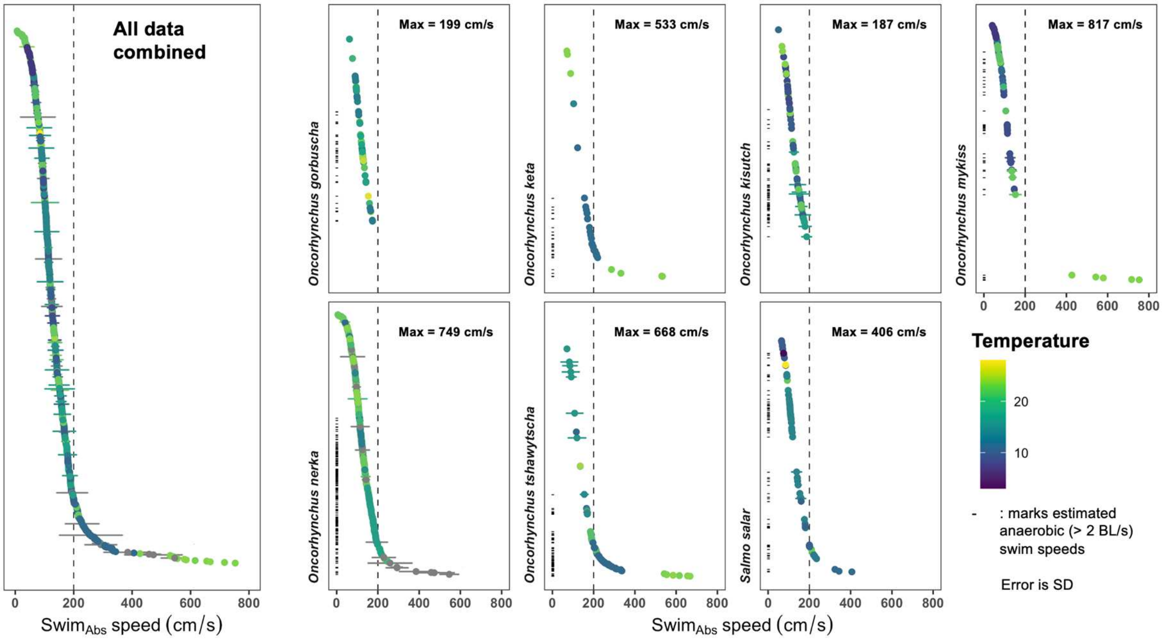

Figure 22: Ordered absolute swim speeds (centimeters /second) of adult salmonids. Species-specific ordered absolute (cm/s) swim speed performance of salmon. Values shown are either single maximum speeds per individual or group of individuals per laboratory tests (U_{crit} or U_{max}) (repeat swim trials are included) or up to 5 individual maximum burst speeds reported in the field. The dashed line is at 200 cm/s, color refers to temperature, and line marks on the left indicate reports at an estimated > 2 BL/s speed (a commonly referred to velocity threshold at which fish transition from aerobic to anaerobic swimming; Figure 20).

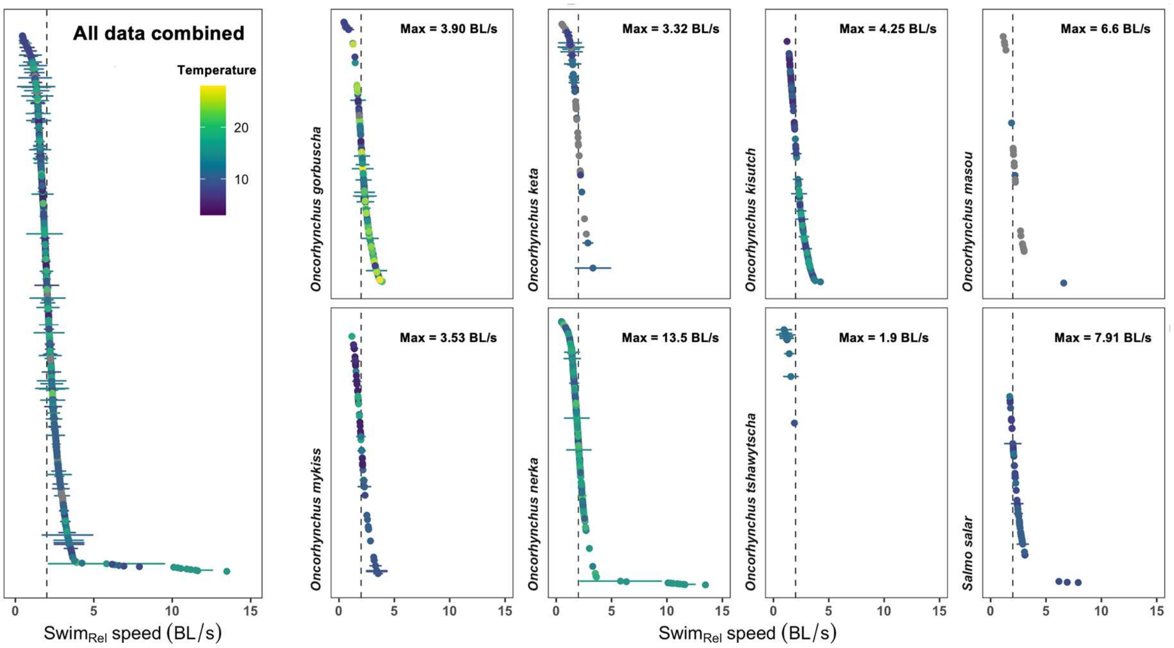

Figure 23: Ordered relative swim speeds (body lengths/second) of adult salmonids.

Species-specific ordered relative swim speed performance of salmon. Values shown are either single maximum speeds per individual or group of individuals per laboratory test (U_{crit} or U_{max}) (repeat swim trials are included) or up to 5 individual maximum burst speeds reported in the field. The dashed line is at 2 BL/s, the color is temperature, and line marks on the left indicate reports at estimated > 2 BL/s speed (an average velocity threshold at which fish transition from aerobic to anaerobic swimming; Figure 20).

The *true* maximum swim speed and the durations at which these speeds can be sustained are largely unknown for adult salmon. Between all approaches, the critical swim speed tests (U_{crit}) provide the most data on swim performance in adult salmon (Figure 24, Tables 5 and 6; the top swim speed achieved during U_{crit} or author reported U_{crit} swim speed estimate), but these results do not provide the true *maximum* swim performance, because of the limitations of the swim tunnel (e.g., Peake, 2004; Peake and Farrell, 2006; Dockery et al., 2017). Still, U_{crit} swim performance is an ecologically relevant measure of fish's *aerobic* swimming capacity (Plaut, 2001), which fish are likely to prioritize over costly anaerobic swimming. For example, 94.9 % (571 / 602) of compiled U_{crit} swim speeds of sockeye salmon (all populations together) were < 200 cm/s (Figure 24), while in the field, sockeye salmon were found to avoid flows ~ 240 cm/s (~ 4 BL/s) (Li et al., 2021; Bett et al., 2022). This intensity of flow (~ 240 cm/s) should be passable to sockeye salmon and other Pacific salmon species if they rely on anaerobic swimming (Hinch and Bratty, 2000), but it does exceed many top U_{crit} speeds reported across studies. Therefore, U_{crit} can come with limitations when it is used to evaluate the ability of salmon to swim anaerobically in order to overcome dam structures, pass fast-flowing fishways, jump, and navigate rapids and narrow canyons.

The highest swim speeds in salmon are reported from field studies. Migrating salmon are reported to pass high-velocity barriers while swimming at velocities from 300 cm/s and all the way up to 800 cm/s in *O. keta, O. nerka, O. tshawytscha, O. mykiss* (3 BL/s and greater) (Figure 24, Tables 5 and 6) (Hinch et al., 2002; Burnett et al., 2014a). The distribution of swim speeds measured in the field is positively skewed (few fast swim speeds, many slow swim speeds), likely reflecting the balance between aerobic *versus* anaerobic swimming in wild fish (Figure 24). Aerobic swimming is likely to be used much more frequently compared to anaerobic swimming because bursting is energetically costly and requires recovery. However, data specifically reporting burst swimming (speeds, duration, frequency) are scarce. These gaps in knowledge reveal the necessity of studies examining anaerobic swimming in adult salmon in the field and in laboratories.

Species	***Test perf.***	***Mean swim speed (n) (range), cm/s***	***Body length, cm(range)***	***Body mass, kg (range)***	***Mean temperature during swim (ºC) (range)***
Oncorhynchus gorbuscha	Field	118.83 (6) (95 - 138)	50.55 (49.05 - 52.05)	1.49 (1.18 - 1.79)	15 (15 - 15)
	U_{crit}	117.16 (52) (62.226 - 173.926)	53.26 (50.25 - 55.5)	1.73 (1.61 - 1.78)	13.92 (9 - 22)
Oncorhynchus keta	Field	273.45 (7) (70.104 - 533.4)	50.8 (35.56 - 60.96)		19 (19 - 19)
	Swim	190.22 (27) (155.448 - 219.456)	56.37 (44.45 - 67.31)		10 (10 - 10)
	U_{crit}	112.65 (2) (103 - 122.3)	65.25 (63.75 - 66.75)		11 (10 - 12)
Oncorhynchus kisutch	Field	85.34 (6) (67.056 - 106.68)			19 (19 - 19)
	U_{crit}	130.69 (85) (50 - 176.762)	57.78 (49.8 - 71.4)	2.15 (1.357 - 4.108)	11.91 (8 - 18)
	U_{max}	159.8 (9) (125 - 187)	66 (66 - 66)		14 (14 - 14)
Oncorhynchus mykiss	Field	317.78 (14) (66.457 - 816.864)	51.96 (34.75 - 81.28)		17.86 (17 - 19)

	U_{crit}	89.5 (60) (40.6 - 152.833)	40.83 (34.523 - 51)	0.8 (0.437 - 1.471)	9.15 (6 - 19)
	U_{max}	85.86 (5) (70.6 - 93.6)	34.91 (34.91 - 34.91)	0.45 (0.452 - 0.452)	10 (10 - 10)
Oncorhynchus nerka	Field	98.92 (206) (6.455 - 292.7)	59.08 (52.255 - 73.1)	1.99 (1.68 - 2.64)	17.32 (10 - 19)
	Jump	328 (9) (114 - 546)	49.33 (29 - 59.5)	1.89 (0.28 - 2.7)	
	Swim	176.72 (51) (112.776 - 216.408)	64.43 (54.61 - 75.565)		14.57 (14 - 15)
	TTF	79.6 (5) (65.2 - 85)	51.5 (47.9 - 55.1)	1.79 (1.615 - 1.969)	19.8 (13 - 24)
	U_{crit}	122.17 (139) (40.11 - 197.3)	59.25 (41.8 - 64.2)	2.25 (0.746 - 3.56)	14.94 (10 - 21)
Oncorhynchus tshawytscha	Field	278.48 (50) (70.6 - 667.512)	77.33 (50.8 - 96.52)	5.92 (5.9 - 6)	11.64 (10 - 19)
	U_{crit}	185.91 (31) (135 - 230)	75.25 (73.9 - 95.197)	5.29 (5 - 11.5)	13.3 (8 - 20)
Salmo salar	Field	357.87 (3) (323.9 - 406)	51.2 (51.2 - 51.2)	1.16 (1.16 - 1.16)	10 (10 - 10)
	Swim	91 (1) (91 - 91)	40 (40 - 40)		11 (11 - 11)
	TTF	158.3 (45) (60 - 240.46)	54.97 (52 - 64)	2.18 (1.199 - 3.158)	7.42 (4 - 18)
	U_{crit}	131.44 (80) (65 - 234.744)	45.15 (34 - 63.8)	1.01 (0.408 - 2.535)	11.41 (3 - 23)
Oncorhynchus spp. *	Field	85.34 (2) (82.296 - 88.392)			

Table 5. Summary of swim speeds, temperature and morphometrics across species. Summary on absolute speeds, body size metrics (length and mass), and temperature for each salmon species. Field is left empty when data were not available. * indicates combined species (*O. nerka* and *O. kisutch*).

Species	***Test perf.***	***Mean swim speed (n) (range), BL/s***	***Body length, cm (range)***	***Body mass, kg (range)***	***Mean temperature during swim (ºC) (range)***
Oncorhynchus gorbuscha	Field	1.5 (18) (0.45 - 3.27)	62.13 (49.05 - 79.6)	3.43 (2.38 - 4.45)	11.67 (9 - 15)
	U_{crit}	2.23 (61) (1.252 - 3.39)	52.61 (46.1 - 55.5)	1.72 (1.361 - 1.823)	14.07 (9 - 22)
	U_{max}	2.76 (132) (1.276 - 3.904)	51 (51 - 51)	1.6 (1.6 - 1.6)	17.52 (7 - 28)
Oncorhynchus keta	Field	1.67 (37) (0.514 - 3.32)	62.17 (53.6 - 68.7)	2.03 (1.55 - 2.32)	10.09 (9 - 12)
	U_{crit}	1.54 (20) (1.25 - 2.556)	63.17 (62.1 - 68.3)	2.38 (1.9 - 2.86)	12.79 (10 - 13)
Oncorhynchus kisutch	U_{crit}	2.38 (113) (1.23 - 4.248)	57.85 (49.8 - 71.4)	2.2 (1.357 - 4.108)	11.12 (5 - 18)
	U_{max}	2.3 (21) (1.98 - 2.97)	62.91 (60.6 - 66)	2.56 (2.56 - 2.56)	13.14 (10 - 15)
Oncorhynchus masou	Field	2.46 (22) (1.13 - 6.6)	53.7 (51.45 - 55.95)		12 (12 - 12)
	U_{crit}	1.89 (1) (1.89 - 1.89)	53.3 (53.3 - 53.3)	1.7 (1.7 - 1.7)	13 (13 - 13)
Oncorhynchus mykiss	U_{crit}	2.03 (60) (1.17 - 3.535)	37.36 (30.1 - 42)	0.64 (0.445 - 0.871)	10.6 (7 - 19)
Oncorhynchus nerka	Field	2.5 (80) (0.48 - 13.476)	61.47 (53.95 - 73.1)	2.22 (1.8 - 2.8)	15.81 (10 - 20)
	U_{crit}	1.93 (273) (0.64 - 3.6)	60.03 (41.8 - 64.2)	2.33 (0.746 - 3.56)	16.07 (10 - 26)
Oncorhynchus tshawytscha	Field	1.22 (7) (0.96 - 1.58)	76 (76 - 76)	6 (6 - 6)	14 (14 - 14)
	U_{crit}	1.57 (2) (1.23 - 1.9)	45.5 (45.5 - 45.5)	1.31 (1.31 - 1.31)	11 (11 - 11)
Salmo salar	Field	7 (3) (6.165 - 7.906)	51.2 (51.2 - 51.2)	1.16 (1.16 - 1.16)	10 (10 - 10)
	Swim	2.03 (1) (2.03 - 2.03)	40 (40 - 40)		11 (11 - 11)

	TTF	2.41 (69) (1.958 - 3.461)	43.9 (43.9 - 43.9)	0.79 (0.592 - 0.916)	12.35 (12 - 13)

Table 6. Summary of relative swim speeds, temperature and morphometrics across species.

4.2.2. Inter- and Intra-specific differences in swimming

Swimming ability in fishes varies between species (Katopodis and Gervais, 2016), across populations (Lee et al., 2003b; Eliason et al., 2017), and between individuals from the same population (Clark et al., 2011), and temporally within individuals (Killen et al., 2016). In adult salmon, swim performance (measured as U_{crit}) is highly repeatable across short timescales (i.e., consecutive swim tests with < 1 hour recovery in between (Jain et al., 1998; Eliason et al., 2013b), but it can change across intermediate timescales, for example throughout the migration as fish reach maturity (Williams and Brett, 1987).

Species-specific differences may be best conceptualized by comparing swim performance across both absolute and relative swim speeds (Figure 20). Ecologically relevant absolute swim speeds (200 cm/s, flow fish are known to avoid, Figure 22) and biologically relevant relative swim speeds (2 BL/s, when fish typically transition to anaerobic swimming, Figure 23) reveal interesting species-specific trends that may be highly related to body size. For example, pink salmon, *O. gorbuscha,* and coho salmon, *O. kisutch,* can achieve > 2 BL/s (assumed burst-and-coast) (Figure 23) but have not been reported to achieve absolute speeds above 200 cm/s. Although this discrepancy could be attributed to their relatively smaller body sizes in these particular studies (~ < 60 cm, Figures 20 and 25), it also may suggest a limitation to swim performance and species- or population-specific conservation concerns. In contrast, larger chinook salmon *O. tshawytscha* (~ > 70 cm, Figure 25) can swim at speeds 200 cm/s and faster (Figures 22 and

23; Tables 5 and 6), but they are not reported to swim at relative swim speed > 2 BL/s (i.e., assumed anaerobic threshold). These trends suggest a need for more refined absolute swim speed data across species, particularly for the large-size species such as chum salmon.

We were unable to evaluate population-specific differences in swim performance due to data deficiency or unknown population-origin for fish included in the database. However, this may be one of the major factors responsible for the high variation in swim speeds within species (Standen et al., 2002; Eliason et al., 2013b). Aerobic and anaerobic swim performances vary between populations of the same fish species (Peake et al., 1997; Billerbeck et al., 2001; Lee et al., 2003b; Eliason et al., 2013b; Fu et al., 2013; Camarillo et al., 2020; Jones et al., 2020). In brown trout, swim performance (U_{crit}) was higher in the upstream population compared to downstream populations (Jones et al., 2020). In adult sockeye salmon, swim performance and metabolic efficiency across swim speeds are population-specific (Lee et al., 2003b; Eliason et al., 2013b; sockeye parr: Eliason et al., 2017). These differences are likely to translate into population-specific migration capacities (Eliason et al., 2011). Other types of stock and life-history differences can influence swim performance. For example, hatchery fish had higher swimming capacity than their wild counterparts (Atlantic salmon U_{crit}: Peake et al., 1997). Additionally, swim performance can differ between fish from the same species, but different stocks that are exposed to different flows (e.g., swim training), different predation regimes, and urbanization levels (Pearson et al., 1990; Nelson et al., 2003, 2008; Zhang et al., 2016; Auer et al., 2018). This experimental evidence reinforces the importance of intraspecific variation in swimming.

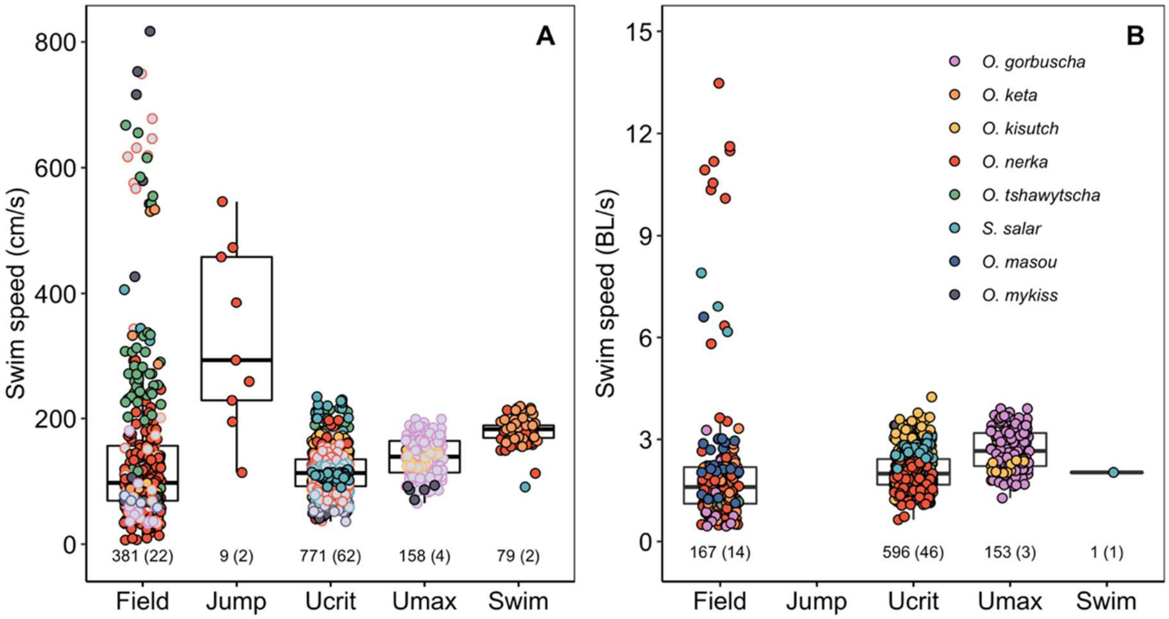

Figure 24: Swim performance from different swim tests.
Presented are the highest achieved swim performance at each swim performance test in the laboratory (U_{crit}, U_{max}; repeat swim tests are included), or up to 5 repeat maximum speed bursts from the field studies in cm/s (**A**) and BL/s (**B**). In panel A, the grey-filled circles are estimated swim speeds using body length (BL, cm) of the fish and reported relative swim speed (BL/s). The numbers indicate sample sizes: n datapoints (n studies).

4.3. TEMPERATURE

4.3.1. Effects on aerobic and anaerobic swimming

Temperature is a master regulator of physiological and ecological performances in fish and has a profound influence on swim performance (Fry,, 1971). Thermal performance curves describe how swim performances, such as U_{crit}, U_{max}, burst, and endurance swimming, change with temperature (Schulte et al., 2011). Swim performance is the lowest in the cold, and then it quickly increases with increasing temperatures until it reaches a peak swim performance at optimal temperature (T_{opt}, ºC). At temperatures beyond $T_{opt,}$ swim performance may decrease, not change, or cease entirely (e.g., Lee et al., 2003b; Clark et al., 2011; fish not swimming in warm conditions: Steinhausen et al., 2008). These trends are best applied to dominantly aerobically powered prolonged swimming (e.g., U_{crit}) and endurance swimming (e.g., time to fatigue) because of the close links between swimming and physiology (Eliason et al., 2013a, 2013b). Acute sensitivity to temperature change and thermal acclimation of aerobic swimming varies across salmon species and populations, but thermal performance in salmonids is typically locally adapted to historical thermal conditions (Eliason et al., 2011; Abe et al., 2019; but see Clark et al., 2011).

The temperature effects on anaerobic swimming are less broadly examined in fish but can be significant (Beddow et al., 1997; Guderley et al., 2001; O'Steen and Bennett 2003). The thermal performance curve of anaerobic swimming, however, is unlikely to follow the same relationships as aerobic swimming (Sylvestre et al., 2007; Muhawenimana et al., 2021). Burst or sprint performance can be nearly insensitive to temperature (Sylvestre et al., 2007; Dockery et al., 2017; Hardison et al., 2021), can increase with temperature, as shown in juvenile European bass sprinted at 12ºC to 22ºC (Claireaux et al., 2007), or can decrease, as observed in burst swimming sockeye salmon at 12ºC, 14ºC and 16ºC (Burt et al., 2012). An alternative ecologically relevant metric to evaluate may be the temperature at which fish transition from steady to burst swimming. For instance, juvenile Atlantic cod began burst-and coast swimming at higher flow speeds when temperatures were higher (Sylvestre et al., 2007), while several studies on adult salmon show that fish increase their reliance on anaerobic metabolism at higher temperatures (Brett, 1964; Jain and Farrell 2003; Eliason et al., 2013a; Abe et al., 2019; Steinhausen et al., 2008). Lastly, temperature effects on anaerobic swimming capacity may be indirectly evaluated using indicators such as lactate levels after exercise, lactate clearance time, glycogen depletion, or changes in metabolic enzyme capacity (e.g., Sänger 1993). Burst capacity is linked with physiological capacity and thus may be expected to change with temperature in fishes, but these ideas require further study.

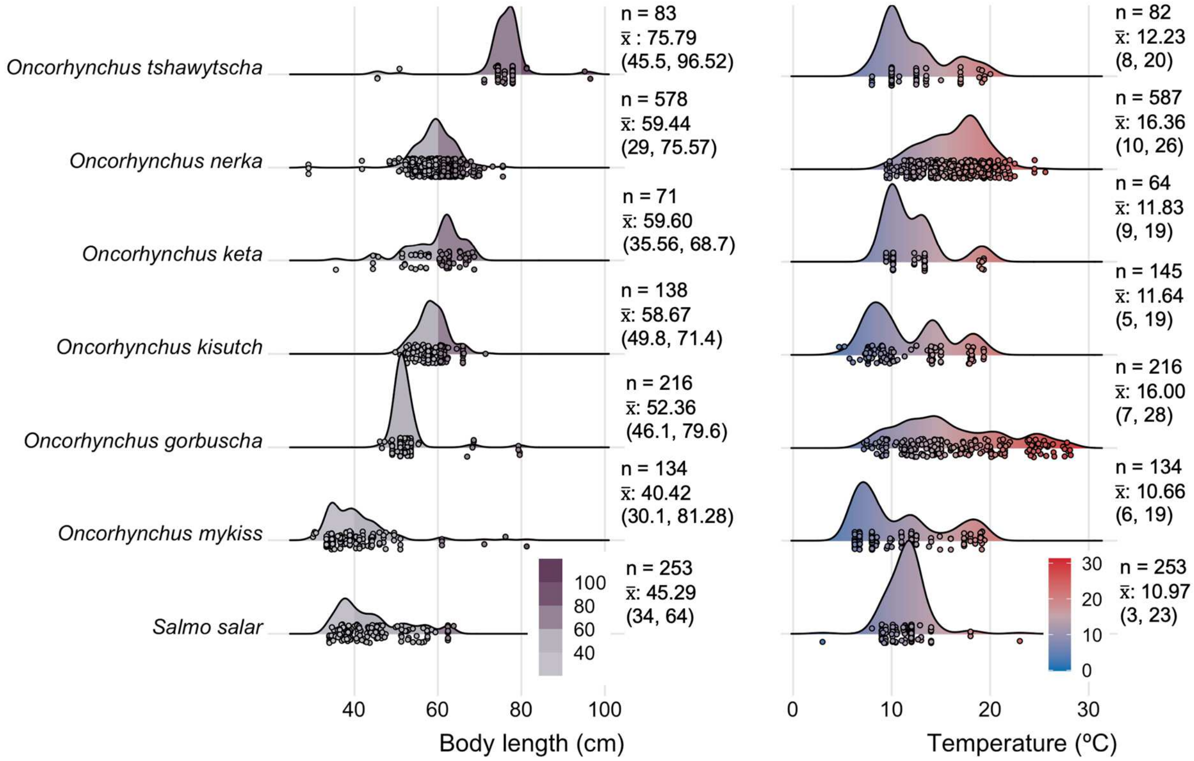

Figure 25. Body lengths (cm) and temperatures of adult salmon included in database. Most length measurements are fork lengths with few exceptions where only total length was available. The peaks are relative density frequencies. All data are plotted in circles at the base of each density plot. The sample size (n), the mean ($\bar{x}$), and the range (minimum, maximum value) of each species and metric subsets are denoted on the right side. Masu salmon (*O. masou*) are not included because the database only includes n = 5 data points with temperature and length measures.

4.3.2. Thermal performance curves: contextual variation in salmonids

The interindividual variation in swim speeds across and within salmonid species and temperatures is substantial. Swim performance has been measured across a ~ 10ºC temperature range in each species (Figure 25), but the sample size across the temperature range is uneven (Figure 25). Therefore, only sub-grouped data from laboratory tests (U_{crit} and U_{max}) were data sufficient to evaluate swim performance across species. In sockeye salmon, the T_{opt} was 16.8ºC (Figure 26b); in coho salmon, T_{opt} = 15.9ºC (Figure 26c), rainbow and steelhead trout T_{opt} = 12.8ºC (Figure 26d), and Atlantic salmon T_{opt} = 14.5ºC (Figure 26f). Swim performance in these species was characterized by expected bell-shaped thermal performance curves with species-specific peak performance temperatures (Figure 26, Table 7). Swim performance in Chinook salmon was measured across the range of 8 ºC to 20 ºC, but the relationship did not show robust T_{opt} (Figure 26j), likely due to low sample sizes and high interindividual variation (Table 7). Species specific swim performance are shown in Appendix 3, Figure 2 (cm/s) and in Appendix 3, Figure 3 (BL/s).

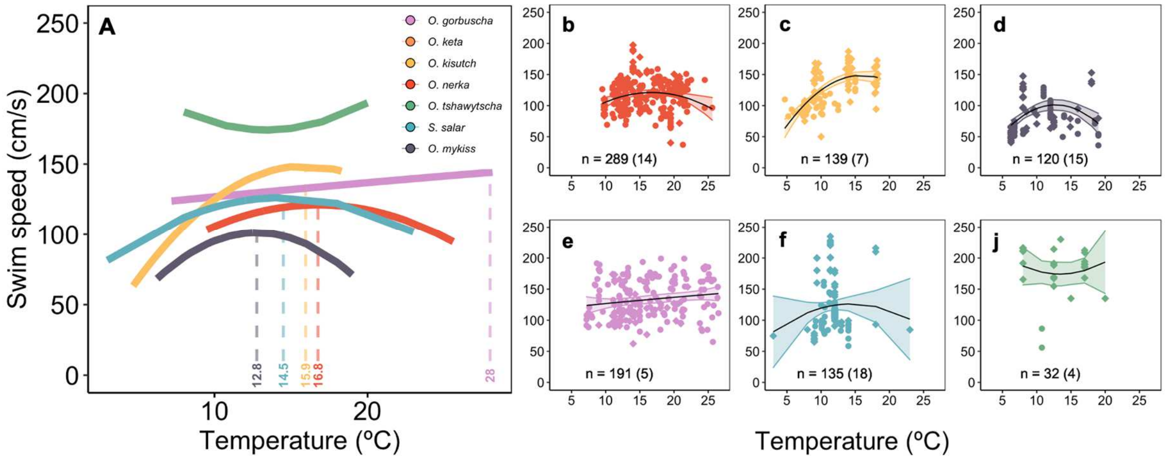

Figure 26: Swim performance across temperatures and species.
Species-specific optimal temperatures (T_{opt}) for only experimental U_{crit} and U_{max} performance tests. All species that were swum across at least 10 ºC are presented. The swim performance across temperatures is modeled using simple regression 2nd order polynomial functions (panel **A**: all species together, panels **b-j** show species-specific data, fitted models, and 2.5 and 97.5% CI bounds). The T_{opt} or the temperature at which each species had the greatest estimated swim performance is indicated by the dashed lines and marked in panel **A**. The numbers indicate sample sizes: n datapoints (n studies). The diamonds are reported swim speeds in cm/s and circles are estimated swim speeds from BL/s. The quadratic equations for each species are reported in Table 7.

The greatest interindividual variation across a broad temperature range (7.19 ºC to 28.16 ºC) was found in pink salmon (Figure 26e). Their swim performance across temperatures was characterized by a nearly linear positive relationship (Table 7) with no clear peak performance (~ 70 to 200 cm/s; 2 to 4 BL/s) or T_{opt} (Figure 26e) (but see Clark et al., 2011). Pink salmon were almost exclusively swum using a U_{max} swim protocol (N (U_{max}) = 132, N (U_{crit}) = 59 U_{crit}) and after acute 4-10 h temperature change (Clark et al., 2011), which makes them difficult to compare with the other species that often have longer temperature acclimation times (≥ 1 day) and are swum following U_{crit} protocol. Study designs are essential to consider when combining results for a broader comparative context.

The spawning migration success of salmon is contingent on temperature conditions (Eliason et al., 2011; Lennox et al., 2018a; Crozier et al., 2019; Snyder et al., 2020). During migration, swim performance can suffer due to constrained metabolic capacity, which may be a direct consequence of temperature (Eliason et al., 2011; Abe et al., 2019; Anlauf-Dunn et al., 2022) or combined adverse effects of temperatures and increased infection rates (Teffer et al., 2018), prolonged recoveries (Kraskura and Hardison et al., 2021), and rapid energy depletion (Martin et al., 2015; Lennox et al., 2018a). Temperature and water discharge levels (high and too low) have been identified as two primary factors that affect depletion rates of finite somatic energy in migrating salmon (Rand et al., 2006), which ultimately can lead to mortality (Westley 2020; von Biela et al., 2022). The combined effects of temperature on swimming (especially anaerobic swimming, and recovery, repeat swimming) can be particularly challenging to test using standard swim tests, such as U_{crit} or U_{max}, but are necessary to understand for management and conservation (Lennox et al., 2019; Cooke et al., 2020; Thorstad et al., 2021; Eliason et al., 2022). Because T_{opt} differs between species and populations (Eliason et al., 2011), this may best be evaluated across species, populations, and individuals from the ecologically relevant subgroups (e.g., Anttila et al., 2014), such as summer or fall runs (Crozier et al., 2019).

Species	**N**	**Model Estimates**					
		intercept		***Temp term***		***Temp^2 term***	
		β	P-val	β	P-val	β	P-val
O. gorbuscha	191	115.653 (21.41)	< 0.001	1.167 (2.61)	0.655	-0.005 (0.07)	0.942
Equation:	~ 115.65 + 1.17 Temperature - 0.01 Temperature^2 + *re*						
O. kisutch	139	-22.554 (21.52)	0.296	21.474 (3.79)	< 0.001	-0.673 (0.15)	< 0.001
Equation:	~ -22.55 + 21.47 Temperature - 0.67 Temperature^2 + *re*						
O. mykiss	120	-24.791 (22.07)	0.264	19.747 (4.11)	< 0.001	-0.774 (0.17)	< 0.001
Equation:	~ -24.79 + 19.75 Temperature - 0.77 Temperature^2 + *re*						
O. nerka	289	26.321 (28.74)	0.361	11.299 (3.65)	0.002	-0.337 (0.11)	0.003
Equation:	~ 26.32 + 11.3 Temperature - 0.34 Temperature^2 + re						
O. tshawytscha	32	253.285 (94.78)	0.012	-11.821 (14.98)	0.437	0.441 (0.57)	0.441
Equation:	~ 253.28 - 11.82 Temperature + 0.44 Temperature^2 + *re*						
S. salar	135	54.996 (47.69)	0.251	9.832 (7.16)	0.172	-0.339 (0.27)	0.211
Equation:	~ 55 + 9.83 Temperature - 0.34 Temperature^2 + *re*						

Table 7. Estimates and models of species-specific swim performance across temperatures.

4.4. BODY SIZE

4.4.1. Anaerobic swimming and aerobic recovery: trade-offs

A larger body size offers several fitness advantages to fish, including the ability to swim faster (Bainbridge, 1958; Brett, 1965b; Webb, 1976; Hammer, 1995; Mesa et al., 2008; Vogel, 2008; Bellinger et al., 2014; Oldham et al., 2019; Cano-Barbacil et al., 2020). Additionally, larger individuals have increased survival because they tend to out-compete smaller counterparts for resources, they can store more energy reserves (e.g., fat, ATP, glycogen stores, and somatic energy), larger males can gain mating priority (Quinn, 1999), and larger females have higher fecundity (Barneche et al., 2018). However, a larger body size can also come with disadvantages. Larger fish are more sought after by fishers. Larger fish also need more food to support metabolic needs and growth and may be more vulnerable to climate-related stressors, especially warming (Gardner et al., 2011; Clark et al., 2012; but see Lennox et al., 2018a; Thorstad et al., 2021). Therefore, there are contexts where a larger body size is beneficial and contexts where larger-sized individuals are more vulnerable compared to their smaller counterparts.

Aerobic and anaerobic power and performance for swimming differ in fish based on their body size (Goolish, 1991; Figure 20C). Aerobic swimming follows negative exponential relationships with body size, which could partly be explained by the negative scaling of mass-specific aerobic enzyme activities in muscle tissue (Somero and Childress, 1980; Goolish, 1991). In contrast, anaerobic swimming follows a positive power function, which mechanistically is supported by positive mass-specific scaling of anaerobic enzyme activity with size (Somero and Childress, 1980; Goolish, 1991). Additionally, larger fish have higher mass-specific storage of anaerobic metabolic fuel sources when at rest (ATP and glycogen g^{-1}) (Ferguson et al., 1993), which would support proportionally higher bursting capacity in large individuals (McDonald et al., 1998). However, the recovery after anaerobic bursting is an aerobic process and thus may be under constraints of lower mass-specific metabolism in larger fish (Brett, 1965ab; Clarke and Johnston, 1999). Body size plays a critical role in salmon swimming capacity and recovery, but it is unsure how aerobic and anaerobic capacities change with body size at inter- and intraspecific levels.

4.4.2. Size-specific salmon swimming: field and laboratory

In the collated dataset, the size range of adult salmonids falls within narrow ranges between 30 cm in body length (*O. mykiss and S. salar*, young adults) and 80 cm (*O. tshawytscha)* (Figure 25). When all species and all swim tests were combined, no clear relationship between absolute swim speed (cm/s) and relative swim speed (BL/s) was evident (Appendix 3, Figure 4). However, there were significant relationships between body length and absolute swim speed when separately considering laboratory swim tests only (U_{crit} and U_{max}) and swim speeds from the field (Figure 27, Appendix 3, Table 10).

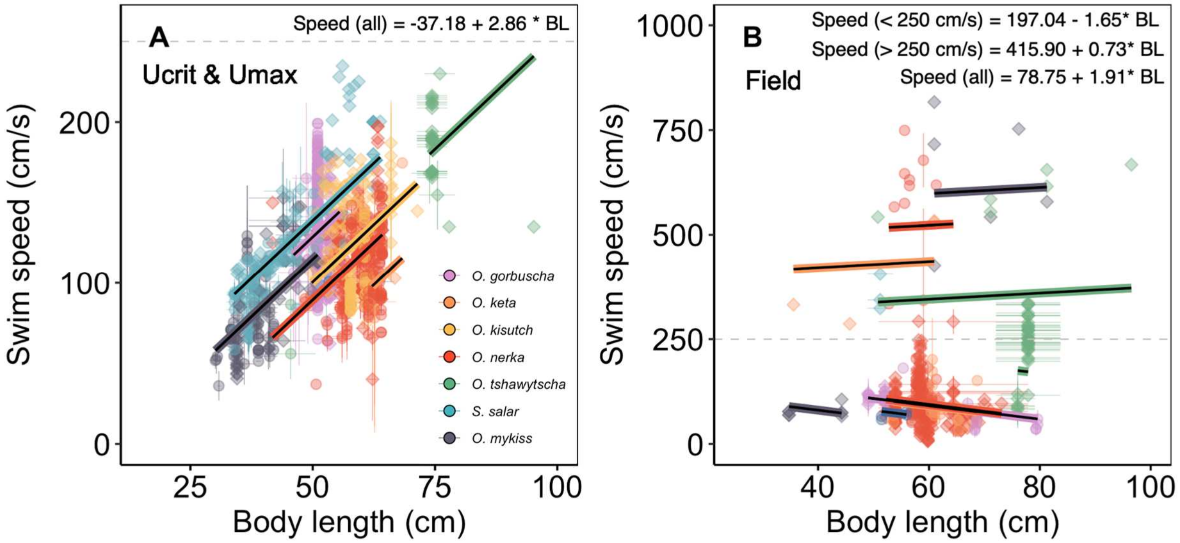

Figure 27. Scaling of swim performance from the laboratory tests and the field. Swim performance is positively related to body length in classic swim tunnel experiments (U_{crit} and U_{max}) (A), but swimming speeds are not strongly related to body length in adult salmon in the wild (B). All species are plotted together in both panels, indicated by color, and plotted regressions are mixed model estimated species-specific slopes (random intercept effect). The dashed line marks 250 cm/s speed. The error is s.d. for data points that represent groups of fish. The regressions are estimated relationships using mixed-effect models where intercept was allowed to vary across species. For the field reported swim speeds, plotted are two sets of regressions i) for speeds above 250 cm/s (assumed anaerobic), and ii) for speeds below 250 cm/s (within range of U_{crit} and U_{max} reported speeds). All equations are provided on the Figure panels. BL = body length, 'all' is for regression where all data were used to construct models. Model parameters and significance are provided in Appendix 3, Table 10.

Different takeaways emerge when evaluating field-measured compared to laboratory-measured swim speeds. The U_{crit} and U_{max} laboratory data suggest that swim speed in adult salmon increases by 2.86 cm/s with each cm increase in body length (SE: 0.18; Anova: $\chi^2 = 240.55$, df = 1, $p < 0.001$) (Figure 27A, Appendix 3, Table 10) supporting the idea that larger fish can swim faster than smaller fish. Notably, the size effect on swimming was different in field measurements (Figure 27B), where anaerobic speed (> 250 cm/s) scaled positively with body size (0.73, SE: 2.65, Anova: p = *ns*), but mostly aerobic speeds (< 250 cm/s) scaled negatively with body size (-1.65, SE: 0.56, Anova: $\chi^2 = 8.6249$, df = 1, $p = 0.003$) (Figure 27B, Appendix 3, Table 10). This negative relationship was rather unexpected but was also seen in adult Atlantic salmon at passage (Lindberg et al., 2016). In either context (laboratory or field), there was no detectable difference between speed to body size relationships across species (no change in scaling slope) or any intra-specific level below species (i.e., populations), but swimming speed did vary between species (varying intercepts). It must be noted that these relationships are not normalized with respect to any covariate (e.g., temperature, sex, maturity).

One of the major factors influencing the differences between laboratory and field results may simply be behavior and choice (Castro-Santos, 2005; Peake and Farrell, 2006). In the laboratory, the conditions are carefully controlled and manipulated, and the flows in the swim tunnel are typically laminar. In the field flows are often turbulent, and the fish can choose how fast to swim, which path to travel, and which flows to avoid (Standen et al., 2004; Castro-Santos, 2005; Bett et al., 2022). Large fish may be avoiding fast flows and choosing easier paths and slower speeds because it is more energy-efficient, not because they cannot swim faster (Lindberg et al., 2016, but see Standen et al., 2004). Accordingly, the field data must be interpreted cautiously. Similarly, the comparisons between field and laboratory swim scaling relationships must consider the specific physical and biological contexts.

Rapidly changing conditions, including river flows, temperatures, and drought, can alter the size structure of the returning adult salmon and possibly even remove the advantages that body size may offer to large migrating adult salmon (Oke et al., 2020). Larger adult salmon may have higher swimming capacity simply because they possess greater muscle mass that allows for greater thrust generation (Webb, 1976) and have greater energy reserves to support long migrations (e.g., fat, ATP, glycogen stores, and somatic energy (Lennox et al., 2018a). At a sex-specific level, larger males may gain mating priority on spawning grounds (Quinn, 1999), while larger females can produce more and larger eggs, thus ensuring a higher survival likelihood of their offspring (Beacham et al., 1985; Beacham and Murray, 1985), and larger females can dig deeper reds which provide better protection from predation and physical disturbance (Berghe and Gross, 1984; Quinn, 1999). On the other hand, larger individuals tend to have lower recovery capacity, which can directly and negatively impact migration. Specifically, larger salmonids take longer to metabolically recover after strenuous anaerobic exercise (McDonald et al., 1998; Clark et al., 2012), and they have more disturbed osmo- and ion-balance than their smaller counterparts (Ferguson et al., 1993; Clark et al., 2012; but see: Oldham et al., 2019). Also, fishers seek larger fish, making them more prone to exhaustion and injury from catch and release impacts before and during spawning migration. However, larger fish take longer to reach fatigue than smaller fish at comparable water velocities or when presented with equal swimming challenges (Figure 20) (McDonald et al., 1998; Ojanguren and Brañta 2000; Nikora et al., 2003). In the wild, a longer time to fatigue may help large adult salmon successfully pass rapid flows before accumulating a recovery burden that is detrimental to their migration success (for time to fatigue data with body size see Appendix 3, Figure 6). There are *pros* and *cons* to having a large body size, which may be different across species and populations and under multi-stressor conditions. This affirms the importance of including body size in adult swimming studies on climate change.

4.5. SEX

4.5.1. Why can swim performance differ between males and females?

In migrating adult salmon, energy is allocated towards competing performances: swimming (e.g., escaping predation, migration) and reproduction (gonad development and maintenance, parental care). The reproductive investment is often disproportional between the sexes. Specifically, females tend to invest more energy in reproduction than males, suggesting sex-specific energy trade-offs between swimming and reproduction (and other performances, not discussed herein; reviewed by (Fenkes et al., 2016). Studies that examine swim performance between sexes in salmonids, or any fish species, are slowly increasing in number (e.g., Williams and Brett, 1987; Plaut, 2002; Standen et al., 2002; Cooke, 2004; Ghalambor et al., 2004; Mateus et al., 2008; Svendsen et al., 2009; Clark et al., 2011; Burnett et al., 2014b; Hockley et al., 2014; Conradsen and McGuigan, 2015; Srean et al., 2017; Kraskura and Hardison et al., 2021). Most of these studies examine swim performance differences between reproductively active, mature males and females (Plaut, 2002; Kraskura and Hardison et al., 2021) or study dimorphic species with sex-specific morphologies (Oufiero et al., 2014; Conradsen and McGuigan, 2015). Fewer studies address swim performance in males and females across their reproductive season (Nelson, 1989; Cooke, 2004) and maturity states (Williams and Brett, 1987; Svendsen et al., 2009).

Sex-specific differences in swim performance in fish are context, species, and population-specific. In some studies, females had lower swim (U_{crit} or U_{max}) performance compared to males across species (Williams and Brett, 1987; Nelson, 1989; Reidy et al., 1995; Plaut, 2002; Ghalambor et al., 2004; Belk and Tuckfield, 2010; Clark et al., 2011; Conradsen and McGuigan, 2015; Makiguchi et al., 2017), but in other studies swim performance did not differ between sexes (e.g., Mateus et al., 2008; Kraskura and Hardison et al., 2021; Makiguchi et al., 2008). The reduction in swim performance in females could be driven by various factors, including morphological differences (reduced streamlining in females; Booth, 1998; Conradsen and McGuigan, 2015), lower metabolic scope for activity in females (Clark et al., 2011), and female-biased physiological constraints due to higher energy investments associated with egg development (reproductive *versus* swimming investment, e.g., Booth, 1998). The extent to which female and male salmon swimming capacity differ is unresolved. When possible, sex-specific swimming will be critical to evaluate in adult fish to best predict species population stability (Hanson et al., 2008b).

4.5.2. Sex-specific swimming in adult salmonids

Most swim performance data in the adult pacific salmon dataset were not sex-specific (803/1443 data points, N(females) = 255, N(males) = 385). In the two most common swim test approaches, laboratory swim tunnel (U_{crit} and U_{max}) and field studies, female adult salmonids achieved swim speeds between 36.00 and 305.96 cm/s in the swim tunnel tests and between 31.9 and 816.9 cm/s in the field. Male salmon swam between 31.9 and 292.7 cm/s in the swim tunnel and between 18.8 and 716.3 cm/s in the field (Appendix

3, Figure 5). We were unable to detect sex-specific differences in swim performance in adult salmon broadly or at species-specific levels (Roscoe et al., 2011), which could be due to data deficiency. It is common to pool male and female performance measures together and report a single mean swimming speed for a mixed-sex group of fish. Consequently, we also pooled male and female swim performances to report the data.

A collection of experimental evidence advocates for the need to report sex-specific swim performance and migration success in salmonids. For example, pink and sockeye salmon females were more energy conservative compared to males while swimming across the studied reaches of Fraser River, BC, Canada (Rand and Hinch, 1998; Standen et al., 2002), which may indicate that females are diverting additional aerobic capacity towards gonad development (Fenkes et al., 2016). This field observation has been further supported by laboratory swim studies where female pink salmon had lower swim performance than males (U_{max}: Clark et al., 2011, U_{crit}: Williams and Brett, 1987; Makiguchi et al., 2017). In contrast, male and female U_{crit} swim performances were comparable in sockeye salmon (Farrell et al., 2003; Steinhausen et al., 2008; Wilson et al., 2013; Eliason et al., 2013b) and Shibetsu River chum salmon (Makiguchi et al., 2008). However, an early study by William and Brett (1987) showed that swim performance of female and male sockeye salmon depends on maturity state therefore, it is possible that differences in swim performance between sexes may only emerge when approaching peak reproductive state (Plaut, 2002; Cooke, 2004; Svendsen et al., 2009).

Sex-specific swimming capacity and recovery performance may contribute to female-biased mortality observed across salmon species and populations (Bowerman et al., 2018; Hinch et al., 2021). Female biased mortality is particularly prevalent in the presence of secondary stressors, including high flow conditions. For example, female sockeye salmon and some Atlantic salmon populations were up to 30% less successful passing dams and fishways compared to males (Calles and Greenberg, 2009; Roscoe et al., 2011; Burnett et al., 2014b). Female salmon also had higher mortality than males under flow rates of 38 - 39 cm/s (speeds that may be classified as aerobic, sustained swimming, Figure 19) (Nadeau et al., 2010). Further, female-biased mortality post exhaustive swimming effort may be due to impaired exercise recovery in females compared to males, which several physiological trends have supported: female counterparts *i)* had higher lactate levels at 0.5 to 1 hours post exhaustive exercise (adult sockeye and pink salmon: Donaldson et al., 2014), *ii)* had longer recovery times for lactate (sockeye adults: Eliason et al., 2020), *iii)* had higher plasma glucose levels h after reaching exhaustion (sockeye adults: Gale et al., 2011; Donaldson et al., 2014), and *iv)* had higher plasma K^+ levels at 3 and 4 hours after exercise (Donaldson et al., 2014; Eliason et al., 2020). At a whole-animal level, the elevated recovery burden has been captured through elevated metabolic costs in females (Kraskura and Hardison et al., 2021). Recovery performance could be one of the key indicators of impaired sex-specific swim performance, especially in field settings where migrating adult salmon swim and recover simultaneously.

4.6. RECOVERY

4.6.1. Recovery mechanisms

Recovery is an aerobic physiological (Zhang et al., 2018) and behavioral performance (Peake and Farrell, 2006; Eliason et al., 2020) and is necessary after exhausting anaerobic as well as aerobic capacities in fish (Kieffer, 2000). Once fatigued and exhausted from maximal swimming, an individual must replenish its energy stores (oxygen stores, ATP, glycogen, phosphocreatine stores), restore the balance of metabolites (clear built-up plasma and tissue level lactate, decrease plasma cortisol levels, return plasma glucose to baseline levels), and re-establish ion and osmotic balance, and balance blood pH (clear built-up CO_2, decrease plasma K^+, Cl^-, Na^+) (reviewed by (Wood et al., 1983; Milligan, 1996; Kieffer, 2000; Zhang et al., 2018). All the factors mentioned above are relevant in swimming and recovery. Specifically, higher lactate indicates higher anaerobic effort, higher K^+ indicates higher muscle contraction and the consequent efflux of K^+ ions in the blood and thus indicate possible muscle fatigue (Wood et al., 1983; Sejersted and Sjøgaard, 2000), and higher plasma glucose levels indicate greater fuel mobilization and thus indirectly indicate higher energy expenditure. Additionally, glucose was higher in unsuccessful (mortalities) compared to successful migrant sockeye (Cooke et al., 2006; Roscoe et al., 2011). These physiological measures are recovered at different time scales, from minutes to several hours (Zhang et al., 2018).

The physiological disturbance associated with exhaustive exercise can surpass an individual's capacity to recover, which may lead to post-exercise mortality (Wood et al., 1983; McLean et al., 2016; Hvas et al., 2021). For example, post-exercise plasma lactate levels that exceed 10 mmol/l may serve as an early warning sign for mortality in some salmonids (Cooke et al., 2006; Eliason et al., 2022). Another indicator of exercise-related delayed mortality may be an individual's inability to recover their heart rates to the pre-exercise levels. Heart rates can take hours up to a day to recover after experiencing an acute stressor, including strenuous exercise or temperature change (Eliason et al., 2013b; Prystay et al., 2017; Bjarnason et al., 2019; Hvas et al., 2021; Doherty et al., 2022). This timeframe is longer than the recovery of blood lactate levels, ion balance, and metabolites (Zhang et al., 2018). Undoubtedly, impaired recovery can lead to mortality, but it is not well understood what processes are responsible for immediate or delayed mortality after exhaustive burst swimming episodes (Roscoe et al., 2011; Burnett et al., 2014a). Therefore, it remains crucial to understand the temporal scales of recovery and factors that can impede any aspect of recovery.

4.6.2. Evaluating recovery in adult salmon swimming: approaches

Quantitative data on post-swim recovery performance was not directly collated and analyzed for this review. Instead, we qualitatively reviewed each original study to understand the extent to which recovery is considered in adult salmonid swimming studies (Figure 28). Of 91 studies, 52 addressed recovery and its importance (Figure 28). Specifically, 29 studies discussed recovery in the context of swim performance of fish but did not test any recovery metrics. Twenty-three studies examined recovery performance complementary to measuring swim performance in adult salmonids. In these studies, recovery was most commonly evaluated by *i)* taking a blood sample to examine plasma ion and metabolite levels during or after recovery (Cl^-, K^+, Na^+, osmolality, glucose, lactate, cortisol, sex hormones (Estradiol, Testosterone)), to examine oxygen levels in the blood (e.g., arterial blood oxygen levels;), or hematocrit and hemoglobin levels, (n = 18 studies), by *ii)* measuring post-exercise excess oxygen consumption rates (metabolic costs) or recovery metabolism (n = 18), and by *iii)* measuring recovery capacity indirectly through repeat prolonged swim tests (U_{crit}, U_{max}), with minimal (< 1 h) recovery time between the tests. Cardiovascular capacity can be the "weak link" in fish's aerobic capacity (Eliason et al., 2013a) and thus their recovery capacity. This was examined in 11 studies. There is more than one way to evaluate recovery in fish, and some studies adopt multiple approaches.

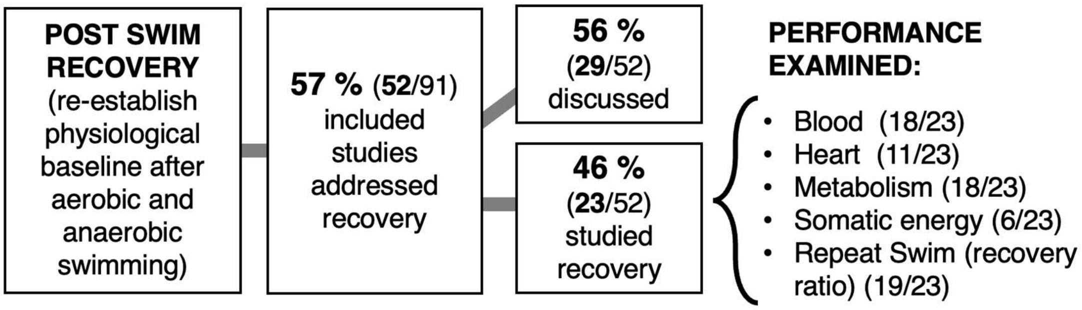

Figure 28. Summary of number of studies evaluating recovery in reviewed swim studies. A step flow diagram presenting how many studies were included in our review (total n = 91), directly examined or discussed recovery performance. Each mechanistic performance examined is described in more detail in the text.

4.7. WHAT ARE THE NEXT STEPS?

The *individual variation* in swim performance of adult salmon is strong, but itself is crucial to understand better how salmon will fare in short time scales (e.g., annual migration success) and across evolutionary timescales (e.g., inter-annual shifts in performance). Equally important is to continue addressing *species-specific variation* in swim performance across diverse ecologically and economically important species across life stages (meta-analysis by Rodgers et al., 2019). Depending on the research question, it may be crucial to separate aerobic and anaerobic swimming, ideally in the same individual fish, to examine trade-offs between these modes (Marras et al., 2010; Ejbye-Ernst et al., 2016). An essential contribution to the field of swimming literature comes from studies that examine the stability and context-dependent repeatability of swimming (Nelson et al., 2008; Marras et al., 2010; Bellinger et al., 2014; Killen et al., 2014, 2016; Conradsen and McGuigan 2015), especially provided that swim performance can change across habitats, migration sections

(Hinch et al., 2002), and life stages (Rodgers et al., 2019). Using the existing telemetry tools to measure swimming in the field (Cooke et al., 2013; Brownscombe et al., 2018; Matley et al., 2022) and standardized tests in the laboratory setting (Farrell, 2008; Little et al., 2020) provide a fantastic breadth of information about swimming capacity, recovery, and behavior in fish. These tools also provide an infrastructure to continue addressing many exciting research questions in fish swimming. Below we outline a series of questions that may continue to motivate research on fish swimming and migration performance of adult salmon.

Estimating and understanding aerobic and anaerobic swimming capacity:

1. What is the absolute maximum swimming capacity of adult salmon across species and populations, measured in cm/s?
2. How long can fish burst at different speeds (burst speed and duration relationship)?
3. How much consecutive bursting activity can be sustained (duration and frequency, e.g., bursts/min), and how does this bursting effort relate to recovery. How much bursting is '*bad*' [for recovery/survival]?
4. How does bursting behavior differ between individuals? Bursting patterns differ between individuals (e.g., some burst often using lower top speeds, some burst less frequently using higher burst speeds) – what are the physiological (intrinsic) or environmental (extrinsic) drivers determining these behaviors?
5. * How much bursting can be sustained and not lead to pre-spawn mortality?
6. Do fish choose to swim at identified optimal speeds? What causes any mismatches between predicted and observed optimal swim speeds: Inter- and intra-individual variation in aerobic and anaerobic swimming behaviors?
7. What are the aerobic and anaerobic contributions in the most used critical swim speed test, U_{crit}?
8. How do aerobic and anaerobic swimming and time to fatigue vary across temperatures?
9. How do aerobic and anaerobic swimming change under multi-stressor contexts? (e.g., temperature and infection loads, low energy density and high temperature, hypoxia, and temperature; e.g., Appendix 3, Figure 7).
10. How does swimming capacity differ between vulnerable groups, like mature females, when exposed to secondary stressors (e.g., temperature, hypoxia)?

Recovery post anaerobic swimming:

1. How much recovery is necessary between anaerobic swimming bursts? (the duration, amount of energy, blood analysis, time to 50%MMR, % aerobic scope)

2. What are the key bioindicators to determine sufficient recovery? (e.g., %MMR, % aerobic scope, lactate levels, cortisol levels)
3. How does recovery duration change if fish are exposed to different flow conditions during recovery? (e.g., 20 cm/s current, 50 cm/s current)
4. How do recovery requirements differ in fish after bursting at higher speeds and lower frequency or vice versa (speed, cm/s)?
5. How do recovery requirements differ across fish across body size and sex?
6. * Are the largest females the most compromised after bursting?
7. How do recovery requirements differ across temperatures?
8. What are various swimming recovery behaviors, and can they serve as indicators for impaired recovery?

4.7.1. Testing burst swimming in the laboratory and field:

There is a multitude of approaches to test swim performance in fish. One goal to address questions related to maximum swimming capacity is to design a swim performance test that captures anaerobic swimming and that can be performed in a setting where flows and under known and abiotic conditions (e.g., temperature, turbulence) are known or controlled. Another goal is to incorporate recovery metrics (at least one, ideally more).

A few valuable but more uncommon approaches that have been used for diverse species in a laboratory setting include: *i)* gait-transition tests in large plexiglass raceway (Peake 2008; e.g., Marras et al., 2010), *ii)* swim performance tests in custom-designed swim raceway system with controllable turbulent conditions resembling natural structures (Nikora et al., 2003; Hockley et al., 2014), *iii)* sprint swimming tests (Starrs et al., 2011, Nelson et al., 2002), *iv)* jump and leap performance tests in tunnel-type adjustable waterfalls (Kondratieff and Myrick 2006). In a recent review by Bett et al. (2022), the authors advocate for measuring swim performance in regulated natural experimental systems and provide an exemplary case study. Additionally, Lauritzen and colleagues measured the jump performance of adult migrating salmon (Lauritzen et al., 2005), which may serve as a rare and valuable study approach.

The much-discussed critical swim speed test (Plaut, 2002) is popular but comes with several limitations: *i)* positive ground speed and *true* acceleration to burst performance cannot be measured, *ii)* the calculated U_{crit} depends on the acceleration pattern of the fish, *iii)* swim tests carry a strong behavioral component. If possible, extending the swimming area for fish in the swim tunnel could be a valuable modification to allow fish to engage in longer burst swimming during the tests (Deslauriers et al., 2017). Fish will produce greater U_{crit} in longer swim tunnels (Kern et al., 2018), which presents one way to extend the value of the U_{crit} test and open the opportunity to better evaluate anaerobic swimming abilities in fish (Peake 2004; Peake and Farrell, 2006; Dockery et al., 2017). Most field swim performance values come from data collected using EMG tags. However, telemetry technology is growing rapidly, which will help capture anaerobic swim speeds in the field across greater velocity ranges, for longer durations, and at higher frequencies (Matley et al., 2022).

4.8. CONCLUDING REMARKS

Adult salmonids are exceptional swimmers that can achieve anaerobically fueled burst speeds up to 800 cm/s and 13 BL/s during their migration (Figures 22, 23, Table 5). These speeds are likely to be maintained for only short durations < 15 seconds and only for a few consecutive bursts before fish must recover. Salmon routinely swim at much lower swim speeds and commonly reported top swimming speeds are near 200 cm/s or 3-4 BL/s. Understanding swim performance between 200 cm/s and 800 cm/s (3 BL/s and ~13 BL/s) and understanding the required recovery needs following these swimming efforts is critical to developing effective management, conservation, and mitigation efforts to support the success of Pacific salmon across species and populations. A critical remaining knowledge gap remains: *how fast can salmon swim and how long?*

This review was motivated by the Big Bar Landslide that occurred in Spring 2018 at a remote section of the Fraser River, 64 km north of Lillooet, BC. The Big Bar entirely blocked the migration path for Pacific salmon in BC, Canada. Returning adult Chinook, Coho, Sockeye, and Pink Pacific salmon, and steelhead trout populations, including Fraser Steelhead (Chilcotin), Spring/Summer Chinook, Interior Fraser Coho, Early Stuart Sockeye, Early Summer Sockeye, Summer Run Sockeye, and Fraser Pinks were stopped facing water flows and turbulence at the Big Bar, on the way to their spawning grounds (Government of Canada 2019a). This raised an urgent conservation and management concern, to which researchers, stakeholders, commercial and recreational fishers, and indigenous peoples responded to identify actionable items for mitigation. It was clear that managers needed to know more about the swimming capacity of salmon and how biotic and abiotic factors impact it. However, salmonids are impacted by numerous natural and anthropogenic stressors across their range, and thus salmon swimming capacity has a broad scientific interest.

The results of this review signify that most swim speeds in adult salmon are measured using a critical swim speed test (U_{crit}) or in the field using different tagging methods, that the most studied species is sockeye salmon (*O. nerka*), and that the least studied are species with comparatively larger body sizes, namely, chum salmon (*O. keta*) and chinook salmon (*O. tshawytscha*). The species-specific maximum (anaerobic) speeds reported for salmon were: pink salmon, *O. gorbuscha* (199 cm/s, 3.90 BL/s), chum salmon, *O. keta* (533 cm/s, 3.32 BL/s), sockeye salmon, *O. nerka* (749 cm/s, 13.5 BL/s), chinook salmon, *O. tshawytscha* (668 cm/s, 1.9 BL/s), coho salmon *O. kisutch* (187 cm/s, 4.25 BL/s), Atlantic salmon, *S. salar* (406 cm/s, 7.91 BL/s), rainbow and steelhead trout, *O. mykiss* (817 cm/s, 3.53 BL/s), and masu salmon, *O. masou* (6.6 BL/s). The temperature effects on maximum swim performance in adult salmon are species-specific with estimated optimal temperatures ranging between 12.8ºC and 16.8 ºC (*O. nerka, O. keta, O. kisutch, S. salar*). Except, in pink salmon, they increased swim performance within the tested range (maximum 28ºC). Expectedly, larger adult salmon reached higher maximum swim speeds than smaller individuals in laboratory tests. However, body size was not associated with greater observed swim speeds in the field. Lastly, there appeared to be no consistent quantitative way to quantify recovery capacity for adult salmon robustly. Still, growing evidence shows that excessive anaerobic burst swimming is related to high mortality, but it is unknown how much burst activity is excessive or how this trend varies with temperature, sex, species, or population.

CONCLUSION

Many fish species are declining in body size in response to warming suggesting they are limited by a size-specific vulnerability to temperature (Audzijonyte et al., 2020, 2016, 2013; Daufresne et al., 2009; Dulvy and Reynolds, 2002; Gardner et al., 2011; Lindmark et al., 2022, 2018; Rubalcaba et al., 2020). However, we require a better understanding of the causes and consequences of body size-specific vulnerability to warming in fishes. For example, consequences to declining body size with temperature may include alter size-structure of communities leading to decreased population productivity (Lindmark et al., 2022, 2018) that depend on the fecundity of vulnerable large spawners and offspring (Barneche et al., 2018; Dahlke et al., 2020). Additionally, a decline in fish body can lead to declining fisheries value. The mechanism behind of declining body size are debated and poorly understood (Audzijonyte et al., 2019; Lefevre et al., 2021, 2017; Lindmark et al., 2022; Pauly and Cheung, 2018). Therefore, careful selection of physiological traits to study is necessary to help reveal underlying causes of size-specific vulnerability in fishes.

We approached our questions about *causes* and *consequences* from three angles: first, using aerobic metabolic scaling relationships (whole-animal level); second, examining the possible physiological mechanisms of altered aerobic metabolism-scaling relationships (organ level); and third, exploring the consequences of size-specific vulnerability in the field of applied conservation physiology (interdisciplinary research). Aerobic metabolic scaling relationships varied profoundly across fish species and thus helped to identify size-specific constraints with warming. However, we believe that temperature-modulated aerobic metabolism scaling relationships bring value only in the context of species-specific ecologies, life histories, and morphologies (*Chapter 2*; Baudron et al., 2014; Killen et al., 2010; Kozłowski et al., 2020). Further, our work demonstrated that scaling relationships of aerobic metabolism (MMR, RMR, and thus AAS and FAS) do not directly determine thermal tolerance in fishes and therefore may not reveal the underlying causes of '*Why fish are declining in body size.'* Further, temperature-dependent scaling relationships merit further investigation for their use in ecology and physiology (Brown et al., 2004; Lindmark et al., 2022, 2018).

Mechanistically, size-specific vulnerability may be best understood when scaling relationships of aerobic metabolism are experimentally examined together with thermal dependence of other physiological performances such as cardiac thermal performance (*Chapter 3*). For example, in contrast to our predictions, the greater cardiac thermal tolerance in larger barred surfperch revealed that larger individuals were more tolerant to warming than smaller individuals. We also identified vulnerability in fishes by examining other performances beyond metabolism (Audzijonyte et al., 2013; Bernhardt et al., 2018; Fryxell et al., 2020; Lindmark et al., 2018). Specifically, we studied the swim performance of migrating adult salmon returning to their natal streams to spawn. During most of their spawning migration, salmon swim aerobically; however, they must also burst anaerobically and recover *en route* (Burnett et al., 2014; Hinch and Rand, 2000). Therefore, salmon require both aerobic and anaerobic swim performances to successfully reach their spawning grounds with enough energy left to spawn. We showed that larger salmonids *can* swim faster (i.e., reach higher absolute swim speeds in cm/s), but in the wild, where flows vary at spatial and temporal scales, larger salmon may not *choose* to swim at their maximum ability. Nevertheless, body size is only one factor that can predict swim performance in salmon (the review, *Chapter 4,* touched on the effects of temperature and sex on swimming and recovery performances and emphasized inter- and intra-specific variation in swimming). In addition, a key question remains unanswered due to the logistical challenges of working with such large, athletic fishes: *How fast can adult salmon swim?* Understanding fish swimming helps us evaluate the effects of changing climates and the impacts of ecological disasters, like landslides that alter flow. Together, this thesis combined a complementary selection of approaches – meta-analyses, laboratory empirical studies, and a collated data-based review covering performances at whole-animal and organ levels. Interdisciplinary research is necessary to conceptualize the mechanisms and consequences of size-specific vulnerability of fishes.

The trend of declining body size with warming in fishes is not observed in all fish species (Audzijonyte et al., 2020; Baudron et al., 2014). This observation aligns with the prominent variation in metabolic scaling relationships we found across fishes. However, it is clear that the metabolic scaling relationships of fishes do not solely determine the decrease in body size with warming (Wootton et al., 2022). Moving forward, there are many avenues for ongoing and future research that will bring us closer to understanding the *causes* of declining body size in fish. For example, a very exciting area of research is exploring life-stage specific thermal tolerance (Dahlke et al., 2020). However, it remains challenging to disentangle the overlapping effects of life stage and body size. Further, we may continue to study the variation in aerobic metabolism, cardiac thermal tolerance, and swimming performance at higher levels of biological organization (individual, population, species, and species with shared ecologies). Specifically, we may study the sources and consequences (good and bad) of this variation (Auer et al., 2020; Burton et al., 2011; Eliason et al., 2011; Killen et al., 2010; Metcalfe et al., 2016), while considering body size and life-stage as contributing factors. Another area of research may address the timescales of physiological responses and the roles of each determining size-specific vulnerability in fishes. For example, an outstanding question is, how does physiological tolerance differ across varying sizes of individuals in response to acute exposure, long-term acclimation, and acclimatization (e.g., Gilbert et al., 2022; Schulte et al., 2011) or with developmental conditions (i.e., developmental plasticity; Atkinson et al., 2006)? Alternatively, studying size-specific environmental tolerance may be approached considering factors acting across generations (parental effects, transgenerational plasticity, and epigenetics; see reviews: Kozłowski et al., 2020; Verberk et al., 2021). Certainly, there are a myriad of study objectives to address that will advance our knowledge about body size-specific vulnerability to warming in fishes.

There are also many areas for future research that will bring us closer to understanding the *consequences* of declining body size in fish. For example, having smaller fish can jeopardize food security through shifts or losses of fisheries (Oke et al., 2020; Pinsky et al., 2011; Rice and Garcia, 2011). Body size changes could cause unexpected shifts in food webs, possibly leading to loss of ecosystem stability and functioning (Jeppesen et al., 2010; Lindmark et al., 2022; Rice and Garcia, 2011). And possessing a smaller body size can negatively affect an individual's reproductive output (Barneche et al., 2018). Therefore, the consequences of declining body size in fish are widespread and can emerge at the level of an individual fish and span all the way to ecosystem function.

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APPENDICES

APPENDIX 1, CHAPTER 2.

Ref ID	Full reference	MR terminology	MMR	RMR
2	Auer SK, Salin K, Rudolf AM, Anderson GJ, Metcalfe NB. 2015 The optimal combination of standard metabolic rate and aerobic scope for somatic growth depends on food availability. Funct. Ecol. 29, 479–486. (doi:10.1111/1365-2435.12396) **Data:** *Supplemental Material*	SMR		Y
3	Behrens JW, van Deurs M, Christensen EAF. 2017 Evaluating dispersal potential of an invasive fish by the use of aerobic scope and osmoregulation capacity. PLOS ONE 12, e0176038. (doi:10.1371/journal.pone.0176038) **Data:** *Supplemental Material*	MMR/SMR	Y	Y
73	Blasco FR, Esbaugh AJ, Killen SS, Rantin FT, Taylor EW, McKenzie DJ. 2020 Using aerobic exercise to evaluate sub-lethal tolerance of acute warming in fishes. J. Exp. Biol. 223. (doi:10.1242/jeb.218602) **Data:** McKenzie, David (2020), Using aerobic exercise to evaluate sub-lethal tolerance of acute warming in fishes, Dryad, Dataset, https://doi.org/10.5061/dryad.cjsxksn2v	AMR	Y	-
7	Boldsen MM, Norin T, Malte H. 2013 Temporal repeatability of metabolic rate and the effect of organ mass and enzyme activity on metabolism in European eel (*Anguilla anguilla*). Comp. Biochem. Physiol. A. Mol. Integr. Physiol. 165, 22–29. (doi:10.1016/j.cbpa.2013.01.027) **Data:** *Personally received*	SMR	-	Y
26	Bonneaud C, Wilson RS, Seebacher F. 2016 Immune-Challenged Fish Up-Regulate Their Metabolic Scope to Support Locomotion. PLOS ONE 11, e0166028. (doi:10.1371/journal.pone.0166028) **Data:** Bonneaud, Camille; Wilson, Robbie S.; Seebacher, Frank (2017), Data from: Immune-challenged fish up-regulate their metabolic scope to support locomotion, Dryad, Dataset, https://doi.org/10.5061/dryad.km3qd	Maximum and resting metabolic rates	**Y**	Y

43	Chen Z, Farrell AP, Matala A, Narum SR. 2018 Mechanisms of thermal adaptation and evolutionary potential of conspecific populations to changing environments. Mol. Ecol. 27, 659–674. (doi:10.1111/mec.14475) **Data**: Chen, Zhongqi; Farrell, Anthony P.; Matala, Amanda; Narum, Shawn R. (2017), Data from: Mechanisms of thermal adaptation and evolutionary potential of conspecific populations to changing environments, Dryad, Dataset, https://doi.org/10.5061/dryad.s04ng	MMR/RMR	Y	Y
56	Christensen EAF, Stieglitz JD, Grosell M, Steffensen JF. 2019 Intra-Specific Difference in the Effect of Salinity on Physiological Performance in European Perch (*Perca fluviatilis*) and Its Ecological Importance for Fish in Estuaries. Biology 8, 1–17. (doi:10.3390/biology8040089) **Data**: [dataset] Christensen EAF (2018). Intra-Specific Difference in the Effect of Salinity on Physiological Performance in European Perch (*Perca fluviatilis*) and Its Ecological Importance for Fish in Estuaries., biostudies, V1. https://www.ebi.ac.uk/biostudies/studies/S-EPMC6956070.	MMR	Y	-
70	Christensen EAF, Svendsen MBS, Steffensen JF. 2020 The combined effect of body size and temperature on oxygen consumption rates and the size-dependency of preferred temperature in European perch *Perca fluviatilis*. J. Fish Biol. 97, 794–803. (doi:10.1111/jfb.14435) **Data**: *Supplemental material*	MMR/SMR	Y	Y
10	Collins GM, Clark TD, Carton AG. 2016 Physiological plasticity v. inter-population variability: understanding drivers of hypoxia tolerance in a tropical estuarine fish. Mar. Freshw. Res. 67, 1575. (doi:10.1071/MF15046) **Data**: Collins, G. (2017). Physiological plasticity vs.inter-population variability: understanding drivers of hypoxia tolerance in a tropical estuarine fish. James Cook University. (dataset). http://dx.doi.org/10.4225/28/58c62cb87ebfd	Resting MO$_2$	-	Y
22	Collins GM, Clark TD, Rummer JL, Carton AG. 2013 Hypoxia tolerance is conserved across genetically distinct sub-populations of an iconic, tropical Australian teleost (*Lates calcarifer*). Conserv Physiol 1. (doi:10.1093/conphys/cot029) **Data**: Collins, Geoffrey (2017): Hypoxia tolerance is conserved across genetically-distinct sub-populations of an iconic, tropical Australian teleost (*Lates calcarifer*). James Cook University. https://doi.org/10.4225/28/58be1a4623491	Resting MO$_2$	-	Y
15	Cooper B, Adriaenssens B, Killen SS. 2018 Individual variation in the compromise between social group membership	MMR/SMR	Y	Y

	and exposure to preferred temperatures. Proc. R. Soc. B Biol. Sci. 285, 20180884. (doi:10.1098/rspb.2018.0884) **Data**: Killen, Shaun; Cooper, Ben; Adriaenssens, Bart (2018), "Data for Cooper et al.", Mendeley Data, V1, doi: 10.17632/34npwr97vn.1			
60	Eliason EJ et al. 2011 Differences in Thermal Tolerance Among Sockeye Salmon Populations. Science 332, 109–112. (doi:10.1126/science.1199158) Data: *Personal data*	MAX/MIN O2 cons	Y	Y
18	Eliason EJ, Higgs DA, Farrell AP. 2007 Effect of isoenergetic diets with different protein and lipid content on the growth performance and heat increment of rainbow trout. Aquaculture 272, 723–736. (doi:10.1016/j.aquaculture.2007.09.006) Data: *Personal data*	SMR	-	Y
32	Fugère V, Mehner T, Chapman LJ. 2018 Impacts of deforestation-induced warming on the metabolism, growth and trophic interactions of an afrotropical stream fish. Funct. Ecol. 32, 1343–1357. (doi:10.1111/1365-2435.13065) **Data**: Fugère, Vincent; Mehner, Thomas; Chapman, Lauren J. (2019), Data from: Impacts of deforestation-induced warming on the metabolism, growth, and trophic interactions of an afrotropical stream fish, Dryad, Dataset, https://doi.org/10.5061/dryad.qg78q	AMR/RMR	Y	Y
27	Hess S, Prescott LJ, Hoey AS, McMahon SA, Wenger AS, Rummer JL. 2017 Species-specific impacts of suspended sediments on gill structure and function in coral reef fishes. Proc. R. Soc. B Biol. Sci. 284, 20171279. (doi:10.1098/rspb.2017.1279) **Data**: Hess, S. (2017). Species-specific impacts of suspended sediments on gill structure and function in coral reef fishes. James Cook University. (dataset). http://dx.doi.org/10.4225/28/59364b00c5bce	MO_2 rest	-	Y
31	Hooker OE, Leeuwen TEV, Adams CE. 2017 The physiological costs of prey switching reinforce foraging specialization. J. Anim. Ecol. 86, 605–614. (doi:10.1111/1365-2656.12632) **Data**: Hooker, Oliver E.; Van Leeuwen, Travis E.; Adams, Colin E. (2017), Data from: The physiological costs of prey switching reinforce foraging specialization, Dryad, Dataset, https://doi.org/10.5061/dryad.v65m0	SMR	-	Y
42	Huang Q, Zhang Y, Liu S, Wang W, Luo Y. 2013 Intraspecific Scaling of the Resting and Maximum Metabolic Rates of the	MMR/RMR	Y	Y

	Crucian Carp (*Carassius auratus*). PLoS ONE 8, e82837. (doi:10.1371/journal.pone.0082837) **Data**: Huang, Qingda et al. (2014), Data from: Intraspecific scaling of the resting and maximum metabolic rates of the crucian carp (*Carassius auratus*), Dryad, Dataset, https://doi.org/10.5061/dryad.cr3p			
71	Huang Y, Fu S, Cooke SJ, Xia J. 2020 Is repeatability of metabolic rate influenced by social separation? A test with a teleost fish. Biol. Lett. 16, 20190825. (doi:10.1098/rsbl.2019.0825) **Data**: Yan, Huang; Fu, Shijian; Cooke, Steven; Xia, Jigang (2020), Data from: Is repeatability of metabolic rate influenced by social separation? a test with a teleost fish, Dryad, Dataset, https://doi.org/10.5061/dryad.n2z34tmsr	RMR	-	Y
11	Khan JR, Pether S, Bruce M, Walker SP, Herbert NA. 2014 Optimum temperatures for growth and feed conversion in cultured hapuku (*Polyprion oxygeneios*) — Is there a link to aerobic metabolic scope and final temperature preference? Aquaculture 430, 107–113. (doi:10.1016/j.aquaculture.2014.03.046) Data: *Personally received*	SMR	-	Y
14	Khan JR, Pether S, Bruce M, Walker SP, Herbert NA. 2015 The effect of temperature and ration size on specific dynamic action and production performance in juvenile hapuku (*Polyprion oxygeneios*). Aquaculture 437, 67–74. (doi:10.1016/j.aquaculture.2014.11.024) Data: *Personally received*	SMR	-	Y
13	Khan JR, Johansen D, Skov PV. 2018 The effects of acute and long-term exposure to CO2 on the respiratory physiology and production performance of Atlantic salmon (*Salmo salar*) in freshwater. Aquaculture 491, 20–27. (doi:10.1016/j.aquaculture.2018.03.010) Data: *Personally received*	SMR	-	Y
12	Khan JR, Lazado CC, Methling C, Skov PV. 2018 Short-term feed and light deprivation reduces voluntary activity but improves swimming performance in rainbow trout *Oncorhynchus mykiss*. Fish Physiol. Biochem. 44, 329–341. (doi:10.1007/s10695-017-0438-0) **Data**: *Personally received*	SMR	-	Y
55	Killen SS, Croft DP, Salin K, Darden SK. 2016 Male sexually coercive behaviour drives increased swimming efficiency in	MMR	Y	-

	female guppies. Functional Ecology 30, 576–583. (doi:https://doi.org/10.1111/1365-2435.12527) **Data**: Killen, Shaun S.; Croft, Darren P.; Salin, Karine; Darden, Safi K. (2016), Data from: Male sexually coercive behaviour drives increased swimming efficiency in female guppies, Dryad, Dataset, https://doi.org/10.5061/dryad.vh8v4			
28	Killen SS, Mitchell MD, Rummer JL, Chivers DP, Ferrari MCO, Meekan MG, McCormick MI. 2014 Aerobic scope predicts dominance during early life in a tropical damselfish. Funct. Ecol. 28, 1367–1376. (doi:10.1111/1365-2435.12296) **Data**: Killen, et al. (2015), Data from: Aerobic scope predicts dominance during early life in a tropical damselfish, Dryad, Dataset, https://doi.org/10.5061/dryad.7gc05	MMR/RMR	Y	Y
4	Killen SS. 2014 Growth trajectory influences temperature preference in fish through an effect on metabolic rate. J. Anim. Ecol. 83, 1513–1522. (doi:10.1111/1365-2656.12244) **Data**: Killen, et al. (2015), Data from: Aerobic scope predicts dominance during early life in a tropical damselfish, Dryad, Dataset, https://doi.org/10.5061/dryad.7gc05	MMR/SMR	Y	Y
8	Kunz KL et al. 2016 New encounters in Arctic waters: a comparison of metabolism and performance of polar cod (*Boreogadus saida*) and Atlantic cod (*Gadus morhua*) under ocean acidification and warming. Polar Biol. 39, 1137–1153. (doi:10.1007/s00300-016-1932-z) **Data**: Kunz, Kristina Lore; Frickenhaus, Stephan; Hardenberg, Silvia; Torild, Johansen; Leo, Elettra; Pörtner, Hans-Otto; Schmidt, Matthias; Windisch, Heidrun Sigrid; Knust, Rainer; Mark, Felix Christopher (2016): New encounters in Arctic waters: a comparison of metabolism and performance of polar cod (*Boreogadus saida*) and Atlantic cod (*Gadus morhua*) under ocean acidification and warming. PANGAEA, https://doi.org/10.1594/PANGAEA.870468	Standard metabolic rate (MO_2)	-	Y
8	Kunz KL, Claireaux G, Pörtner H-O, Knust R, Mark FC. 2018 Aerobic capacities and swimming performance of polar cod (*Boreogadus saida*) under ocean acidification and warming conditions. Journal of Experimental Biology 221: jeb184473. (doi:10.1242/jeb.184473) **Data**: Kunz, Kristina Lore; Claireaux, Guy; Pörtner, Hans-Otto; Knust, Rainer; Mark, Felix Christopher (2018): Swimming and respiration data of Polar cod (*Boreogadus saida*) under ocean acidification and warming conditions. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.889445	MMR	Y	-

16	McArley TJ, Hickey AJR, Herbert NA. 2017 Chronic warm exposure impairs growth performance and reduces thermal safety margins in the common triplefin fish (*Forsterygion lapillum*). J. Exp. Biol. 220, 3527–3535. (doi:10.1242/jeb.162099) **Data**: *Personally received*	SMR	-	Y
17	McArley TJ, Hickey AJR, Herbert NA. 2018 Hyperoxia increases maximum oxygen consumption and aerobic scope of intertidal fish facing acutely high temperatures. J. Exp. Biol., jeb.189993. (doi:10.1242/jeb.189993) **Data**: *Personally received*	SMR	-	Y
6	McLean S, Persson A, Norin T, Killen SS. 2018 Metabolic Costs of Feeding Predictively Alter the Spatial Distribution of Individuals in Fish Schools. Curr. Biol. 28, 1144–1149. (doi:https://doi.org/10.1016/j.cub.2018.02.043) **Data**: Killen, Shaun; McLean, Stephanie; Persson, Anna; Norin, Tommy (2018), “Data for McLean et al Metabolic costs of feeding predictively alter the spatial distribution of individuals in fish schools”, Mendeley Data, V1, doi: 10.17632/8g955t3r9g.1	MMR/SMR	Y	Y
30	Morozov S, Leinonen T, Merilä J, McCairns RJS. 2018 Selection on the morphology–physiology-performance nexus: Lessons from freshwater stickleback morphs. Ecol. Evol. 8, 1286–1299. (doi:10.1002/ece3.3644) **Data**: Morozov, Sergey et al. (2018), Data from: Selection on the morphology-physiology-performance nexus: lessons from freshwater stickleback morphs, Dryad, Dataset, https://doi.org/10.5061/dryad.73kb7	SMR	-	Y
34	Motson K, Donelson JM. 2017 Limited capacity for developmental thermal acclimation in three tropical wrasses. Coral Reefs 36, 609–621. (doi:10.1007/s00338-017-1546-0) **Data**: Motson, K. (2017). Limited capacity for developmental thermal acclimation in three tropical wrasses. James Cook University. (dataset). http://dx.doi.org/10.4225/28/586c8ca7f09a5	MO2 rest/MO2max	Y	Y
21	Nadler LE, Killen SS, McClure EC, Munday PL, McCormick MI. 2016 Shoaling reduces metabolic rate in a gregarious coral reef fish species. J. Exp. Biol. 219, 2802–2805. (doi:10.1242/jeb.139493) **Data**: Nadler, L.; Killen, S.; McClure, E.; Munday, P.; McCormick, M. (2016). Shoaling reduces metabolic rate in a	MRmin	-	Y

	gregarious coral reef fish species. James Cook University. (dataset). http://dx.doi.org/10.4225/28/5745456AD6433			
19	Norin T, Malte H. 2011 Repeatability of standard metabolic rate, active metabolic rate and aerobic scope in young brown trout during a period of moderate food availability. J. Exp. Biol. 214, 1668–1675. (doi:10.1242/jeb.054205) **Data**: *Personally received*	AMR/SMR	Y	Y
20	Norin T, Malte H. 2012 Intraspecific Variation in Aerobic Metabolic Rate of Fish: Relations with Organ Size and Enzyme Activity in Brown Trout. *Physiol. Biochem. Zool.* **85**, 645–656. (doi:10.1086/665982) **Data**: *Personally received*	MMR/SMR	Y	Y
5	Norin T, Clark TD. 2017 Fish face a trade-off between ‘eating big’ for growth efficiency and ‘eating small’ to retain aerobic capacity. Biology Letters 13, 20170298. (doi:10.1098/rsbl.2017.0298) **Data**: *Supplemental material*	MO2max/MO2min	Y	Y
9	Norin T, Malte H, Clark TD. 2016 Differential plasticity of metabolic rate phenotypes in a tropical fish facing environmental change. Funct. Ecol. 30, 369–378. (doi:10.1111/1365-2435.12503) **Data**: *Supplemental material*	MMR/SMR	Y	Y
1	Norin T, Gamperl AK. 2018 Metabolic scaling of individuals vs. populations: Evidence for variation in scaling exponents at different hierarchical levels. Funct. Ecol. 32, 379–388. (doi:10.1111/1365-2435.12996) **Data**: Norin, Tommy; Gamperl, A. Kurt (2018), Data from: Metabolic scaling of individuals vs. populations: evidence for variation in scaling exponents at different hierarchical levels, Dryad, Dataset, https://doi.org/10.5061/dryad.fp32k	AMR/SMR	Y	Y
35	Nyboer EA, Chapman LJ. 2017 Elevated temperature and acclimation time affect metabolic performance in the heavily exploited Nile perch of Lake Victoria. J. Exp. Biol. 220, 3782–3793. (doi:10.1242/jeb.163022) **Data**: Nyboer, Elizabeth A.; Chapman, Lauren J. (2017), Data from: Elevated temperature and acclimation time affect metabolic performance in the heavily exploited Nile perch of Lake Victoria, Dryad, Dataset, https://doi.org/10.5061/dryad.2s590	MMR/SMR	Y	Y
33	Nyboer EA, Chapman LJ. 2018 Cardiac plasticity influences aerobic performance and thermal tolerance in a tropical,	MMR/SMR	Y	Y

	freshwater fish at elevated temperatures. J. Exp. Biol. 221, jeb178087. (doi:10.1242/jeb.178087) **Data**: Nyboer, Elizabeth A.; Chapman, Lauren J. (2018), Data from: Cardiac plasticity influences aerobic performance and thermal tolerance in a tropical, freshwater fish at elevated temperatures, Dryad, Dataset, https://doi.org/10.5061/dryad.2k527b8			
54	Pang X, Shao F, Ding S, Fu S, Zhang Y. 2020 Interspecific differences and ecological correlations of energy metabolism traits in freshwater fishes. Funct. Ecol. 34, 616–630. (doi:10.1111/1365-2435.13505) **Data**: Fu, Shi-Jian et al. (2019), Interspecific differences and ecological correlations of energy metabolism traits in freshwater fishes, Dryad, Dataset, https://doi.org/10.5061/dryad.5mkkwh71w	MMR/RMR	Y	Y
72	Pilakouta N, Killen SS, Kristjánsson BK, Skúlason S, Lindström J, Metcalfe NB, Parsons KJ. 2020 Multigenerational exposure to elevated temperatures leads to a reduction in standard metabolic rate in the wild. Funct. Ecol. 34, 1205–1214. (doi:10.1111/1365-2435.13538) **Data**: Pilakouta, Natalie et al. (2020), Multigenerational exposure to elevated temperatures leads to a reduction in standard metabolic rate in the wild, Dryad, Dataset, https://doi.org/10.5061/dryad.rfj6q576x	MMR/SMR	Y	Y
40	Raffard A, Cucherousset J, Prunier JG, Loot G, Santoul F, Blanchet S. 2019 Variability of functional traits and their syndromes in a freshwater fish species (*Phoxinus phoxinus*): The role of adaptive and nonadaptive processes. Ecol. Evol. 9, 2833–2846. (doi:10.1002/ece3.4961) **Data**: Raffard, Allan; Cucherousset, Julien; Prunier, Jérôme G.; Loot, Géraldine; Santoul, Frédéric; Simon, Blanchet (2019): Variability of functional traits and their syndromes in a freshwater fish species (*Phoxinus phoxinus*): The role of adaptive and non□adaptive processes. figshare. Dataset. https://doi.org/10.6084/m9.figshare.7623854.v1	Metabolic rate	-	Y
38	Rodgers GG, Rummer JL, Johnson LK, McCormick MI. 2019 Impacts of increased ocean temperatures on a low-latitude coral reef fish – Processes related to oxygen uptake and delivery. J. Therm. Biol. 79, 95–102. (doi:10.1016/j.jtherbio.2018.12.008) **Data**: Rodgers, G. (2018). Impacts of increased ocean temperatures on a low-latitude coral reef fish – processes related to oxygen uptake and delivery . James Cook University. (dataset). http://dx.doi.org/10.25903/5c0eff685e349	MO2routine/ MO2max	Y	Y

53	Rupia EJ, Binning SA, Roche DG, Lu W. 2016 Fight-flight or freeze-hide? Personality and metabolic phenotype mediate physiological defense responses in flatfish. J. Anim. Ecol. 85, 927–937. (doi:10.1111/1365-2656.12524) **Data**: Rupia, Emmanuel; Binning, Sandra; Roche, Dominique; Lu, Weiqun (2016): Fight-flight or freeze-hide? Personality and metabolic phenotype mediate physiological defense responses in a benthic fish. figshare. Dataset. https://doi.org/10.6084/m9.figshare.1365473.v7	MMR/SMR	Y	Y
41	Sandersfeld T, Davison W, Lamare MD, Knust R, Richter C. 2015 Elevated temperature causes metabolic trade-offs at the whole-organism level in the Antarctic fish *Trematomus bernacchii*. J. Exp. Biol. 218, 2373–2381. (doi:10.1242/jeb.122804) **Data**: *Supplemental material*	RMR	-	Y
75	Ste-Marie E, Watanabe YY, Semmens JM, Marcoux M, Hussey NE. 2020 A first look at the metabolic rate of Greenland sharks (*Somniosus microcephalus*) in the Canadian Arctic. Sci. Rep. 10, 19297. (doi:10.1038/s41598-020-76371-0) **Data**: *Supplemental material*	Active routine MR/ resting routine MR	Y	Y
36	Strobel A, Bennecke S, Leo E, Mintenbeck K, Pörtner HO, Mark FC. 2012 Metabolic shifts in the Antarctic fish *Notothenia rossii* in response to rising temperature and PCO_2. Front. Zool. 9, 28. (doi:10.1186/1742-9994-9-28) **Data**: Strobel, Anneli; Bennecke, Swaantje; Leo, Elettra; Mintenbeck, Katja; Pörtner, Hans-Otto; Mark, Felix Christopher (2014): Experiment: Metabolic shifts in the Antarctic fish *Notothenia rossii* in response to rising temperature and PCO2. PANGAEA, https://doi.org/10.1594/PANGAEA.829830, Supplement to: Strobel, A et al. (2012): Metabolic shifts in the Antarctic fish *Notothenia rossii* in response to rising temperature and PCO2. Frontiers in Zoology, 9(1), 28, https://doi.org/10.1186/1742-9994-9-28	Routine metabolic rate	-	Y
24	Zhang Y, Timmerhaus G, Anttila K, Mauduit F, Jørgensen SM, Kristensen T, Claireaux G, Takle H, Farrell AP. 2016 Domestication compromises athleticism and respiratory plasticity in response to aerobic exercise training in Atlantic salmon (*Salmo salar*). Aquaculture 463, 79–88. (doi:10.1016/j.aquaculture.2016.05.015) **Data**: *Personally received*	SMR	-	Y
23	Zhang Y, Mauduit F, Farrell AP, Chabot D, Ollivier H, Rio-Cabello A, Le Floch S, Claireaux G. 2017 Exposure of	SMR	-	Y

	European sea bass (*Dicentrarchus labrax*) to chemically dispersed oil has a chronic residual effect on hypoxia tolerance but not aerobic scope. Aquat. Toxicol. 191, 95–104. (doi:10.1016/j.aquatox.2017.07.020) **Data**: *Personally received*			
51	Pope EC et al. 2014 European sea bass, *Dicentrarchus labrax*, in a changing ocean. Biogeosciences 11, 2519–2530. (doi:https://doi.org/10.5194/bg-11-2519-2014) **Data**: Pope, E C; Ellis, Robert P; Scolamacchia, M; Scolding, J W S; Keay, A; Chingombe, P; Shields, R J; Wilcox, R; Speirs, Douglas C; Wilson, R W; Lewis, Ceri N; Flynn, K J (2014): European sea bass, *Dicentrarchus labrax*, in a changing ocean. PANGAEA, https://doi.org/10.1594/PANGAEA.835574	MMR /RMR	Y	-
52	Yan G-J, He X-K, Cao Z-D, Fu S-J. 2013 An interspecific comparison between morphology and swimming performance in cyprinids. J. Evol. Biol. 26, 1802–1815. (doi:10.1111/jeb.12182) **Data**: Yan, Guan-Jie et al. (2013), Data from: An interspecific comparison between morphology and swimming performance in cyprinids, Dryad, Dataset, https://doi.org/10.5061/dryad.vk820	MMR	Y	-
62	Van Wert, J.C., A. Ekstrom, B. Hendriks, D.A. Patterson, S.J. Cooke, S.G. Hinch, E.J. Eliason. Thermal tolerance in Chinook salmon. **Data**: *Personally received*	MMR/RMR	Y	Y
61	Kraskura K*, Hardison EA*, Little AG, Dressler T, Prystay TS, Hendriks B, Farrell AP, Cooke SJ, Patterson DA, Hinch SG, and Eliason EJ. Sex-specific differences in swimming, aerobic metabolism, and recovery from exercise in adult coho salmon (*Oncorhynchus kisutch*) across ecologically relevant temperatures. Conservation Physiology. Volume 9: 10.1093/conphys/coab016 **Data**: *Personal data*	MMR/RMR	Y	Y
203	Auer, S.K., Salin, K., Rudolf, A.M., Anderson, G.J. & Metcalfe, N.B. 2016. Differential effects of food availability on minimum and maximum rates of metabolism. *Biology Letters,* 12, 20160586. ***Data***: Auer, S.K., Salin, K., Rudolf, A.M., Anderson, G.J. & Metcalfe, N.B. 2016. Data from: Differential effects of food availability on minimum and maximum rates of metabolism. http://datadryad.org/stash/dataset/doi:10.5061/dryad.g0q0q	MMR/SMR	Y	Y

77	Lv X, Xie H, Xia D, Shen C, Li J, Luo Y. 2018 Mass scaling of the resting and maximum metabolic rates of the black carp. J Comp Physiol B 188, 591–598. (doi:10.1007/s00360-018-1154-5) ***Data:*** *Supplemental material*	RMR/MMR	Y	Y
204	Andersson ML, Sundberg F, Eklöv P. 2020 Chasing away accurate results: exhaustive chase protocols underestimate maximum metabolic rate estimates in European perch *Perca fluviatilis*. Journal of Fish Biology 97, 1644–1650. (doi:https://doi.org/10.1111/jfb.14519) ***Data:*** Andersson M. 2020 Data for: Chasing away accurate results: exhaustive chase protocols underestimate maximum metabolic rate estimates in European perch *Perca fluviatilis.* (doi:10.5281/zenodo.3873396)	MMR/SMR	Y	Y
79	Killen, S.S., Esbaugh, A.J., Martins, N.F., Rantin, F.T. & McKenzie, D.J. (2018b). Aggression supersedes individual oxygen demand to drive group air-breathing in a social catfish. Journal of Animal Ecology, 87, 223–234. ***Data****:* Killen, S.S., Esbaugh, A.J., Martins, N., Rantin, F.T., McKenzie, D.J., F. Martins, N., et al. (2018). Data from: Aggression supersedes individual oxygen demand to drive group air-breathing in a social catfish. https://doi.org/10.1111/1365-2656.12758	SMR	-	Y
78	Shi, C., Yao, M., Lv, X., Zhao, Q., Peng, Z. & Luo, Y. (2018). Body and organ metabolic rates of a cave fish, *Triplophysa rosa*: influence of light and ontogenetic variation. J Comp Physiol B, 188, 947–955. https://doi.org/10.1007/s00360-018-1178-x ***Data:*** *Supplemental material*	Resting MO_2	-	Y
76	Li, Q., Zhu, X., Xiong, W., Zhu, Y., Zhang, J., Djiba, P.K., et al. (2020). Effects of temperature on metabolic scaling in black carp. PeerJ, 8, e9242. https://peerj.com/articles/9242 ***Data:*** *Supplemental material*	RMR	-	Y
301	Binning, S. A., Ros, A. F. H., Nusbaumer, D. and Roche, D. G. (2015). Physiological Plasticity to Water Flow Habitat in the Damselfish, *Acanthochromis polyacanthus*: Linking Phenotype to Performance. PLOS ONE 10, e0121983. ***Data:*** Binning, S., 2015. Data from "Physiological plasticity to water flow habitat in the damselfish, *Acanthochromis polyacanthus*: linking phenotype to performance." https://doi.org/10.6084/m9.figshare.923561.v6	MO_2max (swimming MO_2)	Y	

302	Christensen, Emil A. F., Norin, T., Tabak, I., van Deurs, M., Behrens, J.W., 2021. Effects of temperature on physiological performance and behavioral thermoregulation in an invasive fish, the round goby. Journal of Experimental Biology 224. https://doi.org/10.1242/jeb.237669 ***Data***: Christensen, Emil A F, Norin, T., Behrens, J.W., 2021. Data and R script for: Effects of temperature on physiological performance and behavioral thermoregulation in an invasive fish, the round goby. Figshare. https://doi.org/10.6084/m9.figshare.13204841.v1	MMR/SMR	Y	Y
303	Cooper, C.J., Kristan, W.B., Eme, J., 2021. Thermal tolerance and routine oxygen consumption of convict cichlid, *Archocentrus nigrofasciatus*, acclimated to constant temperatures (20 °C and 30 °C) and a daily temperature cycle (20 °C → 30 °C). J Comp Physiol B 191, 479–491. https://doi.org/10.1007/s00360-021-01341-5 ***Data***: Cooper, C.J., Thermal tolerance and routine oxygen consumption of convict cichlid, *Archocentrus nigrofasciatus*, acclimated to constant temperatures (20°C and 30°C) and a daily temperature cycle (20°C→30°C). Dryad. https://datadryad.org/stash/share/sMIFBjzyNmhCGD6STtHbgpt5gOxgqCwjAx4RWlFBkPo (accessed 5.28.21).	MO_2	-	Y
304	Cortese, D., Norin, T., Beldade, R., Crespel, A., Killen, S. S. and Mills, S. C. (2021). Physiological and behavioural effects of anemone bleaching on symbiont anemonefish in the wild. Functional Ecology 35, 663–674. ***Data***: Cortese, D., Norin, T., Beldade, R., Crespel, A., Killen, S.S., Mills, S.C., 2020. Physiological and behavioural effects of anemone bleaching on symbiont anemonefish in the wild. https://doi.org/10.5281/zenodo.4167473	SMR	-	Y
305	Johansen, J.L., Esbaugh, A.J., 2017. Sustained impairment of respiratory function and swim performance following acute oil exposure in a coastal marine fish. Aquatic Toxicology 187, 82–89. https://doi.org/10.1016/j.aquatox.2017.04.002 ***Data***: Johansen, Jacob; Esbaugh, Andrew, 2017. Injury and recovery of respiratory performance and swimming performance of red drum following acute oil exposure. https://doi.org/10.7266/N74M92M5	MMR (swimming)	Y	-
306	Killen, S.S., Nadler, L.E., Grazioso, K., Cox, A., McCormick, M.I., 2021. The effect of metabolic phenotype on sociability and social group size preference in a coral reef fish. Ecology and Evolution 11, 8585–8594. https://doi.org/10.1002/ece3.7672	MMR/SMR	Y	Y

	Data: Killen, Shaun; Nadler, Lauren; Grazioso, Kathryn; Cox, Amy; McCormick, Mark (2021), "Data for Killen et al The Effect of Metabolic Phenotype on Sociability and Social Group Size Preference in a Coral Reef Fish", Mendeley Data, V1, doi: 10.17632/4x5k9hsfrf.1			
309	Reemeyer, J.E., Rees, B.B., 2020b. Plasticity, repeatability and phenotypic correlations of aerobic metabolic traits in a small estuarine fish. Journal of Experimental Biology 223. https://doi.org/10.1242/jeb.228098 ***Data**:* Reemeyer, J.E., Rees, B.B., 2020. Data from Reemeyer and Rees, 2020. https://doi.org/10.6084/m9.figshare.12431813.v1	MMR/SMR	Y	Y
310	Slesinger, E., Andres, A., Young, R., Seibel, B., Saba, V., Phelan, B., Rosendale, J., Wieczorek, D., Saba, G., 2019. The effect of ocean warming on black sea bass (*Centropristis striata)* aerobic scope and hypoxia tolerance. PLOS ONE 14, e0218390. https://doi.org/10.1371/journal.pone.0218390 ***Data***: Slesinger, E., 2019. The effect of ocean warming on black sea bass (*Centropristis striata*) aerobic scope and hypoxia tolerance. https://doi.org/10.1371/journal.pone.0218390	MMR/SMR	Y	Y
311	Wheeler, C.R., Rummer, J.L., Bailey, B., Lockwood, J., Vance, S., Mandelman, J.W., 2021. Future thermal regimes for epaulette sharks (*Hemiscyllium ocellatum*): growth and metabolic performance cease to be optimal. Scientific Reports 11, 454. https://doi.org/10.1038/s41598-020-79953-0 Wheeler, C., 2021. Future thermal regimes for epaulette sharks (*Hemiscyllium ocellatum*): growth and metabolic performance cease to be optimal. https://doi.org/10.25903/YTXC-N035	MO2rest/ MO2max	Y	Y
313	Zhu, Y., Xiong, W., Xu, Y., Zhang, P., Zhang, J., Luo, Y., 2021. Comparison of metabolic scaling between triploid and diploid common carp. J Comp Physiol B. https://doi.org/10.1007/s00360-021-01365-x ***Data***: Zhu, Y., 2021. Metabolic scaling of triploid and diploid common carp. Figshare. https://doi.org/10.6084/m9.figshare.13621544.v1	RMR	-	Y
315	Ye, X., Lu, L., Jiang, M., Jia, J., Li, W., Wu, H., Liao, Y., Li, J., 2021. Metabolic scaling: individual versus intraspecific scaling of Nile tilapia (*Oreochromis niloticus*). J Comp Physiol B. 191, 721–729. https://doi.org/10.1007/s00360-021-01376-8 ***Data***: *Electronic supplement*	RMR	-	Y
316	Li, G., Lv, X., Zhou, J., Shen, C., Xia, D., Xie, H., Luo, Y., 2018. Are the surface areas of the gills and body involved with changing metabolic scaling with temperature? Journal of	RMR	-	Y

	Experimental Biology 221 (8): jeb174474 https://doi.org/10.1242/jeb.174474 Li, X., 2018. Data for “Are the surface areas of gill and body involved with changing metabolic scaling with temperature?”. Figshare. https://doi.org/10.6084/m9.figshare.5844930.v1			
317	Clark, T.D., Brandt, W.T., Nogueira, J., Rodriguez, L.E., Price, M., Farwell, C.J., Block, B.A., 2010. Postprandial metabolism of Pacific bluefin tuna (*Thunnus orientalis*). Journal of Experimental Biology 213, 2379–2385. https://doi.org/10.1242/jeb.043455 ***Data***: *Table embedded within the original article*	RMR	-	Y
315-1	Metadata article: Scheuffele, H., Jutfelt, F., Clark, T.D., 2021. Investigating the gill-oxygen limitation hypothesis in fishes: intraspecific scaling relationships of metabolic rate and gill surface area. Conservation Physiology 9. https://doi.org/10.1093/conphys/coab040 ***Metadata article - data:*** *supplementary material* Original publication: Li, G., Xie, H., He, D., Luo, Y., 2016. Effects of body chemical components on the allometric scaling of the resting metabolic rate in four species of cyprinids. Fish Physiol Biochem 42, 295–301. https://doi.org/10.1007/s10695-015-0137-7	RMR	-	Y
315-2	Metadata article: Metadata article: Scheuffele, H., Jutfelt, F., Clark, T.D., 2021. Investigating the gill-oxygen limitation hypothesis in fishes: intraspecific scaling relationships of metabolic rate and gill surface area. Conservation Physiology 9. https://doi.org/10.1093/conphys/coab040 ***Metadata article - data:*** *supplementary material* Original publication: Duthie, G.G., 1982. The respiratory metabolism of temperature-adapted flatfish at rest and during swimming activity and the use of anaerobic metabolism at moderate swimming speeds. J Exp Biol 97, 359–373.	Standard O_2 consumption	-	Y
315-3	Metadata article: Scheuffele, H., Jutfelt, F., Clark, T.D., 2021. Investigating the gill-oxygen limitation hypothesis in fishes: intraspecific scaling relationships of metabolic rate and gill surface area. Conservation Physiology 9. https://doi.org/10.1093/conphys/coab040 ***Metadata article - data:*** *supplementary material* Original publication: Herrmann, J.-P., Enders, E.C., 2000. Effect of body size on the standard metabolism of horse mackerel. Journal of Fish Biology 57, 746–760. https://doi.org/10.1111/j.1095-8649.2000.tb00272.x	Standard (R_S) and routine metabolism (R_R)	-	Y
315-4	Metadata article: Scheuffele, H., Jutfelt, F., Clark, T.D., 2021. Investigating the gill-oxygen limitation hypothesis in fishes: intraspecific scaling relationships of metabolic rate and gill	VO_2	-	Y

	surface area. Conservation Physiology 9. https://doi.org/10.1093/conphys/coab040 ***Metadata article - data:*** *supplementary material* Original publication: Hughes, G.M., 1978. On the respiration of Torpedo marmorata. Journal of Experimental Biology 73, 85–105. https://doi.org/10.1242/jeb.73.1.85			
403	Drown, M.K., DeLiberto, A.N., Ehrlich, M.A., Crawford, D.L., Oleksiak, M.F., 2021. Interindividual plasticity in metabolic and thermal tolerance traits from populations subjected to recent anthropogenic heating. Royal Society Open Science 8, 210440. https://doi.org/10.1098/rsos.210440 ***Data:*** Drown, Melissa et al. (2021), Interindividual plasticity in metabolic and thermal tolerance traits from populations subjected to recent anthropogenic heating, Dryad, Dataset, https://doi.org/10.5061/dryad.0gb5mkm0w	WAM (whole animal metabolism)	-	Y
405	Hardison, E.A., Kraskura, K., Van Wert, J., Nguyen, T., Eliason, E.J., 2021. Diet mediates thermal performance traits: implications for marine ectotherms. Journal of Experimental Biology 224, jeb242846. https://doi.org/10.1242/jeb.242846 Data: Hardison, E., Hardison, E.A., Kraskura, K., Wert, J.V., Nguyen, T., Eliason, E.J., 2021. Diet mediates thermal performance traits: implications for marine ectotherms. https://doi.org/10.25349/D98P66	MMR/ SMR	Y	Y
407	Heuer, R.M., Stieglitz, J.D., Pasparakis, C., Enochs, I.C., Benetti, D.D., Grosell, M., 2021. The Effects of Temperature Acclimation on Swimming Performance in the Pelagic Mahi-Mahi (*Coryphaena hippurus*). Frontiers in Marine Science 8. ***Data***: Heuer, R., Stieglitz, J.D., Pasparakis, C., Enochs, I., Benetti, D., Grosell, M., 2020. Effects of temperature on swim performance of mahi-mahi (*Coryphaena hippurus*). https://doi.org/10.7266/N7-XD7P-YJ29. https://data.gulfresearchinitiative.org/data/R6.x804.000:0008	MMR	Y	-
410	Nadler, L.E., Bengston, E., Eliason, E.J., Hassibi, C., Helland-Riise, S.H., Johansen, I.B., Kwan, G.T., Tresguerres, M., Turner, A.V., Weinersmith, K.L., Øverli, Ø., Hechinger, R.F., 2021. A brain-infecting parasite impacts host metabolism both during exposure and after infection is established. Functional Ecology 35, 105–116. https://doi.org/10.1111/1365-2435.13695 ***Data***: Nadler, L., Bengston, E., Eliason, E., Hassibi, C., Helland-Riise, S., Johansen, I., Kwan, G., Tresguerres, M., Turner, A., Weinersmith, K., Øverli, Ø., Hechinger, R., 2020. A brain-infecting parasite impacts host metabolism both during exposure and after infection is established. Marine & Environmental Sciences Faculty Datasets.	MMR/SMR	Y	Y

412	Scheuffele, H., Rubio-Gracia, F., Clark, T.D., 2021. Thermal performance curves for aerobic scope in a tropical fish (*Lates calcarifer*): flexible in amplitude but not breadth. Journal of Experimental Biology 224, jeb243504. https://doi.org/10.1242/jeb.243504 **Data**: Scheuffele, H., Clark, T., Rubio-Gracia, F. (2021): Data and supplementary material associated with Scheuffele et al. (2021) Thermal performance curves for aerobic scope in a tropical fish (*Lates calcarifer*): flexible in amplitude but not breadth. Journal of Experimental Biology. figshare. Dataset. https://doi.org/10.6084/m9.figshare.16624978.v3	MMR/SMR	Y	Y
404	Gilbert, M.J.H., Tierney, K.B., 2018. Warm northern river temperatures increase post-exercise fatigue in an Arctic migratory salmonid but not in a temperate relative. Functional Ecology 32, 687–700. https://doi.org/10.1111/1365-2435.13006 ***Data***: orcid.org/0000-0002-8342-3783 (2017): Data for "Warm northern river temperatures increase post-exercise fatigue in an Arctic migratory salmonid but not in a temperate relative". figshare. Dataset. https://doi.org/10.6084/m9.figshare.5386882.v1	MO_2max	-	Y
413	Sundell, E., Morgenroth, D., Ekström, A., Brijs, J., Axelsson, M., Gräns, A., Sandblom, E., 2021. Energetic savings and cardiovascular dynamics of a marine euryhaline fish (*Myoxocephalus scorpius*) in reduced salinity. J Comp Physiol B 191, 301–311. https://doi.org/10.1007/s00360-020-01336-8 ***Data***: *supplementary material*	SMR	-	Y
414	Xiong, W., Zhu, Y., Zhang, P., Xu, Y., Zhou, J., Zhang, J., Luo, Y., 2022. Effects of temperature on metabolic scaling in silver carp. Journal of Experimental Zoology Part A: Ecological and Integrative Physiology 337, 141–149. https://doi.org/10.1002/jez.2542 ***Data*:** Luo, Y. (2021): Effects of temperature on scaling of routine metabolic rate, gill surface area, ventilation frequency, cell size and cell metabolic rate in silver carp. figshare. Dataset. https://doi.org/10.6084/m9.figshare.14604255.v1	RMR	--	Y
415	Wootton, H.F., Morrongiello, J.R., Schmitt, T., Audzijonyte, A., 2022 Smaller adult fish size in warmer water is not explained by elevated metabolism. Ecology Letters. https://doi.org/10.1111/ele.13989 ***Data***: Wootton, H.F, Morrongliello, J., Audzijonyte, A., Schmidt, T. (2022): Code and data for Wootton et al. (2022) in Ecology Letters. "Smaller adult fish size in warmer water is not	SMR (MMR not used)	-	Y

	explained by elevated metabolism". University of Melbourne. Online resource. https://doi.org/10.26188/6201f08988bdd			
37	Ern, R., Johansen, J.L., Rummer, J.L., Esbaugh, A.J., 2017. Effects of hypoxia and ocean acidification on the upper thermal niche boundaries of coral reef fishes. Biology Letters 13, 20170135. https://doi.org/10.1098/rsbl.2017.0135 ***Data***: *supplementary material*	MMR/ SMR	Y	Y

Appendix 1, Table 1: Reference table for the collated meta-data.
References of the original peer-reviewed article or manuscript that are included in the metadata used for the analysis, and reference specific to the source of the raw data. Abbreviations: Y = yes, data are included in our analysis. MMR = maximum metabolic rates, AMR = Active metabolic rates, RMR = resting/routine metabolic rates, SMR = Standard metabolic rates. MR = Metabolic Rates (other acronyms are defined within the table). The terminology used to define metabolic rate measurement by the original authors. Reference ID is unique to each study (not in consecutive order).

Opt. ºC		**W. ºC**		**Species latin name**	**Lifestyle**	**Morpho-logy**	**Climate**	**Salinity**
RMR	**MMR**	**RMR**	**MMR**		**fishbase.org**	**'rfishbase' in R**	**fishbase.org**	**fishbase.org**
-	Y	-	-	*Abbottina rivularis*	BenPel	Fus	Subtr	F-B
Y	Y	Y	Y	*Acanthochromis polyacanthus*	ReefAs	ShDe	Trop	M
Y	Y	-	-	*Acrossocheilus monticola*	BenPel	Elon	Temp	F
Y	-	Y		*Amatitlania nigrofasciata*	BenPel	ShDe	Trop	F
Y	-	-	-	*Amphiprion chrysopterus*	ReefAs	ShDe	Trop	M
Y	-	-	-	*Amphiprion melanopus*	ReefAs	ShDe	Trop	M
Y	-	-	-	*Amphiprion percula*	ReefAs	Fus	Trop	M
Y	-	-	-	*Anguilla anguilla*	Dem	Eel-l	Temp	M-F-B
Y	-	-	-	*Bellapiscis medius*	Dem	Fus	Temp	M
Y	Y	Y	Y	*Boreogadus saida*	Dem	Elon	Pol	M-B
Y	Y	-	-	*Caesio cuning*	ReefAs	Fus	Trop	M
Y	Y	-	-	*Carassius auratus*	BenPel	Fus	Subtr	F-B
Y	Y	Y	Y	*Centropristis striata*	ReefAs	Fus	Temp	M
Y	Y	-	-	*Channa argus*	BenPel	Elon	Subtr	F
-	-	Y	Y	*Chromis atripectoralis*	ReefAs	ShDe	Trop	M
Y	-	-	-	*Chromis viridis*	BenPel	ShDe	Subtr	F-B
Y	-	-	-	*Clarias gariepinus*	BenPel	Elon	Subtr	F
-	Y	-	Y	*Coryphaena hippurus*	Pel	Elon	Subtr	M-B
Y	Y	-	-	*Ctenopharyngodon idella*	BenPel	Fus	Subtr	F-B
Y	Y	-	-	*Cyprinus carpio*	BenPel	Fus	Subtr	F-B
Y	-	-	-	*Danio rerio*	BenPel	Fus	Trop	F
Y	Y	-	Y	*Dicentrarchus labrax*	Dem	Fus	Subtr	M-F-B
Y	Y	-	-	*Discogobio yunnanensis*	BenPel	Elon	Subtr	F
Y	Y	-	-	*Enteromius neumayeri*	BenPel	Fus	Trop	F
Y	-	Y	-	*Forsterygion lapillum*	BenPel	Elon	Temp	M
Y	Y	Y	Y	*Fundulus grandis*	BenPel	Elon	Trop	F-B

Y	-	-	-	*Fundulus heteroclitus* *	BenPel	Elon	Temp	M-F-B
Y	-	-	Y	*Fundulus parvipinnis*	BenPel	Elon	Subtr	M-B
Y	-	Y	-	*Gadus morhua*	BenPel	Fus	Temp	M-B
Y	Y	-	-	*Gambusia holbrooki* *	BenPel	Fus	Subtr	F-B
Y	Y	Y	Y	*Gasterosteus aculeatus*	BenPel	Fus	Subtr	M-F-B
Y	Y	-	-	*Girella nigricans*	BenPel	ShDe	Subtr	M
Y	Y	-	-	*Gobiocypris rarus*	BenPel	Fus	Temp	F
Y	Y	Y	Y	*Halichoeres melanurus*	ReefAs	Fus	Trop	M
Y	Y	Y	Y	*Halichoeres miniatus*	ReefAs	Fus	Trop	M
Y	Y	-	-	*Hemibagrus macropterus*	Dem	Elon	Temp	F
Y	Y	-	-	*Hemibarbus maculatus*	BenPel	Fus	Temp	F
-	Y	-	-	*Hemiculter leucisculus*	BenPel	Fus	Trop	F-B
Y	Y	Y	Y	*Hemiscyllium ocellatum*	ReefAs	Elon	Trop	M
Y	Y	-	-	*Hypophthalmichthys molitrix*	BenPel	Fus	Subtr	F-B
Y	Y	-	-	*Hypophthalmichthys nobilis*	BenPel	Fus	Temp	F-B
Y	Y	Y	Y	*Lates calcarifer* *	Dem	Fus	Trop	M-F-B
Y	Y	Y	Y	*Lates niloticus*	Dem	Fus	Trop	F
Y	Y	-	-	*Megalobrama pellegrini*	BenPel	ShDe	Subtr	F
Y	Y	-	-	*Metahomaloptera omeiensis*	Dem	Elon	Temp	F
Y	Y	-	-	*Misgurnus anguillicaudatus*	Dem	Elon	Subtr	F-B
Y	Y	-	-	*Mylopharyngodon piceus*	Dem	Fus	Subtr	F-B
Y	-	-	-	*Myoxocephalus scorpius*	Dem	Fus	Pol	M-B
Y	Y	-	-	*Myxocyprinus asiaticus*	Dem	Fus	Subtr	F
Y	Y	Y	Y	*Neogobius melanostomus*	Dem	Fus	Temp	M-F-B
Y	-	Y	-	*Notothenia rossii*	Dem	Fus	Pol	M
Y	Y	Y	Y	*Oncorhynchus kisutch* *	Pel	Fus	Subtr	M-F-B
Y	Y	Y	Y	*Oncorhynchus mykiss*	BenPel	Fus	Subtr	M-F-B
Y	Y	Y	Y	*Oncorhynchus nerka*	Pel	Fus	Temp	M-F-B
Y	Y	Y	Y	*Oncorhynchus tshawytscha*	BenPel	Fus	Subtr	M-F-B
-	Y	-	-	*Onychostoma simum*	BenPel	Elon	Subtr	F
-	Y	-	-	*Opsariichthys bidens*	BenPel	Fus	Temp	F
Y	Y	-	Y	*Oreochromis niloticus*	BenPel	Fus	Trop	F-B
-	Y	-	-	*Parabramis pekinensis*	BenPel	ShDe	Temp	F-B
Y	Y	-	-	*Paralichthys olivaceus*	Dem	Fus	Subtr	M
Y	Y	Y	Y	*Perca fluviatilis*	Dem	Fus	Temp	F-B
Y	Y	-	-	*Percocypris pingi*	BenPel	Elon	Subtr	F
Y	Y	-	-	*Phoxinus phoxinus*	Dem	Fus	Temp	F-B
-	Y	-	Y	*Piaractus mesopotamicus*	Dem	ShDe	Subtr	F
Y	-	-	-	*Platichthys flesus*	Dem	ShDe	Temp	M-F-B
-	Y	-	-	*Poecilia reticulata*	BenPel	Fus	Trop	F-B
Y	-	-	-	*Polyprion oxygeneios*	Dem	Fus	Subtr	M
Y	Y	-	-	*Pomacentrus amboinensis*	ReefAs	ShDe	Trop	M
Y	Y	-	-	*Procypris rabaudi*	BenPel	Elon	Subtr	F
Y	Y	-	-	*Pseudobagrus vachellii*	Dem	Elon	Subtr	F
Y	Y	-	-	*Pseudorasbora parva*	BenPel	Fus	Temp	F-B
Y	Y	-	-	*Rhinogobius giurinus*	Dem	Fus	Subtr	M-F-B
Y	Y	-	-	*Rhodeus ocellatus*	BenPel	Fus	Subtr	F-B
-	Y	-	-	*Rhodeus sinensis* *	BenPel	Fus	Subtr	F-B
Y	-	-	-	*Salmo salar*	BenPel	Fus	Temp	M-F-B

Y	Y	-	-	*Salmo trutta*	Pel	Fus	Subtr	M-F-B
Y	Y	-	Y	*Salvelinus alpinus*	BenPel	Fus	Temp	M-F-B
-	Y	-	-	*Sarcocheilichthys parvus*	BenPel	Fus	Subtr	F
Y	Y	-	-	*Schizothorax wangchiachii* *	BenPel	Elon	Subtr	F
-	Y	-	-	*Sciaenops ocellatus*	Dem	Fus	Subtr	M-B
Y	Y	-	-	*Silurus meridionalis*	Dem	Elon	Subtr	F
Y	Y	-	-	*Sinibrama taeniatus* *	BenPel	Fus	Temp	F
Y	Y	-	-	*Siniperca chuatsi*	BenPel	ShDe	Temp	F
Y	Y	-	-	*Somniosus microcephalus*	BenPel	Elon	Pol	M-B
Y	Y	-	-	*Spinibarbus sinensis*	BenPel	Elon	Subtr	F
Y	Y	-	-	*Tachysurus dumerili*	Dem	Elon	Temp	F-B
Y	Y	-	-	*Tautogolabrus adspersus*	ReefAs	Fus	Temp	M
Y	Y	Y	Y	*Thalassoma amblycephalum*	ReefAs	Fus	Subtr	M
Y	-	-	-	*Thunnus orientalis*	Pel	Fus	Subtr	M-B
Y	-	-	-	*Torpedo marmorata* *	ReefAs	DorsVen	Subtr	M-B
Y	-	-	-	*Trachurus trachurus*	Pel	Fus	Subtr	M
Y	-	Y	-	*Trematomus bernacchii*	Dem	Fus	Pol	M
Y	Y	-	-	*Triplophysa rosa*	Dem	Elon	Subtr	F
Y	Y	-	-	*Zacco platypus*	BenPel	Fus	Subtr	F

- *Fundulus heteroclitus*: Morphology justification. Species was is classified as "fusiform-normal" in fasbase database. Overwriting as "elongated". All species from Genus *Fundulus* are elangated.
- *Gambusia holbrooki*: Morphology justification. Was not available via Fishbase R interface. Classified following two references: 1) Xiong, D., Xie, C. & Xia, L. Threatened fishes of the world: *Gobiocypris rarus* Ye and Fu, 1983 (Cypinidae). Environ Biol Fish 86, 107 (2009). 2) Yan Shao, Jianwei Wang, Ye Qiao, Yongfeng He, Wenxuan Cao "Morphological Variability Between Wild Populations and Inbred Stocks of a Chinese Minnow, *Gobiocypris rarus*," Zoological Science, 24(11), 1094-1102, (1 November 2007)
- *Lates calcarifer*: Morphology justification. Was not available via Fishbase R interface. Classified following the reference: Chen, J., Guo, J., Wang, Z.-Q. and Wang, W.-M. (2020). Morphological variation among the four *Megalobrama* species inferred by X-ray photography. Aquaculture Research 51, 3999–4010.
- *Oncorhynchus kisutch*: Lifestyle classification: Fishbase.org classified as pelagic-oceanic. This species was previously categorised as pelagic in its standalone group by Killen et al Am Nat 2016 (https://doi.org/10.1086/685893)
- *Rhodeus sinensis*: Lifestyle classification. Fishbase.org classified as pelagic-neritic. This species was previously categorised as pelagic in its standalone group by Killen et al Am Nat 2016 (https://doi.org/10.1086/685893)
- *Schizothorax wangchiachii*: Morphology justification. Was not available via Fishbase R interface. Classified following the reference: Xie, Z.-gui., Xie, C-xin, Zhang, E. (2003). Morphological Variations Among the Chinese Species of *Sinibrama* (Pisces： Teleostei: Cyprinidae), with Comments on Their Species Validities. ISSN 0254—5853
- *Sinibrama taeniatus*: Climate classification. Fishbase.org classified as boreal. Classified as polar by the original authors from where the metabolic rate data are obtained: Quoted sentence:

"large polar ectotherm such as the Greenland shark (…)". Ste-Marie, E., Watanabe, Y. Y., Semmens, J. M., Marcoux, M. and Hussey, N. E. (2020). A first look at the metabolic rate of Greenland sharks (*Somniosus microcephalus*) in the Canadian Arctic. Sci Rep 10, 19297.

- *Torpedo marmorata*: Morphology justification. Was not available via Fishbase R interface, specified as "other". Dorsoventrally flattened fish.

Appendix 1, Table 2: Classification of species ecology.
Fishabse links are provided in Apenddix 1, Table3. Abbreviations: Y = yes, data are included on our analysis. With asterisk '*' are denoted species that are author selected; justification of the selection is at the end of the table. Key to each abbreviation: Opt = Optimal temperature, W = warm temperature category. Benthopelagic = BenPel, pelagic = Pel, reef-associated = ReefAs, demersal = Dem, fusiform = Fus, short/deep = ShDe, elongated = Elon, eel-like = Eel-l, subtropical = Subtr, tropical = Trop, Polar = Pol, Temperate = Temp, Freshwater; brackish = F-B, Marine; freshwater; brackish = M-F-B, Freshwater; brackish = F-B, Marine = M, Freshwater = F, Marine; brackish = M-B.

Species Latin name	Last accessed	URL fishbase.org
Abbottina rivularis	11-Jun-2021	https://www.fishbase.de/summary/Abbottina-rivularis.html
Acanthochromis polyacanthus	11-Jun-2021	https://www.fishbase.se/summary/6655
Acrossocheilus monticola	11-Jun-2021	https://www.fishbase.se/summary/55155
Amatitlania nigrofasciata	26-Jun-2021	https://www.fishbase.se/summary/amatitlania-nigrofasciata.html
Amphiprion chrysopterus	26-Jun-2021	https://www.fishbase.in/summary/Amphiprion-chrysopterus.html
Amphiprion melanopus	11-Jun-2021	https://www.fishbase.se/summary/Amphiprion-melanopus
Amphiprion percula	11-Jun-2021	https://www.fishbase.de/summary/amphiprion-percula.html
Anguilla anguilla	11-Jun-2021	https://www.fishbase.se/summary/Anguilla-anguilla.html
Bellapiscis medius	11-Jun-2021	https://www.fishbase.se/summary/Bellapiscis-medius.html
Boreogadus saida	11-Jun-2021	https://www.fishbase.se/summary/Boreogadus-saida.html
Caesio cuning	26-Jun-2021	https://www.fishbase.se/summary/Caesio-cuning.html
Carassius auratus	11-Jun-2021	https://www.fishbase.se/summary/271
Centropristis striata	26-Jun-2021	https://www.fishbase.se/summary/Centropristis-striata.html
Channa argus	11-Jun-2021	https://www.fishbase.de/summary/4799
Chromis atripectoralis	26-Jun-2021	https://www.fishbase.se/summary/chromis-atripectoralis.html
Chromis viridis	11-Jun-2021	https://www.fishbase.se/summary/Ctenopharyngodon-idella.html

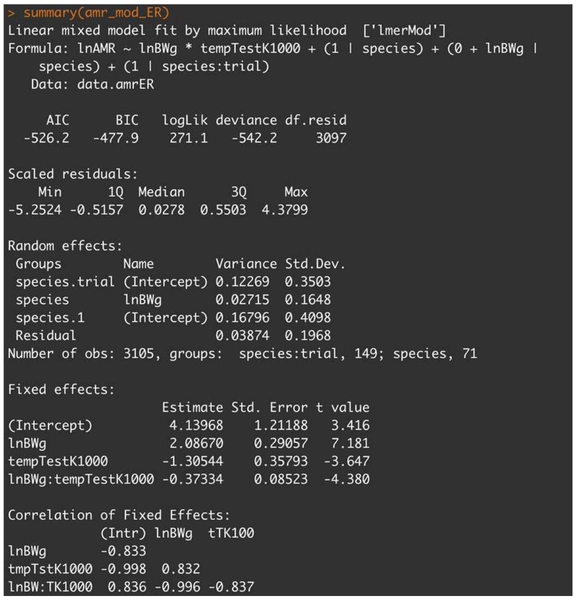
Clarias gariepinus	11-Jun-2021	https://www.fishbase.se/summary/clarias-gariepinus.html
Coryphaena hippurus	22-Mar-2022	https://www.fishbase.se/summary/6
Ctenopharyngodon idella	11-Jun-2021	https://www.fishbase.se/summary/Ctenopharyngodon-idella.html
Cyprinus carpio	11-Jun-2021	https://www.fishbase.se/summary/cyprinus-carpio.html
Danio rerio	22-Mar-2022	https://www.fishbase.se/summary/Danio-rerio.html
Dicentrarchus labrax	11-Jun-2021	https://www.fishbase.se/summary/Dicentrarchus-labrax.html
Discogobio yunnanensis	11-Jun-2021	https://www.fishbase.se/summary/Discogobio-yunnanensis
Enteromius neumayeri	11-Jun-2021	https://www.fishbase.se/summary/11430
Forsterygion lapillum	11-Jun-2021	https://www.fishbase.se/summary/12940
Fundulus grandis	26-Jun-2021	https://www.fishbase.in/summary/Fundulus-grandis.html
Fundulus heteroclitus *	22-Mar-2022	https://www.fishbase.se/summary/Fundulus-heteroclitus.html
Fundulus parvipinnis	22-Mar-2022	https://www.fishbase.se/summary/Fundulus-parvipinnis.html
Gadus morhua	11-Jun-2021	https://www.fishbase.se/summary/gadus-morhua.html
Gambusia holbrooki *	11-Jun-2021	https://www.fishbase.de/summary/gambusia-holbrooki.html
Gasterosteus aculeatus	11-Jun-2021	https://www.fishbase.de/summary/Gasterosteus-aculeatus.html
Girella nigricans	22-Mar-2022	https://www.fishbase.se/summary/Girella-nigricans.html
Gobiocypris rarus	11-Jun-2021	https://www.fishbase.se/summary/Gobiocypris-rarus.html
Halichoeres melanurus	11-Jun-2021	https://www.fishbase.de/summary/4858
Halichoeres miniatus	11-Jun-2021	https://www.fishbase.in/summary/6614
Hemibagrus macropterus	11-Jun-2021	https://www.fishbase.se/summary/hemibagrus-macropterus.html
Hemibarbus maculatus	11-Jun-2021	https://www.fishbase.de/summary/Hemibarbus-maculatus
Hemiculter leucisculus	11-Jun-2021	https://www.fishbase.se/summary/4755
Hemiscyllium ocellatum	26-Jun-2021	https://www.fishbase.de/summary/Hemiscyllium-ocellatum.html
Hypophthalmichthys molitrix	11-Jun-2021	https://www.fishbase.de/summary/274
Hypophthalmichthys nobilis	11-Jun-2021	https://www.fishbase.se/summary/Hypophthalmichthys-nobilis.html
Lates calcarifer *	11-Jun-2021	https://www.fishbase.se/summary/Lates-calcarifer.html
Lates niloticus	11-Jun-2021	https://www.fishbase.se/summary/lates-niloticus.html

Megalobrama pellegrini	11-Jun-2021	https://www.fishbase.in/summary/Megalobrama-pellegrini.html
Metahomaloptera omeiensis	11-Jun-2021	https://www.fishbase.se/summary/Metahomaloptera-omeiensis.html
Misgurnus anguillicaudatus	11-Jun-2021	https://www.fishbase.se/summary/3016
Mylopharyngodon piceus	11-Jun-2021	https://www.fishbase.se/summary/Mylopharyngodon-piceus.html
Myoxocephalus scorpius	22-Mar-2022	https://www.fishbase.se/summary/Myoxocephalus-scorpius.html
Myxocyprinus asiaticus	11-Jun-2021	https://www.fishbase.se/summary/12304
Neogobius melanostomus	11-Jun-2021	https://www.fishbase.de/summary/neogobius-melanostomus.html
Notothenia rossii	11-Jun-2021	https://www.fishbase.se/summary/468
*Oncorhynchus kisutch **	11-Jun-2021	https://www.fishbase.se/summary/245
Oncorhynchus mykiss	11-Jun-2021	https://www.fishbase.de/summary/oncorhynchus-mykiss.html
Oncorhynchus nerka	11-Jun-2021	https://www.fishbase.se/summary/oncorhynchus-nerka.html
Oncorhynchus tshawytscha	11-Jun-2021	https://www.fishbase.de/summary/244
Onychostoma simum	11-Jun-2021	https://www.fishbase.in/summary/Onychostoma-simum
Opsariichthys bidens	11-Jun-2021	https://www.fishbase.se/summary/27264
Oreochromis niloticus	11-Jun-2021	https://www.fishbase.se/summary/oreochromis-niloticus.html
Parabramis pekinensis	11-Jun-2021	https://www.fishbase.in/summary/Parabramis-pekinensis
Paralichthys olivaceus	11-Jun-2021	https://www.fishbase.se/summary/Paralichthys-olivaceus.html
Perca fluviatilis	11-Jun-2021	https://www.fishbase.se/summary/perca-fluviatilis.html
Percocypris pingi	11-Jun-2021	https://www.fishbase.se/summary/56074
Phoxinus phoxinus	11-Jun-2021	https://www.fishbase.de/summary/Phoxinus-phoxinus.html
Piaractus mesopotamicus	11-Jun-2021	https://www.fishbase.se/summary/55383
Platichthys flesus	26-Jun-2021	https://www.fishbase.de/summary/platichthys-flesus.html
Poecilia reticulata	11-Jun-2021	https://www.fishbase.de/summary/3228
Polyprion oxygeneios	11-Jun-2021	https://www.fishbase.se/summary/350
Pomacentrus amboinensis	11-Jun-2021	https://www.fishbase.se/summary/5715
Procypris rabaudi	11-Jun-2021	https://www.fishbase.in/summary/Procypris-rabaudi.html
Pseudobagrus vachellii	11-Jun-2021	https://www.fishbase.se/summary/50950

Pseudorasbora parva	11-Jun-2021	https://www.fishbase.de/summary/4691
Rhinogobius giurinus	11-Jun-2021	https://www.fishbase.se/summary/Rhinogobius-giurinus
Rhodeus ocellatus	11-Jun-2021	https://www.fishbase.se/summary/Rhodeus-ocellatus.html
Rhodeus sinensis *	11-Jun-2021	https://www.fishbase.se/summary/Rhodeus-sinensis.html
Salmo salar	11-Jun-2021	https://www.fishbase.se/summary/salmo-salar.html
Salmo trutta	11-Jun-2021	https://www.fishbase.se/summary/Salmo-trutta.html
Salvelinus alpinus	11-Jun-2021	https://www.fishbase.de/summary/Salvelinus-alpinus.html
Sarcocheilichthys parvus	11-Jun-2021	https://www.fishbase.se/summary/Sarcocheilichthys-parvus.html
Schizothorax wangchiachii *	11-Jun-2021	https://www.fishbase.se/summary/Schizothorax-wangchiachii.html
Sciaenops ocellatus	29-Mar-2022	https://www.fishbase.de/summary/1191
Silurus meridionalis	11-Jun-2021	https://www.fishbase.de/summary/Silurus-meridionalis.html
Sinibrama taeniatus *	11-Jun-2021	https://www.fishbase.se/summary/Sinibrama-taeniatus.html
Siniperca chuatsi	11-Jun-2021	https://www.fishbase.de/summary/Siniperca-chuatsi.html
Somniosus microcephalus	11-Jun-2021	https://www.fishbase.de/summary/Somniosus-microcephalus.html
Spinibarbus sinensis	11-Jun-2021	https://www.fishbase.de/summary/62460
Tachysurus dumerili	11-Jun-2021	https://www.fishbase.de/summary/50980
Tautogolabrus adspersus	11-Jun-2021	https://www.fishbase.se/summary/Tautogolabrus-adspersus.html
Thalassoma amblycephalum	11-Jun-2021	https://www.fishbase.de/summary/5642
Thunnus orientalis	26-Jun-2021	https://www.fishbase.de/summary/14290
Torpedo marmorata *	26-Jun-2021	https://www.fishbase.se/summary/Torpedo-marmorata.html
Trachurus trachurus	26-Jun-2021	https://www.fishbase.se/summary/Trachurus-trachurus.html
Trematomus bernacchii	11-Jun-2021	https://www.fishbase.se/summary/7053
Triplophysa rosa	11-Jun-2021	https://www.fishbase.se/summary/62957
Zacco platypus	11-Jun-2021	https://www.fishbase.in/summary/Zacco-platypus.html

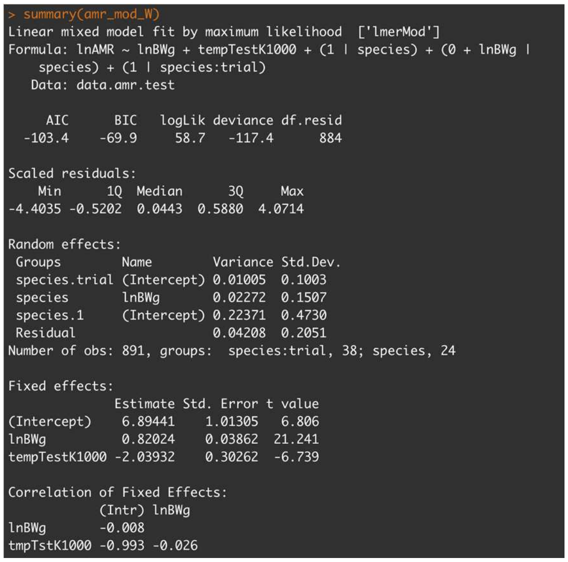
Appendix 1, Table 3: Fishbase.org URL links for the species-specific ecology reference.

MMR, optimal



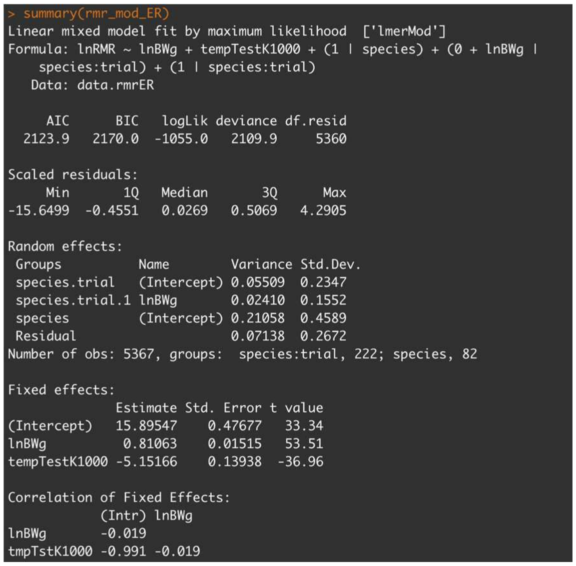
```
> summary(amr_mod_ER)
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: lnAMR ~ lnBWg * tempTestK1000 + (1 | species) + (0 + lnBWg |
    species) + (1 | species:trial)
   Data: data.amrER

     AIC      BIC   logLik deviance df.resid
  -526.2   -477.9    271.1   -542.2     3097

Scaled residuals:
    Min      1Q  Median      3Q     Max
-5.2524 -0.5157  0.0278  0.5503  4.3799

Random effects:
 Groups        Name        Variance Std.Dev.
 species.trial (Intercept) 0.12269  0.3503
 species       lnBWg       0.02715  0.1648
 species.1     (Intercept) 0.16796  0.4098
 Residual                  0.03874  0.1968
Number of obs: 3105, groups:  species:trial, 149; species, 71

Fixed effects:
                    Estimate Std. Error t value
(Intercept)          4.13968    1.21188   3.416
lnBWg                2.08670    0.29057   7.181
tempTestK1000       -1.30544    0.35793  -3.647
lnBWg:tempTestK1000 -0.37334    0.08523  -4.380

Correlation of Fixed Effects:
            (Intr) lnBWg  tTK100
lnBWg       -0.833
tmpTstK1000 -0.998  0.832
lnBW:TK1000  0.836 -0.996 -0.837
```

MMR, warm



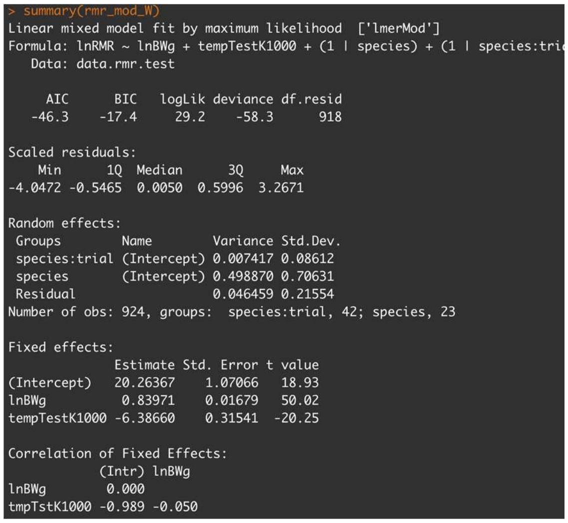
```
> summary(amr_mod_W)
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: lnAMR ~ lnBWg + tempTestK1000 + (1 | species) + (0 + lnBWg |
    species) + (1 | species:trial)
   Data: data.amr.test

     AIC      BIC   logLik deviance df.resid
  -103.4    -69.9     58.7   -117.4      884

Scaled residuals:
    Min      1Q  Median      3Q     Max
-4.4035 -0.5202  0.0443  0.5880  4.0714

Random effects:
 Groups        Name        Variance Std.Dev.
 species.trial (Intercept) 0.01005  0.1003
 species       lnBWg       0.02272  0.1507
 species.1     (Intercept) 0.22371  0.4730
 Residual                  0.04208  0.2051
Number of obs: 891, groups:  species:trial, 38; species, 24

Fixed effects:
              Estimate Std. Error t value
(Intercept)    6.89441    1.01305   6.806
lnBWg          0.82024    0.03862  21.241
tempTestK1000 -2.03932    0.30262  -6.739

Correlation of Fixed Effects:
            (Intr) lnBWg
lnBWg       -0.008
tmpTstK1000 -0.993 -0.026
```

RMR, optimal



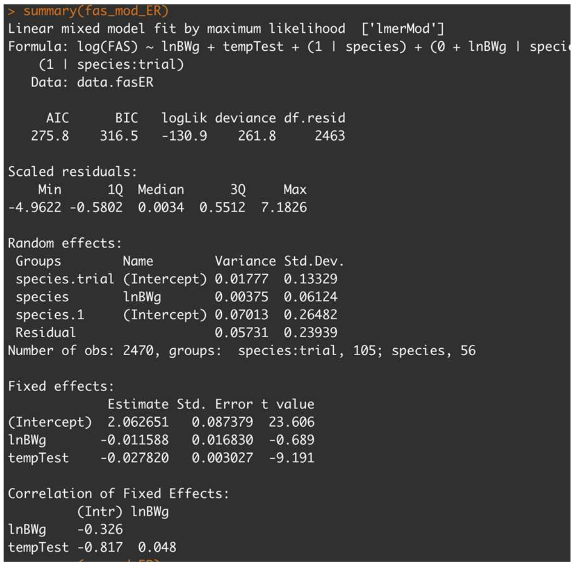
```
> summary(rmr_mod_ER)
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: lnRMR ~ lnBWg + tempTestK1000 + (1 | species) + (0 + lnBWg |
    species:trial) + (1 | species:trial)
   Data: data.rmrER

     AIC      BIC   logLik deviance df.resid
  2123.9   2170.0  -1055.0   2109.9     5360

Scaled residuals:
     Min       1Q   Median       3Q      Max
-15.6499  -0.4551   0.0269   0.5069   4.2905

Random effects:
 Groups          Name        Variance Std.Dev.
 species.trial   (Intercept) 0.05509  0.2347
 species.trial.1 lnBWg       0.02410  0.1552
 species         (Intercept) 0.21058  0.4589
 Residual                    0.07138  0.2672
Number of obs: 5367, groups:  species:trial, 222; species, 82

Fixed effects:
              Estimate Std. Error t value
(Intercept)   15.89547    0.47677   33.34
lnBWg          0.81063    0.01515   53.51
tempTestK1000 -5.15166    0.13938  -36.96

Correlation of Fixed Effects:
            (Intr) lnBWg
lnBWg       -0.019
tmpTstK1000 -0.991 -0.019
```

RMR, warm



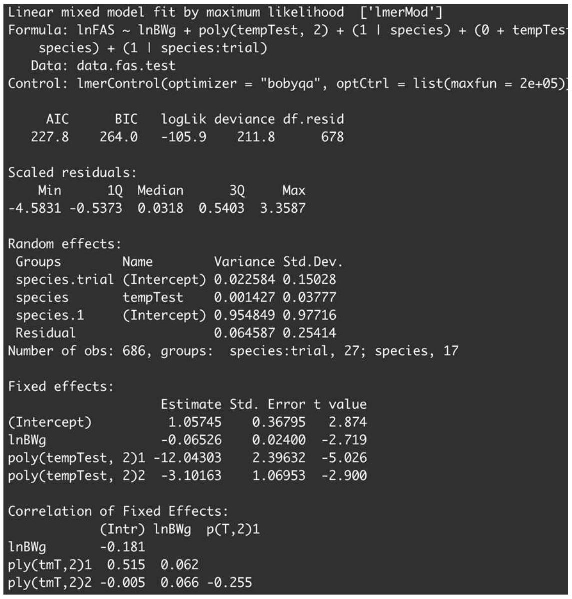
```
> summary(rmr_mod_W)
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: lnRMR ~ lnBWg + tempTestK1000 + (1 | species) + (1 | species:tri
   Data: data.rmr.test

     AIC      BIC   logLik deviance df.resid
   -46.3    -17.4     29.2    -58.3      918

Scaled residuals:
    Min      1Q  Median      3Q     Max
-4.0472 -0.5465  0.0050  0.5996  3.2671

Random effects:
 Groups        Name        Variance Std.Dev.
 species:trial (Intercept) 0.007417 0.08612
 species       (Intercept) 0.498870 0.70631
 Residual                  0.046459 0.21554
Number of obs: 924, groups:  species:trial, 42; species, 23

Fixed effects:
              Estimate Std. Error t value
(Intercept)   20.26367    1.07066   18.93
lnBWg          0.83971    0.01679   50.02
tempTestK1000 -6.38660    0.31541  -20.25

Correlation of Fixed Effects:
            (Intr) lnBWg
lnBWg        0.000
tmpTstK1000 -0.989 -0.050
```

FAS, optimal



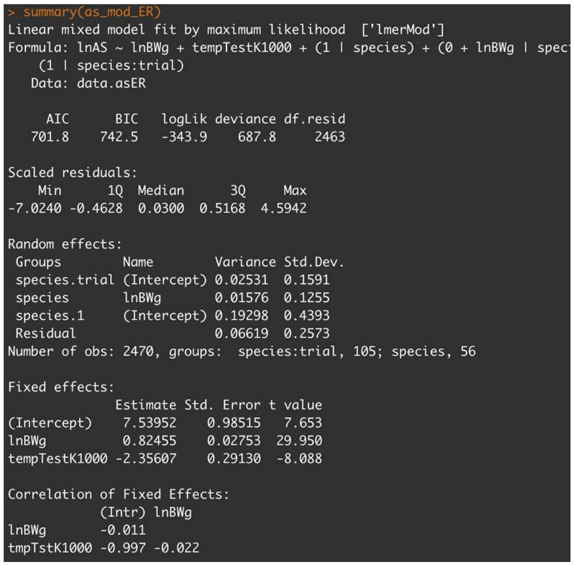
```
> summary(fas_mod_ER)
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: log(FAS) ~ lnBWg + tempTest + (1 | species) + (0 + lnBWg | speci
    (1 | species:trial)
   Data: data.fasER

     AIC      BIC   logLik deviance df.resid 
   275.8    316.5   -130.9    261.8     2463 

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-4.9622 -0.5802  0.0034  0.5512  7.1826 

Random effects:
 Groups        Name        Variance Std.Dev.
 species.trial (Intercept) 0.01777  0.13329 
 species       lnBWg       0.00375  0.06124 
 species.1     (Intercept) 0.07013  0.26482 
 Residual                  0.05731  0.23939 
Number of obs: 2470, groups:  species:trial, 105; species, 56

Fixed effects:
             Estimate Std. Error t value
(Intercept)  2.062651   0.087379  23.606
lnBWg       -0.011588   0.016830  -0.689
tempTest    -0.027820   0.003027  -9.191

Correlation of Fixed Effects:
         (Intr) lnBWg 
lnBWg    -0.326       
tempTest -0.817  0.048
```

FAS, warm



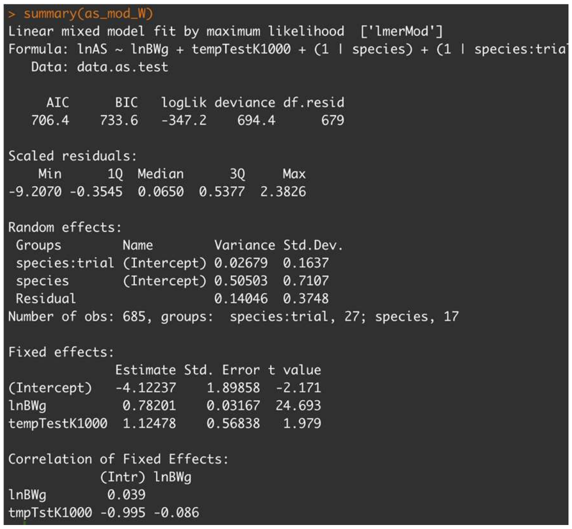
```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: lnFAS ~ lnBWg + poly(tempTest, 2) + (1 | species) + (0 + tempTes
    species) + (1 | species:trial)
   Data: data.fas.test
Control: lmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 2e+05)

     AIC      BIC   logLik deviance df.resid 
   227.8    264.0   -105.9    211.8      678 

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-4.5831 -0.5373  0.0318  0.5403  3.3587 

Random effects:
 Groups        Name        Variance Std.Dev.
 species.trial (Intercept) 0.022584 0.15028 
 species       tempTest    0.001427 0.03777 
 species.1     (Intercept) 0.954849 0.97716 
 Residual                  0.064587 0.25414 
Number of obs: 686, groups:  species:trial, 27; species, 17

Fixed effects:
                    Estimate Std. Error t value
(Intercept)          1.05745    0.36795   2.874
lnBWg               -0.06526    0.02400  -2.719
poly(tempTest, 2)1 -12.04303    2.39632  -5.026
poly(tempTest, 2)2  -3.10163    1.06953  -2.900

Correlation of Fixed Effects:
            (Intr) lnBWg  p(T,2)1
lnBWg       -0.181               
ply(tmT,2)1  0.515  0.062        
ply(tmT,2)2 -0.005  0.066 -0.255 
```

AS, optimal



```
> summary(as_mod_ER)
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: lnAS ~ lnBWg + tempTestK1000 + (1 | species) + (0 + lnBWg | spec
    (1 | species:trial)
   Data: data.asER

     AIC      BIC   logLik deviance df.resid 
   701.8    742.5   -343.9    687.8     2463 

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-7.0240 -0.4628  0.0300  0.5168  4.5942 

Random effects:
 Groups        Name        Variance Std.Dev.
 species.trial (Intercept) 0.02531  0.1591  
 species       lnBWg       0.01576  0.1255  
 species.1     (Intercept) 0.19298  0.4393  
 Residual                  0.06619  0.2573  
Number of obs: 2470, groups:  species:trial, 105; species, 56

Fixed effects:
              Estimate Std. Error t value
(Intercept)    7.53952    0.98515   7.653
lnBWg          0.82455    0.02753  29.950
tempTestK1000 -2.35607    0.29130  -8.088

Correlation of Fixed Effects:
            (Intr) lnBWg 
lnBWg       -0.011       
tmpTstK1000 -0.997 -0.022
```

AS, warm



```
> summary(as_mod_W)
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: lnAS ~ lnBWg + tempTestK1000 + (1 | species) + (1 | species:tria
   Data: data.as.test

     AIC      BIC   logLik deviance df.resid 
   706.4    733.6   -347.2    694.4      679 

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-9.2070 -0.3545  0.0650  0.5377  2.3826 

Random effects:
 Groups        Name        Variance Std.Dev.
 species:trial (Intercept) 0.02679  0.1637  
 species       (Intercept) 0.50503  0.7107  
 Residual                  0.14046  0.3748  
Number of obs: 685, groups:  species:trial, 27; species, 17

Fixed effects:
              Estimate Std. Error t value
(Intercept)   -4.12237    1.89858  -2.171
lnBWg          0.78201    0.03167  24.693
tempTestK1000  1.12478    0.56838   1.979

Correlation of Fixed Effects:
            (Intr) lnBWg 
lnBWg        0.039       
tmpTstK1000 -0.995 -0.086
```

Appendix 1, Table 4: Mixed effect model summary outputs, as provided by R.

OPTIMAL		**Slope (*b*), {C.I., 90%}**	**Slope (*b*), {C.I., 90%}**	**Slope (*b*), {C.I., 90%}**	**Suited for scaling?**			**MMR and RMR scaling inter-relationships.**
		MMR	**RMR**	**FAS**	**MMR**	**RMR**	**FAS**	

Morphology	Dorsov. Flatten	1.08 {0.85, 1.32}	NA	NA	**0**	**0**	**0**	
	Eel-like	1.24 {0.91, 1.57}	NA	NA	**0**	**0**	**0**	
	Elongated	0.74 {0.69, 0.79}	0.98 {0.93, 1.03}	0.01 {-0.03, 0.04}	**1**	**1**	**1**	$b_{MMR} < b_{RMR}$
	Fusiform	0.89 {0.88, 0.89}	0.94 {0.93, 0.95}	0.04 {0.04, 0.05}	**1**	**1**	**1**	$b_{MMR} < b_{RMR}$
	Short-deep	0.75 {0.73, 0.78}	0.71 {0.69, 0.73}	-0.01 {-0.04, 0.01}	**1**	**1**	**1**	$b_{MMR} > b_{RMR}$
Climate	Polar	0.8 {0.7, 0.89}	0.69 {0.65, 0.74}	-0.05 {-0.1, 0.01}	**0**	**0**	**0**	$b_{MMR} > b_{RMR}$
	Subtrop.	0.86 {0.85, 0.87}	0.94 {0.93, 0.96}	0.06 {0.05, 0.07}	**1**	**1**	**1**	$b_{MMR} < b_{RMR}$
	Temperate	0.89 {0.88, 0.9}	0.93 {0.91, 0.94}	0.03 {0.02, 0.04}	**1**	**1**	**1**	$b_{MMR} < b_{RMR}$
	Tropical	0.81 {0.8, 0.82}	0.75 {0.74, 0.77}	0 {-0.01, 0.01}	**1**	**1**	**1**	$b_{MMR} > b_{RMR}$
Lifestyle	Bentho-pelagic	0.91 {0.9, 0.92}	0.88 {0.86, 0.9}	0 {-0.02, 0.02}	**1**	**1**	**1**	$b_{MMR} > b_{RMR}$
	Demersal	0.75 {0.73, 0.76}	0.77 {0.75, 0.78}	0 {-0.01, 0.02}	**1**	**1**	**1**	$b_{MMR} < b_{RMR}$
	Pelagic	1 {0.99, 1.02}	1.02 {1.01, 1.03}	0.01 {0, 0.02}	**1**	**1**	**1**	$b_{MMR} < b_{RMR}$
	Reef-assoc.	0.8 {0.78, 0.81}	0.79 {0.78, 0.8}	0.01 {0, 0.02}	**1**	**1**	**1**	$b_{MMR} > b_{RMR}$
Salinity	Freshw.	0.8 {0.77, 0.83}	1 {0.94, 1.06}	0 {-0.04, 0.05}	**1**	**1**	**1**	$b_{MMR} < b_{RMR}$
	Freshw.-Brackish	0.75 {0.74, 0.76}	0.83 {0.81, 0.85}	-0.02 {-0.04, -0.01}	**1**	**1**	**1**	$b_{MMR} < b_{RMR}$
	Marine	0.83 {0.82, 0.84}	0.78 {0.77, 0.8}	0.02 {0.01, 0.03}	**1**	**1**	**1**	$b_{MMR} > b_{RMR}$
	Marine-brackish	0.82 {0.77, 0.87}	0.69 {0.65, 0.73}	-0.05 {-0.1, 0.01}	**1**	**0**	**0**	$b_{MMR} > b_{RMR}$
	All sal.	0.96 {0.94, 0.97}	0.97 {0.96, 0.97}	0.05 {0.04, 0.06}	**1**	**1**	**1**	$b_{MMR} < b_{RMR}$
WARM		**Slope (b), {C.I, 90%}**	**Slope (b), {C.I, 90%}**	**Slope (b), {C.I, 90%}**	**Suited for scaling?**			**MMR and RMR scaling inter-relationships.**
	MMR	***MMR***	***RMR***	***FAS***	**RMR**	**MMR**	**RMR**	
Morphol	Dorsov. Flatten	NA	NA	NA				

	Eel-like	NA	NA	NA				
	Elongated	0.47 {0.38, 0.57}	0.75 {0.61, 0.88}	-0.25 {-0.31, -0.18}	**0**	**0**	**0**	$b_{MMR} < b_{RMR}$
	Fusiform	0.93 {0.92, 0.95}	0.94 {0.93, 0.95}	0.01 {0, 0.02}	**1**	**1**	**1**	$b_{MMR} < b_{RMR}$
	Short-deep	0.92 {0.82, 1.01}	0.84 {0.77, 0.91}	-0.36 {-0.42, -0.29}	**0**	**0**	**0**	$b_{MMR} > b_{RMR}$
Climate	Polar	0.87 {0.71, 1.02}	1.44 {0.81, 2.07}	0.05 {-0.87, 0.96}	**0**	**0**	**0**	$b_{MMR} < b_{RMR}$
	Subtrop.	0.99 {0.98, 1}	0.97 {0.96, 0.98}	0.05 {0.01, 0.08}	**1**	**1**	**1**	$b_{MMR} > b_{RMR}$
	Temperate	1.06 {1.03, 1.08}	1.02 {0.99, 1.05}	-0.13 {-0.17, -0.09}	**1**	**1**	**1**	$b_{MMR} > b_{RMR}$
	Tropical	0.83 {0.81, 0.86}	0.83 {0.81, 0.86}	-0.01 {-0.03, 0.01}	**1**	**1**	**1**	$b_{MMR} < b_{RMR}$
Lifestyle	Bentho-pelagic	1 {0.98, 1.02}	0.97 {0.96, 0.99}	-0.06 {-0.18, 0.06}	**1**	**1**	**1**	$b_{MMR} > b_{RMR}$
	Demersal	0.78 {0.75, 0.82}	0.71 {0.69, 0.73}	-0.01 {-0.05, 0.03}	**1**	**1**	**1**	$b_{MMR} > b_{RMR}$
	Pelagic	1.25 {0.82, 1.68}	0.74 {0.66, 0.81}	-0.06 {-0.74, 0.63}	**0**	**0**	**0**	$b_{MMR} > b_{RMR}$
	Reef-assoc.	0.88 {0.85, 0.92}	0.84 {0.8, 0.88}	-0.05 {-0.08, -0.02}	**1**	**1**	**1**	$b_{MMR} > b_{RMR}$
Salinity	Freshw.	0.76 {0.7, 0.82}	0.77 {0.71, 0.84}	-0.05 {-0.14, 0.03}	**0**	**0**	**0**	$b_{MMR} < b_{RMR}$
	Freshw.-Brackish	0.87 {0.82, 0.91}	0.96 {0.92, 0.99}	-0.07 {-0.12, -0.02}	**0**	**0**	**0**	$b_{MMR} < b_{RMR}$
	Marine	0.88 {0.85, 0.91}	0.84 {0.8, 0.88}	-0.05 {-0.08, -0.02}	**1**	**1**	**1**	$b_{MMR} > b_{RMR}$
	Marine-brackish	1.04 {0.6, 1.47}	0.8 {0.76, 0.85}	-0.65 {-1.24, -0.06}	**0**	**0**	**0**	$b_{MMR} > b_{RMR}$
	All sal.	1 {0.98, 1.01}	0.97 {0.96, 0.98}	0.02 {0, 0.03}	**1**	**1**	**1**	$b_{MMR} > b_{RMR}$

Appendix 1, Table 5: Ecology – associated variation of scaling relationships.
Data are provided in fish grouped in each ecological and morphological category. Presented are only scaling slopes (b), and their 95% and 5% confidence intervals (C.I.$_{90\%}$ {low; high}) for direct comparison. The indication 0 = No or 1=Yes specifies whether the sample size of the dataset was n =100 or more, and the body size coverage spanned at least an order of magnitude. MMR = maximum metabolic rate, RMR = resting metabolic rate, FAS = factorial aerobic scope (MMR / RMR)

APPENDIX 2, CHAPTER 3.

Date	Location	Fishing method	N (fish)	Coordinates (Lat, Lng)
Spring Housing: 108 gallon (410 L; L: 52 inches, W:30 inches, D: 16, N = 12 fish) and 80 gallon (301 L; L: 52 inches, W:29.5 inches, D: 12, N = 10 fish) tanks, and two 25 gallon tanks (N = 5 fish/tank). Laboratory-born juveniles: 10 gallon tanks (N = 6 to 12 fish/tank).				
April 17, 2021	Goleta Beach, Goleta, CA 93117	30 ft seine no bag	3	34.416967, -119.818091
April 17, 2021	Goleta Beach, Goleta, CA 93117	hook and line	2	
May 10, 2021	Haskell's Beach, Goleta, CA 93117	50 ft seine with bag	5	34.430767, -119.916717
May 11, 2021	Haskell's Beach, Goleta, CA 93117	50 ft seine with bag	11	
May 12, 2021	Haskell's Beach, Goleta, CA 93117	50 ft seine with bag	5	
May 15, 2021	Santa Claus Lane Carpinteria, CA 93013	hook and line	1	34.407207, -119.550873
May 15, 2021	Goleta Beach - pier, Goleta, CA 93117	hook and line	1	34.416967, -119.818091
May 16, 2021	Haskell's Beach, Goleta, CA 93117	50 ft seine with bag	8	34.430767, -119.916717
Summer Housing: n = five 25 gallon tanks (2-13 fish per tank, matched sizes)				
July 27	Haskell's Beach, Goleta, CA 93117	50 ft seine with bag	25	34.430767, -119.916717
31-May, 1-Jun 3-Jun, 6-Jun 7-Jun, 8-Jun, 2021	Newborn in laboratory	NA	79	

Appendix 2, Table 1. Fishing and laboratory residence.

Tests	Origin	Pregnancy	Size class	Sex	N
Respirometry (MMR, RMR, AAS, FAS)	field	No	Adult (> 50 g)	F	12
				M	21
		No	Juvenile (<50 g)	F	5
				M	6
				NA	1
		Yes	Adult (50 g)	F	5
	lab	No	Juvenile (< 50 g)	F	10
				M	20

				NA	3
Arrhenius breakpoint temperature test (f_{Hmax}, T_{AB}, T_{PEAK}, T_{ARR}, $PEAK_{fHmax}$)	field	No	Adult (> 50 g)	F	7
				M	5
		No	Juvenile (< 50 g)	F	4
				M	5
				NA	4
	lab	No		F	1
				M	3
				NA	1

Appendix 2, Table 2: Summary of physiological tests complete.

N = sample size, F = female, M = male, NA = not available. Origin (laboratory-born or field caught).

MODEL	HYPO-THESES	k	BIC	ΔBIC
Maximum metabolic rates (MMR):				
log(MMR) ~ log(BW) + T + Orig + (1|ID)	Temperature treatment (T, categ.), repeat measures (1|ID), Sex (categ.) and Orig (categ.)	8	-195.941	3.25899
log(MMR) ~ log(BW) + T + Sex + Orig + (1|ID)		10	-169.8433	29.35678
log(MMR) ~ log(BW) + T + Sex + (1|ID)		9	-172.9307	26.26938
log(MMR) ~ log(BW) + T + (1|ID)		**7**	**-199.2**	**0**
log(MMR) ~ log(BW) * T + (1|ID)		10	-183.4366	15.76344
log(MMR) ~ log(BW)	temperature specific LM. 12, 16, 20, 22ºC, no covariates			
Minimum metabolic rates (RMR)				
log(RMR) ~ log(BW) + T + Orig + (1|ID)	T (ºC, categ.), repeat measures (1|ID), Sex (categ.), Orig (categ.)	**8**	**-41.75825**	**0**
log(RMR) ~ log(BW) + T + Sex + Orig + (1|ID)		10	-23.74274	18.01551
log(RMR) ~ log(BW) + T + Sex + (1|ID)		9	-19.8973	21.86095
log(RMR) ~ log(BW) + T + (1|ID)		7	-36.90996	4.84829
log(RMR) ~ log(BW) * T + (1|ID)		10	-21.87646	19.8818
log(RMR) ~ log(BW)	temperature specific LM. 12, 16, 20, 22ºC, no covariates			
Absolute Aerobic scopes (AAS = MMR - RMR)				
log(AAS) ~ log(BW) + T + Orig + (1|ID)	T (ºC, categ.), repeat measures (1|ID), Sex (categ.), Orig (categ.)	8	146.7398	3.46968
log(AAS) ~ log(BW) + T + Sex + Orig + (1|ID)		10	156.9671	13.69698
log(AAS) ~ log(BW) + T + Sex + (1|ID)		9	152.9353	9.66521
log(AAS) ~ log(BW) + T + (1|ID)		**7**	**143.2701**	**0**

log(AS) ~ log(BW)	temperature specific LM. 12, 16, 20, 22ºC, no covariates			
Factorial Aerobic scope (FAS = MMR / RMR)				
log(FAS) ~ log(BW) + T + Orig + (1|ID)	T (ºC, categ.), repeat measures (1|ID), Sex (categ.), Orig (categ.)	**8**	**-132.0578**	**0**
log(FAS) ~ log(BW) + T + Sex + Orig + (1|ID)		10	-110.4866	21.5712
log(FAS) ~ log(BW) + T + Sex + (1|ID)		9	-109.556	22.50176
log(FAS) ~ log(BW) + T + (1|ID)		7	-129.8056	2.25222
log(FAS) ~ log(BW) * T + (1|ID)		10	-115.1419	16.91589
log(FAS) ~ log(BW)	temperature specific LM. 12, 16, 20, 22ºC, no covariates			
Maximum heart rate (beats min^{-1}) across temperatures				
log(f_{Hmax}) ~ log(BW) + T + (1|ID)	T (ºC, categ.), repeat measures (1|ID), no covariates	**16**	**-733.2281**	**0**
log(f_{Hmax}) ~ log(BW) * T + (1|ID)		28	-687.8539	45.37416
log(f_{Hmax}) ~ log(BW) + (1|ID)		4	-224.0942	509.13385
Temperature at which the heart became arrhytmic				
log(T_{ARR}) ~ 1	*NULL model*	2	-67.36079	4.2596
log(T_{ARR}) ~ log(BW)	T (ºC, categ.), repeat measures (1|ID), Sex (categ.), Orig (categ.)	**3**	**-71.62039**	**0**
log(T_{ARR}) ~ log(BW) + Orig		4	-68.94095	2.67944
log(T_{ARR}) ~ log(BW) + Sex		4	-54.08455	17.53584
log(T_{ARR}) ~ log(BW) + Sex + Orig		5	-53.68086	17.93953
Temperature at which fish had the peak maximum heart rates				
log(T_{PEAK}) ~ 1	*NULL model*	2	-61.76246	4.43588
log(T_{PEAK}) ~ log(BW)	T (ºC, categ.), repeat measures (1|ID), Sex (categ.), Orig (categ.)	**3**	**-66.19834**	**0**
log(T_{PEAK}) ~ log(BW) + Orig		4	-62.91077	3.28757
log(T_{PEAK}) ~ log(BW) + Sex		4	-50.22768	15.97066
log(T_{PEAK}) ~ log(BW) + Sex + Orig		5	-47.86668	18.33166
Breakpoint temperature of maximum heart rates				
log(T_{AB}) ~ 1	*NULL model*	**2**	-61.80491	11.56258
log(T_{AB}) ~ log(BW)	T (ºC, categ.), repeat measures (1|ID), Sex (categ.), Orig (categ.)	3	-71.29383	2.07366
log(T_{AB}) ~ log(BW) + Orig		**4**	**-73.36749**	**0**
log(T_{AB}) ~ log(BW) + Sex		4	-53.76421	19.60328
log(T_{AB}) ~ log(BW) + Sex + Orig		5	-54.47289	18.8946
The absolute peak maximum heart rates recorded at any temperature				
log($PEAK_{fHmax}$) ~ 1	*NULL model*	**2**	**-49.52628**	**0**
log($PEAK_{fHmax}$) ~ log(BW)		3	-46.4506	3.07568

log(PEAK$_{f\mathrm{Hmax}}$) ~ log(BW) + Orig	T (ºC, categ.), repeat measures (1|ID), Sex (categ.), Orig (categ.)	4	-44.09186	5.43442
log(PEAK$_{f\mathrm{Hmax}}$) ~ log(BW) + Sex		4	-38.18762	11.33866
log(PEAK$_{f\mathrm{Hmax}}$) ~ log(BW) + Sex + Orig		5	-39.11335	10.41293
Ventricular mass (kg)				
log(VM)~log(BW)	VM = ventricular mass, no covariates			

Appendix 2, Table 3. Linear models for metabolic scaling and results of model selection (BIC).

	log(BW)		**Temperature**		**Origin**	
Mixed models	χ^2 *(df)*	*p-value*	χ^2 *(df)*	*p-value*	χ^2 *(df)*	*p-val*
MMR	6989.51 (1)	< 0.0001	463.88 (3)	< 0.0001	--	--
Post-hoc results			12ºC vs 16ºC	***		
			12ºC vs 20ºC	***		
			12ºC vs 22ºC	***		
			16ºC vs 20ºC	***		
			16ºC vs 22ºC	***		
			20ºC vs 22ºC	ns		
RMR	1568.975 (1)	< 0.0001	515.971 (3)	< 0.0001	11.035 (1)	0.0009
Post-hoc results			12ºC vs 16ºC	***		
			12ºC vs 20ºC	***		
			12ºC vs 22ºC	***		
			16ºC vs 20ºC	***		
			16ºC vs 22ºC	***		
			20ºC vs 22ºC	0.018		
AAS	2268.224 (1)	< 0.0001	21.976 (3)	< 0.0001	--	--
Post-hoc results			12ºC vs 16ºC	ns		
			12ºC vs 20ºC	**		
			12ºC vs 22ºC	0.046		
			16ºC vs 20ºC	*		
			16ºC vs 22ºC	ns		
			20ºC vs 22ºC	ns		
FAS	1.567 (1)	0.2106	72.503 (3)	< 0.0001	8.013 (1)	0.0046
Post-hoc results			12ºC vs 16ºC	***		
			12ºC vs 20ºC	***		
			12ºC vs 22ºC	***		
			16ºC vs 20ºC	ns		
			16ºC vs 22ºC	*		
			20ºC vs 22ºC	ns		

f_{Hmax}	30.957 (1)	< 0.0001	1767.892 (12)	< 0.0001	--	--
Simple linear models	*F (df)*	*p-value*	*F (df)*	*p-value*	*F (df)*	*p-val*
T_{ARR}	8.122 (1)	0.0083	--	--	--	--
T_{PEAK}	8.359 (1)	0.0073	--	--	--	--
T_{AB}	8.851 (1)	0.0066	--	--	5.281 (1)	0.0306
$PEAK_{fHmax}$	--	--	--	--	--	--

Appendix 2, Table 4. Statistics results for best fit models.

And Post hoc statistics for models with significant temperature main effects.

Performance	Origin	Treatment ºC	df	n	Estimated marginal mean (mass – specific)	Standard error, SD	Coefficient of variation (SD/mean), %
RMR	Field-collected	12	94.1	44	1.264	1.066	17.80
		16	92.4	46	1.803	1.066	19.60
		20	91.9	48	2.328	1.066	13.10
		22	137.8	19	2.638	1.074	17.20
	Laboratory-born	12	81.7	22	1.529	1.113	16.50
		16	80.3	28	2.182	1.112	8.95
		20	81.8	18	2.816	1.114	9.77
		22	99.9	8	3.191	1.119	6.96
MMR	Field-collected	12	105.9	66	2.747	1.040	12.60
		16	104.8	76	3.439	1.040	12.20
		20	99.4	68	4.203	1.039	9.94
		22	158.0	28	4.468	1.045	7.77
Absolute Aerobic scope	Field-collected	12	108.9	66	1.717	1.079	22.80
		16	108.2	74	1.806	1.079	24.80
		20	103.1	66	2.106	1.077	24.80
		22	166.3	27	2.040	1.093	21.40
Factorial Aerobic scope	Field-collected	12	95.7	44	2.267	1.052	15.00
		16	93.8	46	1.984	1.051	15.80
		20	93.3	48	1.891	1.052	14.00
		22	143.8	19	1.769	1.058	13.10
	Laboratory-born	12	81.5	22	1.998	1.087	14.60
		16	79.8	28	1.749	1.087	11.60
		20	81.6	18	1.667	1.088	9.81
		22	101.8	8	1.559	1.093	5.75

f_{Hmax}	Field-collected	16	37.8	31	75.554	1.036	3.25
		17	38.4	34	80.227	1.036	3.42
		18	38.9	30	86.613	1.036	2.83
		19	38.9	30	92.655	1.036	2.54
		20	38.9	30	98.349	1.036	2.64
		21	38.9	30	103.467	1.036	3.25
		22	39.0	29	107.580	1.036	3.82
		23	39.6	25	110.937	1.036	3.53
		24	39.4	26	112.575	1.036	3.65
		25	40.1	23	114.661	1.036	5.57
		26	41.4	20	116.166	1.036	7.07
		27	66.2	7	106.696	1.041	23.90
		28	176.8	2	112.195	1.056	0.69

Appendix 2, Table 5. Mass-independent mixed model estimates of physiological performances.

Summary of mixed model marginal mean performance estimates for fish adjusted to 1 kg. These values were used to perform post-hoc analysis. Size ranges are provided in Appendix 2, Table 2.

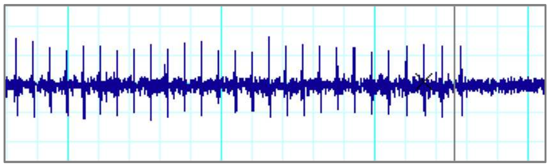
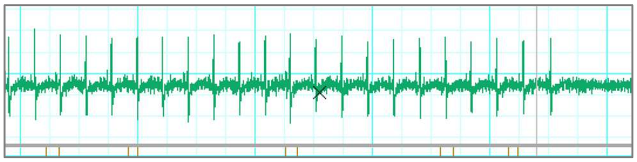
Size Class	Performance	Treatm, °C	Mean value	Minimum value	Maximum value	SD	N
> 50 g fish	PEAK$_{f\mathrm{Hmax}}$		136.50	117.66	157.02	11.35	12
	T_{PEAK}		25.45	23.00	26.90	1.06	12
	T_{ARR}		27.13	25.71	28.90	0.89	11
	T_{AB}		21.83	19.83	24.49	1.46	11
	Body Mass		0.1368	0.0850	0.2490	0.0524	12
< 50 g fish	PEAK$_{f\mathrm{Hmax}}$		137.54	111.54	168.91	14.64	18
	T_{PEAK}		23.66	19.90	26.15	1.95	18
	T_{ARR}		25.41	21.66	27.84	1.82	18
	T_{AB}		20.21	18.34	21.77	1.08	16
	Body Mass		0.0160	0.0083	0.0254	0.0047	18
All fish	PEAK$_{f\mathrm{Hmax}}$		137.12	111.54	168.91	13.22	30
	T_{PEAK}		24.37	19.9	26.9	1.86	30
	T_{ARR}		26.06	21.66	28.9	1.73	29
	T_{AB}		20.87	18.34	24.49	1.47	27
	Body Mass		0.0643	0.0083	0.2490	0.0684	30
All fish	f_{Hmax}	16	88.9	74.4	104	8.03	31
		17	95.5	78.4	111	8.35	34
		18	103	84	120	8.86	30
		19	110	88.8	125	9.1	30
		20	117	94	133	9.76	30

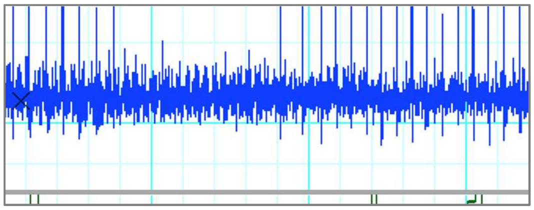
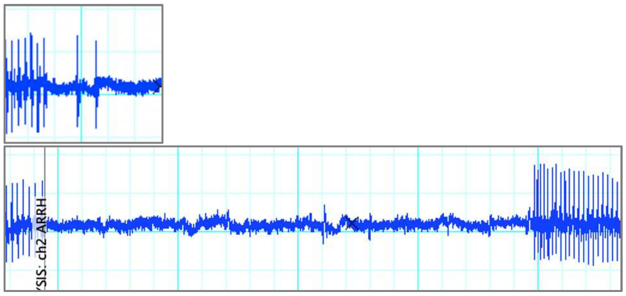
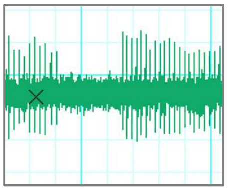
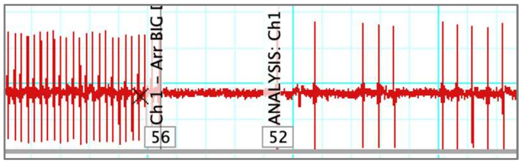
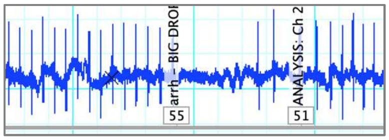
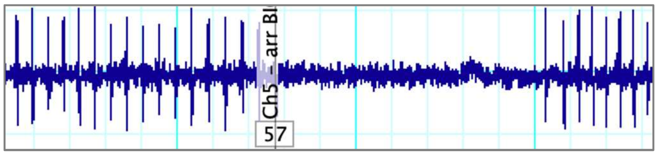
		21	123	100	141	10.2	30
		22	128	107	151	11.1	29
		23	131	113	155	11.3	25
		24	134	117	156	10.4	26
		25	136	108	161	11.8	23
		26	138	109	169	14.7	20
		27	131	57.6	164	35.7	7
		28	133	130	137	4.89	2
> 50 g fish (adult)	RMR	12	0.251	0.073	1.194	0.204	33
		16	0.348	0.094	0.860	0.203	35
		20	0.452	0.167	2.083	0.340	36
		22	0.554	0.339	1.107	0.246	11
	MMR	12	0.537	0.221	2.530	0.408	33
		16	0.635	0.266	1.368	0.294	36
		20	0.802	0.417	3.146	0.485	37
		22	0.874	0.570	1.506	0.324	11
	AAS	12	0.286	0.092	1.336	0.211	33
		16	0.291	0.151	0.762	0.128	35
		20	0.346	0.177	1.063	0.170	36
		22	0.320	0.176	0.511	0.116	11
	FAS	12	2.281	1.554	3.596	0.473	33
		16	2.017	1.290	3.150	0.459	35
		20	1.887	1.363	2.669	0.338	36
		22	1.628	1.342	2.167	0.255	11
< 50 g fish (juvenles)	RMR	12	0.035	0.016	0.115	0.017	33
		16	0.050	0.024	0.118	0.018	39
		20	0.066	0.040	0.171	0.027	30
		22	0.072	0.050	0.105	0.013	16
	MMR	12	0.065	0.038	0.182	0.027	33
		16	0.081	0.041	0.232	0.034	40
		20	0.104	0.061	0.329	0.055	31
		22	0.110	0.072	0.173	0.029	17
	AAS	12	0.030	0.010	0.067	0.013	33
		16	0.031	0.008	0.114	0.019	39
		20	0.039	0.010	0.159	0.031	30
		22	0.040	0.020	0.073	0.017	16
	FAS	12	1.887	1.272	2.554	0.316	33
		16	1.619	1.144	2.232	0.219	39
		20	1.571	1.159	2.088	0.204	30

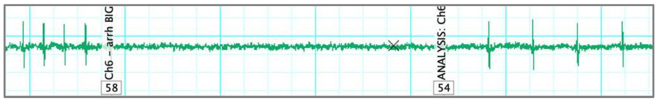
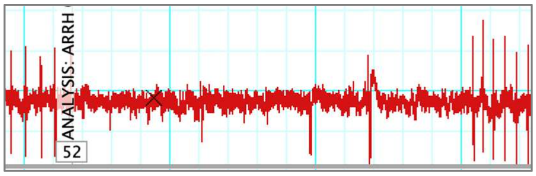
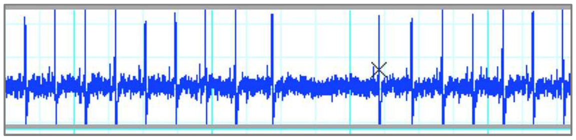
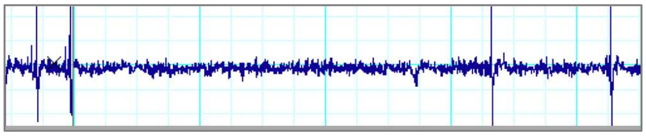
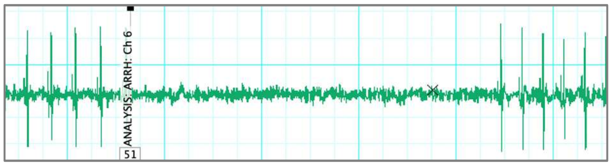
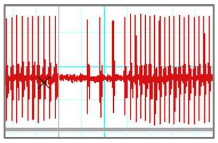
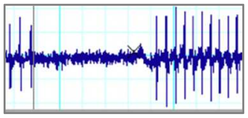
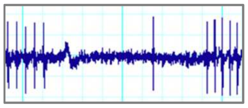
		22	1.538	1.287	1.847	0.176	16
All fish	RMR	12	0.143	0.016	1.194	0.180	66
		16	0.191	0.024	0.860	0.204	74
		20	0.276	0.040	2.083	0.317	66
		22	0.268	0.050	1.107	0.286	27
	MMR	12	0.301	0.038	2.530	0.372	66
		16	0.344	0.041	1.368	0.344	76
		20	0.484	0.061	3.146	0.500	68
		22	0.410	0.072	1.506	0.429	28
	AAS	12	0.158	0.010	1.336	0.197	66
		16	0.154	0.008	0.762	0.158	74
		20	0.207	0.010	1.063	0.199	66
		22	0.154	0.020	0.511	0.158	27
	FAS	12	2.084	1.272	3.596	0.446	66
		16	1.807	1.144	3.150	0.404	74
		20	1.743	1.159	2.669	0.325	66
		22	1.574	1.287	2.167	0.212	27

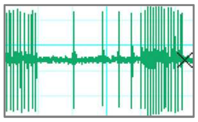
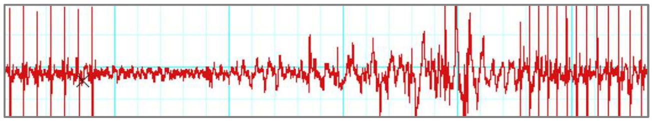
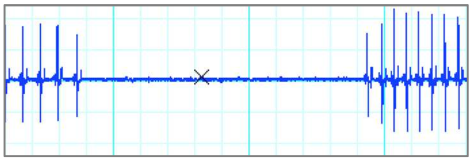
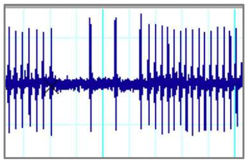
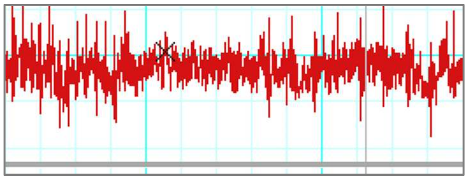
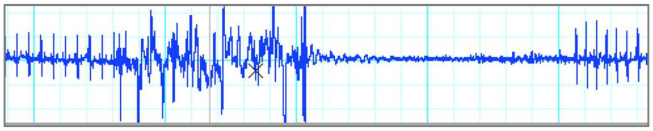
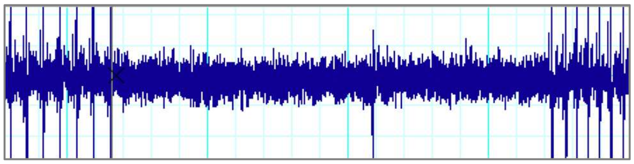
Appendix 2, Table 6. The range of individual measured aerobic and cardiac thermal tolerance values and sample sizes.

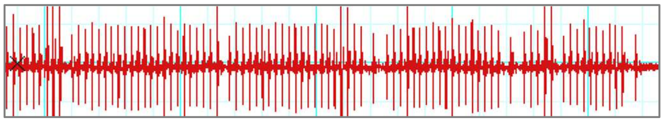
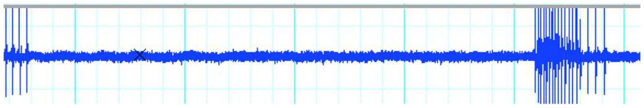
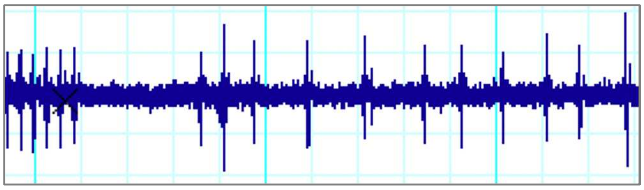
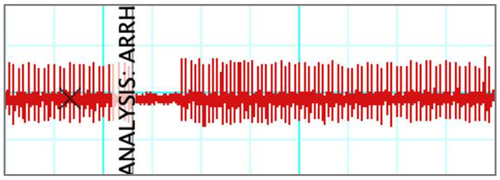
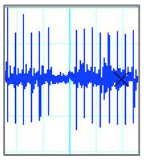
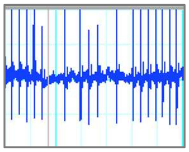
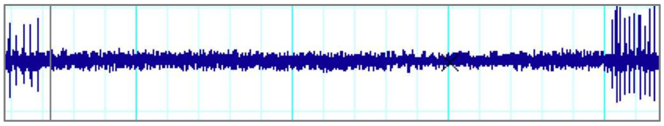
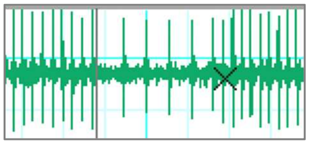
Size range for all performances was between approximately 5 g and 700 g for aerobic performances, and between approximately 8 g and 200 g cardiac thermal tolerance performances. Two size classes were considered: juveniles (< 50 g), and adults (> 50 g). * *note*: 30 fish were tested, a few fish had more than one recording at 16 or 17ºC, because that was the initial temperature at which fish started the trial and the heating element had delay in these few trails.

Channel	Test ID	Time T_{ARR}	Temp Last, setpoint	Electrocardiogram images of arrhythmic, or missing heart beat (direct screenshots from analysis software, LabChart 8, methods in main text)
5	Oct05_2021_test1	0:49:02	23 ºC	 *First occurrence of a missing heart beat.*
6	Oct05_2021_test1	1:17:05 h	27 ºC	 *First occurrence of a missing heart beat.*

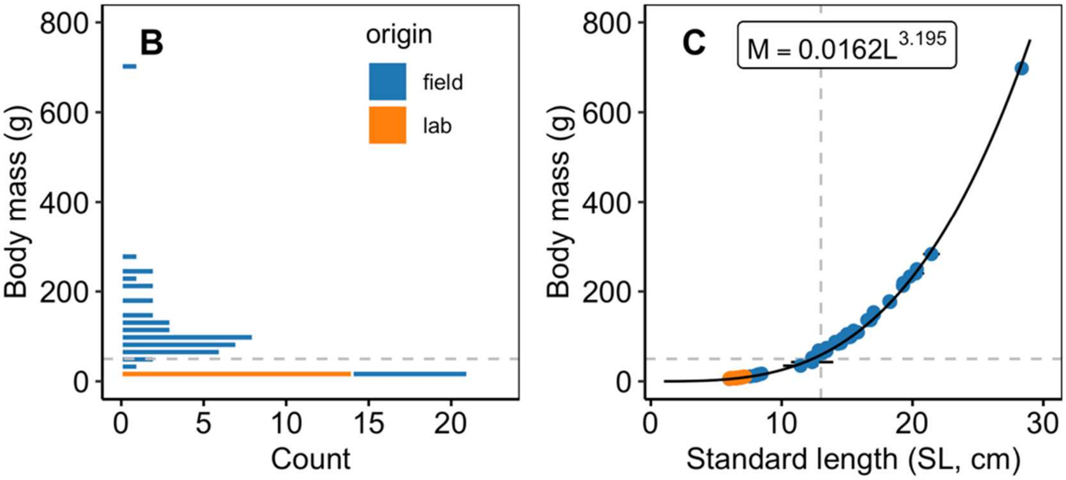
2	Oct05_2021_test1	38:10	21 ºC	 *First occurrence of a missing heart beat.*
2	Oct07_2021_test3	49:08	24 ºC	 *Irregular heart beat and occurrence of a missing heart beat.*
6	Oct07_2021_test3	1:07:18	27 ºC	 *First occurrence of a missing heart beat.*
1	Oct11_2021_test4	1:09:28	26 ºC	 *Irregular heart beat and occurrence of a missing heart beat.*
2	Oct11_2021_test4	1:07:10	26 ºC	 *Irregular heart beat and occurrence of a missing heart beat.*
5	Oct11_2021_test4	1:08:57	26 ºC	 *First occurrence of a missing heart beat.*

6	Oct11_2021_test4	1:10:43	26 ºC	 *Irregular heart beat and occurrence of a missing heart beat.*
1	Oct12_2021_test5	1:14:41	27 ºC	 *First occurrence of a missing heart beat.*
2	Oct12_2021_test5	44:44	22 ºC	 *First occurrence of a missing heart beat.*
5	Oct12_2021_test5	51.38	23 ºC	 *Irregular heart beat and occurrence of a missing heart beat.*
6	Oct12_2021_test5	58:55	24 ºC	 *First occurrence of a missing heart beat.*
1	Oct13_2021_test6	1:01:36	25 ºC	 *Irregular heart beat and occurrence of a missing heart beat.*
5	Oct13_2021_test6	1:08:23	26 ºC	 followed by  *Irregular heart beat and occurrence of a missing heart beat.*

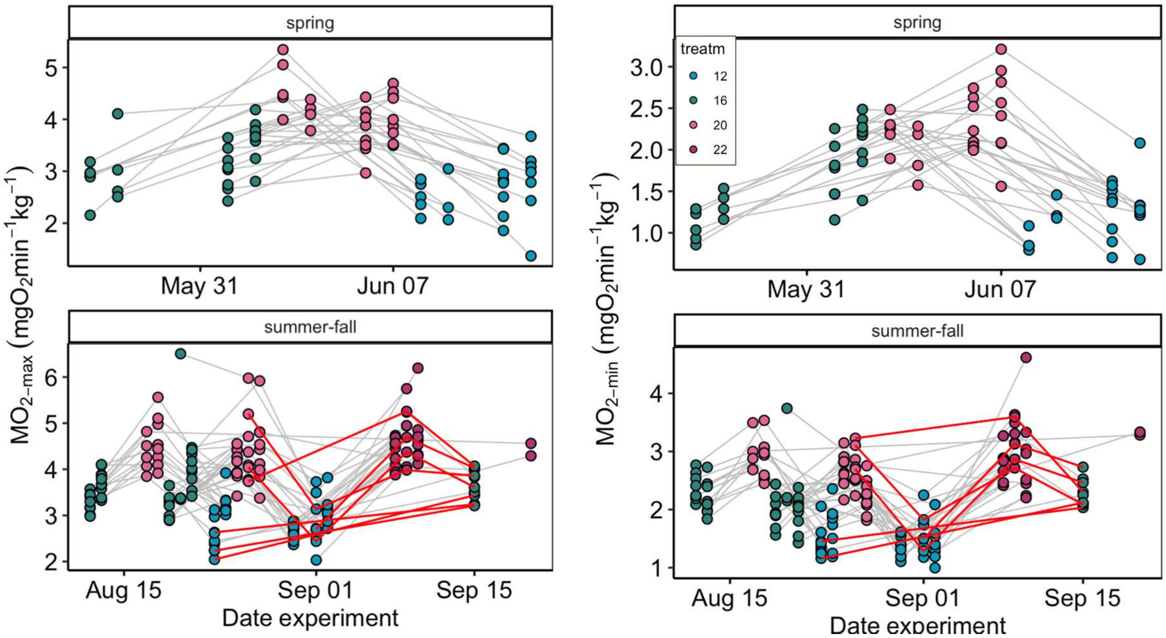
6	Oct13_2021_test6	1:12 41:07 (first long beat)	27 ºC (21- right at 22)	 *Irregular heart beat and occurrence of a missing heart beat.*
1	Oct13_2021_test7	1:16:19	26 ºC	 *First occurrence of a missing heart beat.*
2	Oct13_2021_test7	1:15:08	26 ºC	 *First occurrence of a missing heart beat.*
5	Oct13_2021_test7	1:17:56	26 ºC	 *Irregular heart beat and occurrence of a missing heart beat.*
1	Oct14_2021_test8	1:11:28	27 ºC	 *Irregular heart beat and occurrence of a missing heart beat.* Noisy, but distinguishable.
2	Oct14_2021_test8	1:12:21	27 ºC	 *First occurrence of a missing heart beat.*
5	Oct14_2021_test8	1:16:21	26 ºC	 *First occurrence of a missing heart beat.*

1	Oct15_ 2021_test9	1:21:01	28 ºC	 *Irregular heart beat.*
2	Oct15_ 2021_test9	1:22:	28 ºC	 *Irregular heart beat and occurrence of a missing heart beat.*
5	Oct15_ 2021_test9	1:10:01	26 ºC	 *Irregular heart beat and occurrence of a missing heart beat.*
1	Oct18_ 2021_test10	55:03	24 ºC	 *First occurrence of a missing heart beat.*
2	Oct18_ 2021_test10	1:03:58	25 ºC	 followed by  *Irregular heart beat and occurrence of a missing heart beat.*
5	Oct18_ 2021_test10	58:24	24 ºC	 *First occurrence of a missing heart beat.*
6	Oct18_ 2021_test10	1:06:37	26 ºC	 *Irregular heart beat and occurrence of a missing heart beat.*

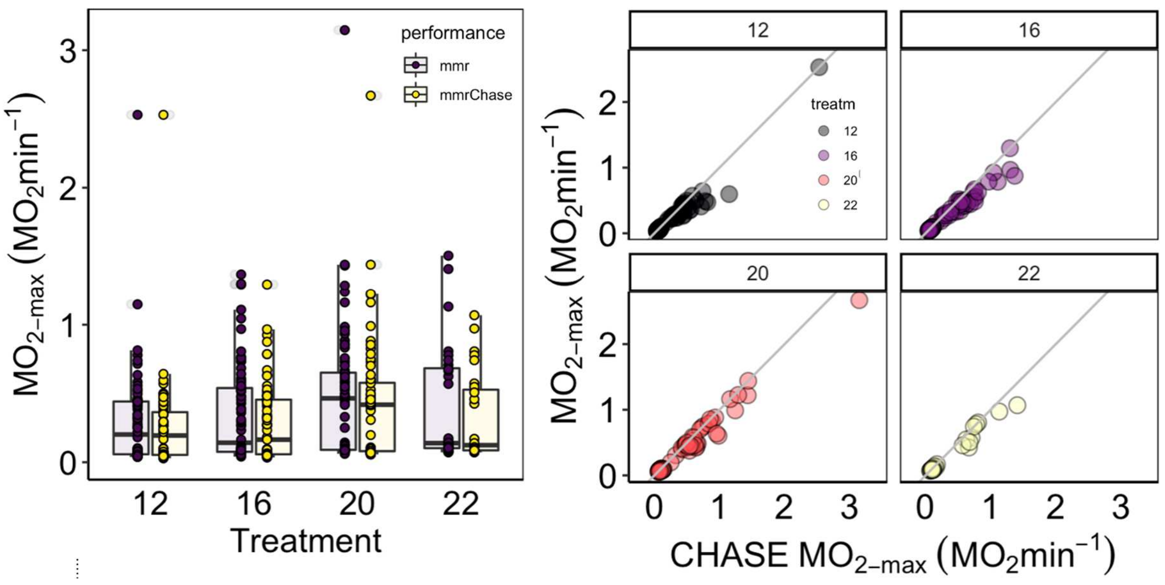
Appendix 2, Table 7. Visual identification of arrhythmias in each fish.
One fish was removed from the experimental sling before the onset of clear arrhythmia.



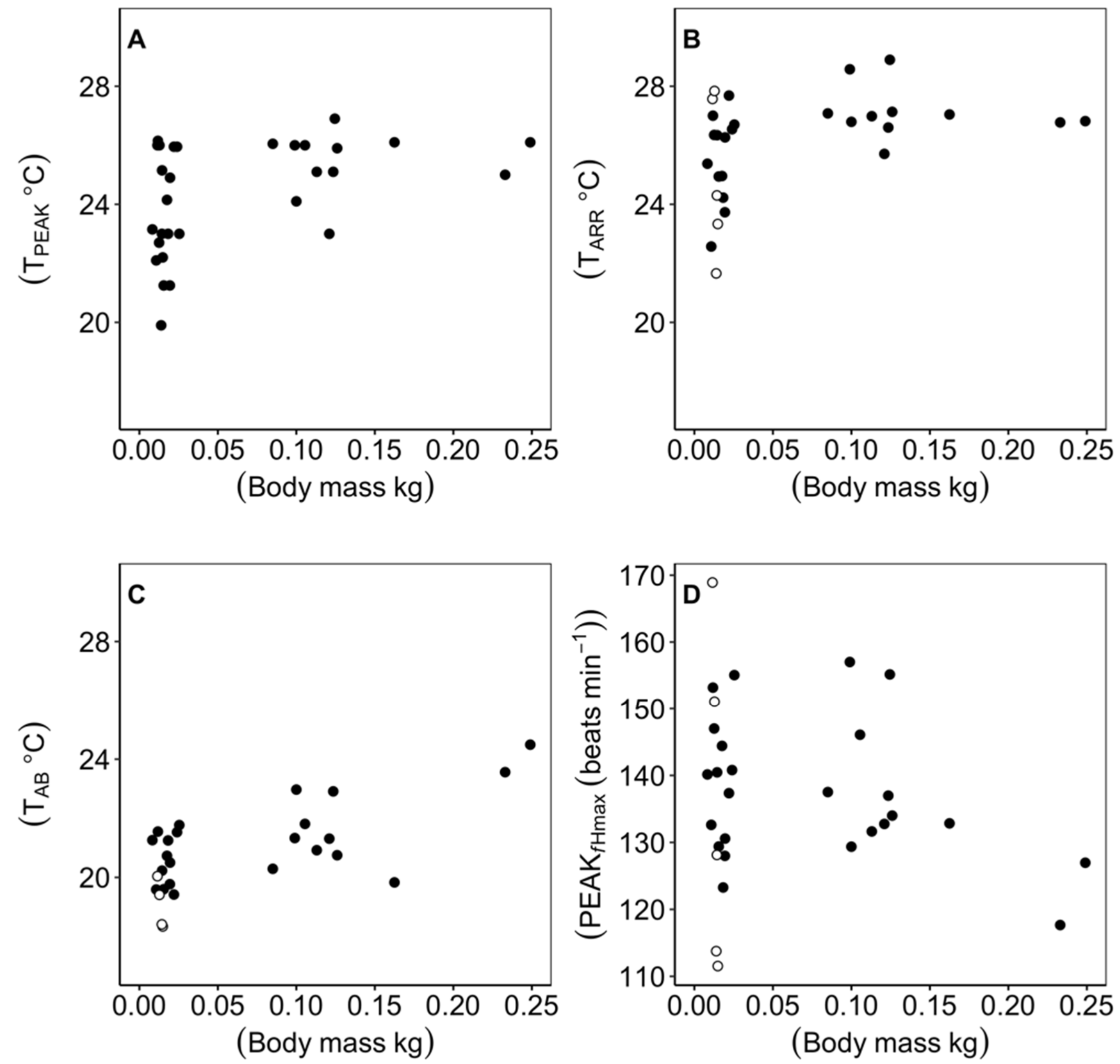
Appendix 2, Figure 1. Body size distribution and mass-length relationships.



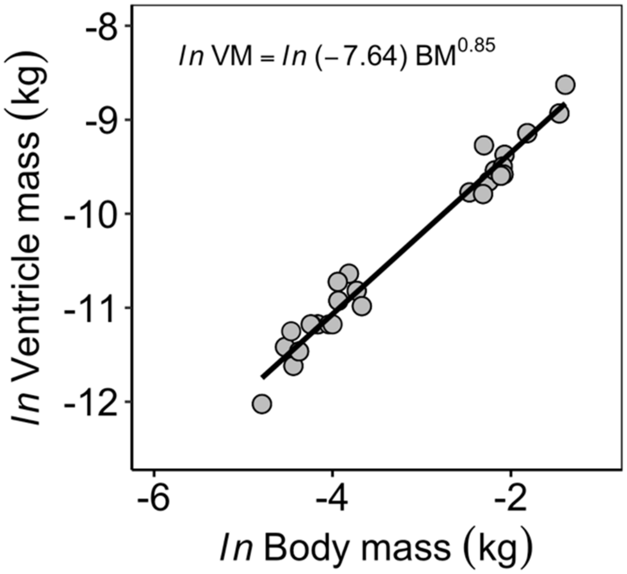
Appendix 2, Figure 2. The time (day) or respirometry trials and measured metabolic rates. The MMR (MO$_2$max) and RMR (MO$_2$min) measured in each individual in respect to time in 2021. Grey lines connect individuals that were tested first in 16ºC, their acclimation temperature. The red lines connect individuals that were tested in one of the acute temperature treatments first. Treatm = treatment.



Appendix 2, Figure 3. Comparison of maximum metabolic rates measurements.
CHASE MMR (MO_{2max}) is following a 3 min chase, 1 min air exposure and MMR (MO_{2max}) the highest reported MO_2 value overnight. If MMR-chase was the highest value, then MMR and MMR-chase will be equivalent. On the left side boxplot showing the distributions of each MMR value for each treatment. On the right-side facet plot, the two MMR values are correlated for each temperature treatment. The line is the "identity line" with slope = 1 and intercept = 0.



Appendix 2, Figure 4. Mass scaling of cardiac thermal performance indices.
Plotted are: T$_{PEAK}$ (**A**), T$_{ARR}$ (**B**), T$_{AB}$ (**C**), f_{Hmax} (**D**). In T$_{AB}$ (**C**) the origin of individual — laboratory-born (open symbols) and wild-collected fish (closed symbols) — was a significant explanatory variable. The peak maximum heart rate at any temperature (PEAK$_{fHmax}$) (**D**) was not significantly explained by body mass. [same as the main text, but not on a log-log scale].



Appendix 2, Figure 5. Scaling of ventricular mass.
Plotted are individuals used in the ABT tests (n = 23). VM = ventricular mas

APPENDIX 3, CHAPTER 4.

SECTION 1: TERMINOLOGY AND EXTENDED METHODS

1.1. Common terminology in fish swimming

- **Aerobic metabolism** – a cellular process that produces energy (ATP) from glucose, fatty acids, and amino acids in the presence of oxygen.
- **Anaerobic metabolism** is a cellular process that produces energy (ATP) using glucose and glycogen without oxygen.
- **Burst (sprint) swimming** – Sprinting, bursting, jumping, and predator escape responses are unsustainable, physiologically exhausting modes that quickly lead to fatigue.
- **Burst and coast (burst and glide) –** A transitional swimming mode that consists of alternating periods of accelerations (burst) and powerless, passive gliding (coast or glide).
- **Exhaustion –** A physiological (and behavioral) state when an individual cannot continue swimming.
- **Fatigue –** A physiological state at which an individual ability to maximally swim (burst) is lost.
- **Oxygen Consumption Rate –** a measurement typically expressed in $mgO_2\ min^{-1}kg^{-1}$ that serves as a proxy for metabolic rates. It is used to study the energetics of swimming.
- **Prolonged swimming** – a combination of aerobic and anaerobic swimming. It is an unsteady swimming mode, where continuous (aerobic) swimming is intersected with rapid bursts, turns, and consecutive burst-and-coast episodes (anaerobic). It will eventually lead to fatigue.
- **Sustained swimming** – aerobic swimming that can be maintained indefinitely. The type of swimming activity used for daily behaviors, foraging, exploring new environments, hovering, and steady swimming against low flows, does not lead to fatigue.
- **Time to fatigue swimming –** swimming test or approach, where fish swims against a constant (pre-determined) current until it reaches fatigue.
- **U_{crit} –** An aerobic and anaerobic swim performance, where water velocity is incrementally increased in a stepwise manner. The test is performed in swim tunnel, and the protocol is most commonly used to examine swimming energetics (oxygen consumption, a proxy for metabolic rate).
- **U_{max} –** An aerobic and anaerobic swim performance similar to U_{crit}, but the water velocity is continuously increased throughout the test. Unlike the U_{crit} test, a U_{max} test is designed to test swimming capacity predominantly.

1.2. Materials and methods

Swim speed can be described using two units, the absolute swim speed units ($Swim_{Abs}$, cm/s, m/s) and relative swim speed units using body length of the fish ($Swim_{Relat}$, BL/s). The $Swim_{Abs}$ is directly comparable across observations and is a more relevant metric in context of natural conditions (e.g. river flows). On the other hand, relative swim speed has merits when considering the swimming physiology and transition states from aerobic to anaerobic swimming. Where possible both, $Swim_{Abs}$ and $Swim_{Relat}$ were compiled for our analysis alongside with body length of the fish (cm). To obtain the most comprehensive outlook of swimming capacity of salmon applicable to ecologically applied settings, we estimated $\mathrm{Swim}_{\mathrm{Abs}}$ swim speeds where possible, but it must be noted that these estimates contain error that. The directly reported and estimated $\mathrm{Swim}_{\mathrm{Abs}}$ are visually discrete in our data presentation.

1.2.1. Data search and selection

Systematic and comprehensive review was performed using Web of Science (https://webofknowledge.com) and Google Scholar (https://scholar.google.com/). To complete a systematic review, we used Web of Science with access through University of California, Santa Barbara in 2020 April, and in January 2022. We queried articles published between 1950 and 2022 using 5 specific searches using keywords "*speed", "salmon", "swim", "burst", "jump", "leap", "sprint", Ucrit, Umax, Ucat, critical swim, maximum swim, adult*" appear in all fields (keywords appear anywhere in the full record), and where keywords "*juvenile"* do not appear in topic fields (abstract, title, author keywords). Search details and number of returns are summarized in Appendix 3, Table 1. The comprehensive and cross-reference review through Google Scholar was performed between December 2019 and April 2020 using keywords in various combinations (examples: *"Pacific salmon swim", "Salmon sprint", "Salmon jump", "Salmon anaerobic swim", "Salmon Ucrit", "Salmon burst swim", "Columbia River salmon swim", "Adult salmon swim"*). Each of different search phrases were used to query literature published between 1950 and 2020. The number of returned reports or literature ranged anywhere from 3 (e.g. "salmon Ucrit" in 1961-1970) up to a several thousand ("Pacific salmon swim" in 2001-2010 resulted in ~ 10 700 returns), results were assessed until at least 30 consecutive results (3 pages) became irrelevant for the goal of this study (most cases > 100 results were assessed; details on this search including keywords, time ranges, date of the search and notes on number of returns are summarized in Appendix 3, table 2).

The retained articles from systemic and comprehensive search were individually assessed against our criteria for inclusion or exclusion in our database, the criteria were: i) quantitative swimming speed of fish (groups or individuals) must be reported either in text, table or be plotted, ii) swim speed must belong to Pacific salmon (*Oncorhynchus spp:* sockeye salmon (*O. nerka*), coho salmon (*O. kisutch*), pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), chinook salmon (*O. tshawytscha*)), rainbow or steelhead trout *(Oncorhynchus mykiss*), and Atlantic salmon, (*Salmo salar*), iii) exclude migration speeds reported on km/d or similarly coarse scales, iv) fish must have reached an adult life stage (Pacific salmon *Oncorhynchus* spp. > 800 g; *O. mykiss* > 500 g; Atlantic salmon *S. salar* > 500 g). Selected studies were individually reviewed to extract targeted information to build the database. Data only presented through figures were digitized using ImageJ v 1.52 (Schneider et al., 2012), to extract reference values on x- and/or y-axis, and swim data points (all in px). All tracks were saved and used to calculate swim speed (in some cases also temperature, swimming speeds, and body size of the fish were obtained from original author published Figures).

1.2.2. Database variables

A goal of this review was to link swimming capacity with environmental conditions and condition of the fish. We compiled different types of entries to ensure all-encompassing database of salmon swimming capacity. An entry of swim speed can represent a mean swim performance value of a group of individuals (n>1 salmon, commonly reported), or a swim speed measured in an individual fish (n=1); to specify the type of entry we created a descriptive variable "group" or "individual". For some studies, there were more than a single datapoint reported for one individual or a group of salmon (for example, repeat swim speed tests, or one individual migrating through different sections of the river). The non-independence and weight of the data (sample size, n=1 or n>1) are considered in primary analyses and inference.

Following our aim to investigate intra-specific variation in swim performance of salmon, we reported the origin of the fish. This was categorized at two levels, i) specific origin of fish (e.g. stock or population, specific collection site, a specific hatchery or farm, or a study site), ii) a coarse scale classification of origin ("collection" (all entries with noted collection site as best estimate of their origin), "farm", "hatchery", "stock" (population), "study" (location of the study, not a reliable metric of fish origin)).

We reported methods used to obtain swim speeds of salmon (swim performance test methods) and the mean temperature during these swim tests. Swim performance tests were defined following an established terminology in fish swimming literature. Swim tests performed under controlled, predominantly, laboratory setting include, "Ucrit" – critical swim speed test, "Umax" – maximum (constant acceleration) swim speed test, and "TTF" – time to fatigue tests or endurance swim tests. We used a category "Field" to describe swim performance measured in migrating fish, and category "Jump" to describe velocity of jumping fish. We compiled swim performance measured using non-traditional methods in a category "Swim" includes. The compiled swim test categories are detailed in Appendix 3, Table 3. Test temperature represents the reported water temperature in the swim tunnels, flumes, tanks, or the mean reported river water temperature from the field tracking studies. Caution may be used when drawing any strong conclusions on temperature effects of swim performance, because the mean temperatures are often not directly representing what fish may have experienced, especially in the field studies.

A selection of additional variables that are known to influence fish swimming performance and that we included in the database when available include: *intrinsic fish condition, extrinsic fish condition, sex, and salinity. surgery and instrumentation, quantitative measures of maturity, water flow velocity and/or discharge, mortality, tracking versus laboratory study.* None of the latter outlined variables were included in the primary analyses due to their low sample sizes per category, but they are discussed in this review.

When possible, we extracted intrinsic fish condition, a variable specifying intrinsic state of the fish. It was used to group fish with similar physiological conditions in common sub-categories. The intrinsic fish conditions that were noted from the literature were subset in 12 sub-categories: “diet", "exercise trained", “density”, “density, exercise trained”, "fallback", "infection", "mature", "pass", "prior anesthetic", "spawned", "toxicant ", "unhealthy". Similarly, also extrinsic swim conditions that define the swimming environment were extracted when possible and were subset in 7 sub-categories: "Dam", "Fall", "Fraser River", "Klickitat River", "other", "Shibetsu River", "Toyohira River". The main intrinsic and extrinsic conditions that were noted and their classification in the corresponding subcategories are detailed in Appendix 3, Tables 5 and 6.

Sex, male or female, was noted when available. Sex was denoted as "mixed" for entries reporting swim speeds of pooled sexes or for entries when the sex was not specified. One exception of sex classification was allowed when the sex distribution for a group of fish was noted 93% female, which we denoted as female for the entry (reference [1; Brett 1965]). Further, the salinity of the water during swim was noted in one of the three categorical groups, saltwater (SW, > 25 ppt), freshwater (FW, 0 ppt) or brackish water (SW/FW <25 ppt and > 0 ppt).

Additional variables that were sparsely reported in the literature, but that can affect swimming ability of fish were extracted when possible. These were grouped as follows: i) *surgery or instrumentation*: in the laboratory most of the surgery is performed to measure cardiovascular performance of salmon while swimming, in the field (tracking studies) fish are instrumented with Electromyogram tags (EMG tags), triaxial accelerometers, magnetic ring, radio tags, and acoustic tags (insertion of PIT, passive integrated transponder, tags were not classified as surgery) (Appendix 3, Table 7); ii) *quantitative measures of maturity:* gonad weight (g) or gonadosomatic index (GSI; gonad weight/body weight); iii) *water flow velocity (cm/s) and/or discharge (cm^3/s)* in field studies; iv) *mortality,* which we included as a binomial variable (1 = mortality reported, 0 = mortality not mentioned, not reported), with general assumption regarding field studies where fish that were not successful migrants were denoted positive for mortality, unless otherwise specified by author; and lastly v) *tracking study*, which was included as a binomial variable (1 or 0), where 1 denotes tracking study where swim speed is measured under field conditions as adult salmon are completing a part of their spawning migration, and 0 denotes controlled (laboratory) study. We caution making meta-analytical inference about how these factors influence swimming ability in adult salmon because the data are very coarse in each sub-category.

1.2.3. Data analysis

All analyses were performed in R 3.5.1 (2018). The sample size of complete data entries was insufficient to robustly estimate how swim capacity differs intra- and inter-specifically and across environmental conditions. For instance, entry of mean swim speed of a group of fish did not have a corresponding body size measurement (length or mass), or the swim speed would be only reported in relative units, body lengths per second ($\mathrm{Swim}_{\mathrm{Relat}}$, BL/s). To populate or database with absolute swim speed ($\mathrm{Swim}_{\mathrm{Abs}}$, cm/s) entries, we used the reported length (cm) of the fish and calculated $\mathrm{Swim}_{\mathrm{Abs}} = \mathrm{Swim}_{\mathrm{Relat}} * \mathrm{BL}$ (Appendix 3, Figure 1). When BL was not reported, but body mass was, we used a weight-length relationship $W=a*\mathrm{BL}^b$ (Jones et al., 1999) to estimate the BL; in this equation W = body mass, BL = body length, *a* and *b* are accepted species-level estimates in many fish species from a linearized form of this equation: log(W) =log(a) +log(BL), where *a* is the intercept and *b* is the slope of the regression. The, the estimated body length was used to calculate the $\mathrm{Swim}_{\mathrm{Abs}}$. The used coefficients (*a* and *b*) for each species, the comparison between the reported $\mathrm{Swim}_{\mathrm{Abs}}$ and estimated $\mathrm{Swim}_{\mathrm{Abs}}$ when available are available in the Appendix 3, Figure 1.

SECTION 2: TABLES AND FIGURES

SEARCH ID1: (ALL=(speed* AND salmon* AND (burst* OR jump* OR leap* OR sprint*)) NOT TS=juvenile) AND LANGUAGE: (English)	
Returns (N studies) and year or the search	55 (April 2020) 64 (January 2022)
Included (N studies)	8 (no additions in 2022)
SEARCH ID2: (ALL=(speed* AND salmon* AND swim* AND (Ucrit OR Umax OR Ucat)) NOT TS=juvenile) AND LANGUAGE: (English)	
Returns (N studies) and year or the search	16 (April 2020) 18 (January 2022)
Included (N studies)	4 (3 added in April 2020, 1 added 2022)
SEARCH ID3: (ALL=(speed* AND salmon* AND swim* AND (critical swim OR maxim* swim)) NOT TS=juvenile) AND LANGUAGE: (English)	
Returns (N studies) and year or the search	252 (April 2020) 265 (January 2022)
Included (N studies)	30 (28 added in April 2020, 2 added in 2022)
SEARCH ID4:	

(ALL=(speed* AND salmon* AND swim* AND adult AND (critical swim OR maximum swim)) NOT TS=juvenile) AND LANGUAGE: (English)	
Returns (N studies) and year or the search	46 (April 2020) 45 (January 2022)
Included (N studies)	19 (all additions from 2020 search)
SEARCH ID5 ***(only 2022)*****:** (ALL=(adult AND salmon* AND (swim fatigue OR time to fatigue OR endurance swim)))	
Returns (N studies) and year or the search	25 (January 2022) _* This search was performed to specifically query studies measuring time to fatigue performance in salmon._
Included (N studies)	0

Appendix 3, Table 1. Summary details of systematic review using Web of Sciences.

Search terms	**Date search was performed**	**Publication years (range)**	**Notes on reviews and returns**
Pacific salmon swim	Dec 26 2019	1950-1960	Returned literature became irrelevant (different species, no swimming) to our topic starting pages 10 - 13, search stopped.
Salmon burst			Unsuccessful search, no fish. Not reviewed passed pages 3-4.
Salmon sprint			Unsuccessful search. Mostly irrelevant literature, even in the page 1.
Burst swim adult trout	March 18 2020		About 761 results (0.08 sec) (march 18, 2020)
Salmon swim	Dec 26 2019	1961 - 1970	About 1,130 results (0.04 sec). Reviewed until 14 and finding no more relevant studies.
Salmon burst			About 805 results (0.13 sec), in around page 4, most relevant pubs already marked and noted, and others are irrelevant.
Burst swim			Returns are not fish (thus salmonid) specific
Salmon Ucrit			3 results (0.06 sec), 2 Brett papers, and a paper that cites & discusses the search term in text.
Salmon swim Columbia river, USA	Jan 15 2020		About 720 results (0.05 sec)
Salmon Ucrit	Dec 27 2019	1971-1980	3 results (0.04 sec), 2 Webb papers, and Dadswell paper on sturgeon

Salmon burst			About 1,480 results (0.08 sec).Pages 5-6 (…) all returns are on different fish species, or focus on irrelevant performances and contexts , e.g. behavioral studies only
Pacific salmon burst			About 1,050 results (0.07 sec). Generally, starting to get a lot of Oregon coho studies and trout, and swimming studies that use tracking. Starting page 9 - mostly yearling, fry, hatchery development, and aquaculture papers, and mostly trout.
Pacific salmon swim			About 1,120 results (0.20 sec); after page 15 returned literature is irrelevant
Salmon swim Columbia river, USA			About 1,450 results (0.10 sec). Page 8 not very relevant
Pacific salmon Ucrit		1981-1990	12 results (0.11 sec)
Salmon burst			About 3,310 results (0.08 sec) - a lot more studies on Atlantic salmon. Page 8 - no more relevant papers.
salmon jump			starting page 4 - returns become completely irrelevant to our goal. Most returns are by author with name Salmon. page 12, no more relevant papers. Mostly young life stages, Atlantic salmon, and not swimming performance
Salmon swim Columbia River			About 2,200 results (0.13 sec): went to page 10, no added directly related studies
Pacific Salmon Ucrit	Dec 28 2019	1991-2000	About 73 results (0.08 sec). All studies reviewed This is the most successful and relevant search
Salmon burst swim			About 3,210 results (0.10 sec); Page 10 - no more relevant papers.
Pacific salmon swim			About 4,100 results (0.10 sec); Page 10 - no more relevant papers, and non-adult lifes stage studies.
Pacific salmon anaerobic swim			About 538 results (0.04 sec); Page 5 - papers are stillAbout swimming but on other fish species, not Pacific salmon
salmon swim Columbia River			Page 10 mostly only smolts and juvies
Salmon Ucrit	Dec 30 2019	2001-2010	About 349 results (0.06 sec); Page 6 starting to deviate from Pacific salmon studies, page 7 no more relevant papers
Salmon anaerobic swim			About 4,240 results (0.09 sec); Page 9 no more relevant papers.
Pacific salmon swim			About 10,700 results (0.12 sec)

Pacific salmon burst swim			About 4,350 results (0.10 sec); Page 6 no more relevant returns.
salmon swim Columbia River	Mar 19 2020		About 11,900 results (0.11 sec); Page 12 - mostly juvenile fish research and other species.
Adult trout swimming	Mar 19 2020		About 15,400 results (0.14 sec); No adult fish studies page 13-17; stop at 18 (18 including)
Adult Atlantic salmon swim	Mar 21 2020		About 14,500 results (0.12 sec)
Pacific salmon burst swim	Dec 31, March 21	2011 - 2020	About 5,800 results (0.08 sec); Page 7,8 no more relevant studies, mostly other species. return a lot of offspring burst swim capacity studies to understand maternal effects.
Salmon Ucrit			About 536 results (0.08 sec); Lots of repeated returns (from previous searches) and studies on Atlantic salmon
Pacific salmon anaerobic swim			About 2,300 results (0.08 sec); reviewed until Page 13
Pacific salmon max swim speed			Unsuccessful.
Adult trout swimming	Mar 21 2020		About 17,100 results (0.08 sec)
Adult Atlantic salmon swim			About 16,900 results (0.10 sec)
Salmon swim Columbia River			About 13,800 results (0.09 sec); Reviewed 18 pages.
Columbia river salmon swim	Jan 14 2020	Not specified	About 28,700 results (0.28 sec)
Burst swim adult trout	Mar 19 2020		About 61,500 results (0.07 sec)
Swimming masu salmon	Mar 21 2020	Not specified	About 2,600 results (0.09 sec); Went through 5 pages, no relevant studies found (except one that was already reported: Miyoshi et al 2014)

Appendix 3, Table 2. Summary details of comprehensive review using Google Scholar.

	ENTRIES IN DATASET		**Absolute swim speed (cm/s)**		**Relative swim speed (BL/s)**		**Entries with both, relative and absolute swim speed**	
	N studies (n entries)	***Ref. ID***	*N (n)*	*Ref.ID*	*N (n)*	*Ref.ID*	*N (n)*	*Ref.ID*

Oncorhynchus gorbuscha	**8 (216)**	**6, 9, 13, 20, 21, 24, 43, 88**	4 (58)	9, 13, 20, 43	7 (211)	6, 9, 13, 21, 24, 43, 88	3 (52)	9, 13, 43
Oncorhynchus keta	**8 (74)**	**39, 41, 42, 44, 50, 53, 54, 88**	5 (36)	39, 41, 50, 53, 54	5 (57)	39, 41, 42, 44, 88	2 (2)	39, 41
Oncorhynchus kisutch	**8 (145)**	**10, 18, 17, 28, 45, 50, 89, 12**	6 (100)	10, 18, 17, 50, 89, 12	6 (134)	10, 18, 28, 45, 89, 12	3 (89)	10, 18, 89
Oncorhynchus masou	**1 (5)**	**44**	NA	NA	2 (23)	63, 44	NA	NA
Oncorhynchus mykiss	**16 (134)**	**53, 65, 68, 69, 72, 73, 74, 75, 76, 77, 80, 87, 90, 92, 94, 95**	8 (79)	53, 65, 68, 69, 73, 76, 87, 95	10 (60)	68, 72, 74, 75, 77, 80, 90, 92, 94, 95	2 (5)	68, 95
Oncorhynchus nerka	**31 (607)**	**1, 2, 3, 5, 19, 7, 8, 9, 13, 14, 15, 16, 20, 21, 22, 23, 25, 26, 27, 29, 30, 31, 38, 47, 50, 48, 54, 40, 58, 79, 12**	21 (410)	1, 2, 3, 5, 7, 9, 13, 20, 25, 27, 29, 30, 31, 38, 50, 48, 54, 40, 58, 79, 12	21 (353)	1, 3, 5, 19, 7, 8, 9, 13, 14, 15, 16, 21, 22, 23, 25, 26, 27, 47, 46, 48, 12	9 (147)	1, 3, 5, 7, 9, 13, 25, 27, 48
Oncorhynchus tshawytscha	**7 (83)**	**4, 36, 35, 37, 53, 66, 33**	6 (81)	36, 35, 37, 53, 66, 33	2 (9)	4, 35	1 (7)	35
Salmo salar	**22 (253)**	**55, 56, 57, 60, 62, 70, 71, 78, 81, 82, 83, 84, 85, 86, 61, 91, 93, 96, 100, 102, 104, 105**	14 (129)	56, 57, 60, 62, 70, 78, 81, 83, 84, 85, 86, 61, 102, 105	14 (139)	55, 56, 71, 78, 81, 82, 84, 91, 93, 96, 100, 102, 104, 105	4 (15)	56, 78, 81, 84

Appendix 3, Table 3. Summary of species-specific sample sizes and corresponding reference IDs.

Provided are summaries for absolute and relative swim speeds (BL/s and cm/s, and studies that report both BL/s and cm/s). Ref. ID = Reference ID Number, the matched references list is provided at Appendix 3, Section 3.

Condition	**Subcategory of the**	***N studies (n data-points)***	**Ref. ID**	**Description**

	condition			
Field	Field	24 (426)	5, 8, 20, 21, 22, 23, 29, 30, 31, 36, 35, 38, 39, 41, 44, 47, 46, 50, 53, 56, 63, 66, 87, 88	Swim speeds reported during migration in the field. In one study [53] swim tests were performed in the filed intersecting spawning migration.
Jump	Jump	2 (9)	40, 58	Jump velocity of fish; this incudes horizontal, vertical, total and take-off velocity
Swim	Swim-1	2 (25)	54, 78	Studies that used a unique type of experimental setup and design, i.e. these were not following one of the standard protocols in fish swimming. The number represents the repeat tests order.
	Swim-2	1 (24)	54	
	Swim-3	1 (23)	54	
	Swim-4	1 (7)	54	
TTF	TTF	7 (119)	2, 57, 60, 79, 84, 61, 105	Time to fatigue. Fish are swum at defined velocity until they reach fatigue (unable to continue swimming)
Ucrit	EMG-Ucrit	7 (21)	35, 37, 41, 62, 87, 88, 33	Critical swim speed (Brett, 1964); established swim performance test in fish swimming. Ucrit is measured in a swim tunnel or flume, where velocity is increased in increments (step-test) until fish reaches fatigue. The number represents the repeat tests order. EMG-Ucrit denote Ucrit test performed on fish instrumented with EMG tags. The results of these test are used to calibrate EMG tags and predict swim speed in field tracking studies.
	Ucrit-1	57 (590)	1, 3, 4, 6, 19, 7, 9, 10, 13, 14, 15, 16, 17, 25, 26, 27, 28, 37, 39, 42, 43, 44, 48, 55, 57, 65, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 80, 81, 82, 83, 84, 85, 86, 87, 89, 90, 91, 92, 93, 94, 95, 96, 100, 12, 102, 104, 105	
	Ucrit-2	18 (144)	19, 7, 10, 13, 14, 15, 16, 25, 48, 68, 69, 76, 81, 82, 90, 92, 93, 12	
	Ucrit-3	4 (14)	19, 69, 90, 93	
	Ucrit-4	2 (4)	69, 93	

Umax	Umax	4 (158)	18, 24, 45, 76	Constant acceleration test; established swim performance test in fish swimming. Umax is measured in a swim tunnel or flume, where velocity is increased continuously at a defined rate until fish reaches fatigue. The number represents the repeat tests order. This is sometimes reported as Ucat for constant acceleration test.

Appendix 3, Table 4. The summary of swim tests defined in the data.
The table contains the main category (the largest grouping that was used for analysis and data presentation), sub-categories (finer scale categories of used swim tests), the reference number of all corresponding studies, and description of the categories. Ref. ID = Reference ID Number, the matched references list is provided at the end of the Appendix 3, Section 3.s

Condition	**Subcategory of the condition**	***N studies (n data-points)***	**Ref. ID**	**Description**
Dam	American-Dam	1 (8)	87	A set of conditions in Fraser River, BC, Canada within a section with dam.
	Columbia-Dam	1 (8)	35	A set of conditions in Columbia River, WA, USA within a section with dam.
	Fraser-Dam	2 (16)	22, 23	A set of conditions in American River, CA, USA within a section with dam.
Fall	Fall-artificial	2 (9)	40, 58	Artificial fall conditions that were used to measure swim performance of salmon during simulated passage
Fraser	Fraser-Difficult	1 (4)	47	Author defined segment in Fraser River, BC, Canada. Swim speeds were recorded for each section. Segment # 1 (Segm-1) includes The Hell's Gate
	Fraser-Easy	1 (4)	47	
	Fraser-Intermediate	1 (4)	47	
	Fraser-Segm1	1 (13)	29	
	Fraser-Segm10	1 (11)	29	
	Fraser-Segm2	3 (22)	20, 21, 29	
	Fraser-Segm3	1 (15)	29	
	Fraser-Segm4	3 (22)	20, 21, 29	
	Fraser-Segm5	1 (12)	29	
	Fraser-Segm6	1 (13)	29	
	Fraser-Segm7	2 (17)	21, 29	
	Fraser-Segm8	1 (11)	29	

	Fraser-Segm9	3 (18)	20, 21, 29	
Klickitat	Klickitat-Falls	2 (37)	36, 66	Natural fall conditions in Klickitat River, WA, USA
other	Ammonia	1 (1)	72	Elevated water ammonia levels
	hypoxia	1 (4)	19	Environmental hypoxia (13.3–18.8 kPa)
	pH 5.15	1 (2)	71	Lower pH in the water
	pH 5.24 + Al	1 (2)	71	Lower pH and Al presence in the water
Shibetsu	Shibetsu-Construction	2 (21)	39, 88	Section in Shibetsu River, Japan that was modified by constructions (either reconstructed or canalized)
Toyohira	Toyohira-GroundSill	2 (12)	41, 44	A set of conditions in Toyohira River, Japan. Section with a groundsill.
Toyohira	Toyohira-Segm1	1 (4)	44	Author defined segment in Toyohira River, Japan. Swim speeds were recorded for each section
	Toyohira-Segm2	1 (4)	44	
	Toyohira-Segm3	1 (4)	44	
	Toyohira-Segm4	1 (4)	44	
	Toyohira-Segm5	1 (4)	44	
	Toyohira-Segm6	1 (4)	44	
	Toyohira-Segm7	1 (4)	44	
	Toyohira-Segm8	1 (4)	44	
NA	N = 80 (n = 1246)	1, 2, 3, 4, 5, 6, 19, 7, 8, 9, 10, 13, 14, 15, 16, 18, 17, 24, 25, 26, 27, 28, 30, 31, 37, 38, 39, 41, 42, 43, 44, 45, 46, 50, 48, 53, 54, 55, 56, 57, 60, 62, 63, 65, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 61, 90, 33, 91, 92, 93, 94, 95, 96, 100, 12, 102, 104, 105		

Appendix 3, Table 5. The summary of swim (extrinsic) conditions defined in the data. The table contains the main category (the largest grouping that was used for analysis and data presentation), sub-categories (finer scale categories that described extrinsic conditions in each study), the reference number of all corresponding studies, and description of the categories. NA = not available; this includes all studies that did not have any of the classifications. Ref. ID = Reference ID Number, the matched references list is provided at the end of the Appendix 3, Section 3.

** All conditions are ecologically relevant; note that Ammonia here is classified as an extrinsic, naturally occurring, condition and not as a toxin (see Appendix, Table 4 ref 72).*

Condition	***N studies (n entries)***	**Ref. ID**	**Description**
Density	1 (2)	94	Fish reared at varying densities (high, and low)

Density exercise trained	1 (2)	94	Fish reared at varying densities and at high flow
Diet	2 (18)	81, 82	Fish fed different types of diets
Exercise trained	2 (9)	73, 75	Fish undergone exercise training
Fallback	4 (18)	8, 36, 38, 41	Fish reported as non-successful migrants in the field studies
Pass	9 (137)	6, 13, 22, 23, 56, 71, 83, 89, 61	Fish reported as successful migrants in the field studies
Infection	4 (17)	8, 36, 38, 41	Fish prone to infection or fish that were infected at different severity levels (prone to fungal infection, weak *Parvicapsula minibirnis* infection, strong *Parvicapsula minibirnis* infection, Sea lice infected 0.02 sealice/g, Sea lice infected 0.13 sea lice/g, *Aeromonas salmonicida*, infection, Sea lice infected 0.13 sea lice/g)
Mature	5 (23)	13, 15, 55, 93, 96	Mature fish. * different terms were used to describe maturity of fish. The subcategory list here represents more common ways, but not all. (gravid, spawning, nearing spawning condition, ripe within days of spawning, At terminal spawning ground, mature, mature; pre stripping near/at spawning)
Prior anesthetic	2 (10)	42, 77	Fish that had undergone anesthesia near before swimming
Spawned	1 (2)	6	Fish that had spawned
Toxicant	3 (9)	19, 7, 72	Fish exposed to a toxin prior swimming. DHA = dehydroabietic acid; PCP = pentachlorophenol; sublethal levels of Ammonia
Unhealthy	3 (59)	7, 14, 18	Fish in unhealthy conditions
NA	N = 76 (n = 1258)	1, 2, 3, 4, 5, 19, 7, 9, 10, 13, 15, 16, 18, 17, 20, 21, 24, 25, 26, 27, 28, 29, 30, 31, 35, 37, 39, 41, 42, 43, 44, 45, 47, 46, 50, 48, 53, 54, 55, 57, 40, 58, 60, 62, 63, 65, 66, 68, 69, 70, 72, 73, 74, 75, 76, 77, 78, 79, 80, 84, 85, 86, 87, 88, 90, 33, 91, 92, 93, 95, 96, 100, 12, 102, 104, 105	

Appendix 3, Table 6. The summary of fish (intrinsic) conditions defined in the data.

The table contains the main category (the largest grouping that was used for analysis and data presentation), sub-categories (finer scale categories that described intrinsic conditions in each study), the reference number of all corresponding studies, and description of the categories. NA = not available; this includes all studies that did not have any of the classifications. Ref. ID = Reference ID Number, the matched references list is provided in Appendix 3, Section 3.

** Note that Ammonia was classified as a toxin and not environmental factor. In the original study [72] sublethal levels of ammonia were used, considered toxic.*

Condition	***N studies (n entries)***	**Ref. ID**	**Description**
Accelerometer	4 (39)	22, 23, 27, 47	Surgically implanted acceleration transmitter used for field tracking.
Acoustic Tag	1 (8)	46	Surgically implanted sound wave emitting tag used for field tracking.
Cannulation	11 (57)	19, 7, 15, 16, 17, 68, 72, 74, 76, 79, 80	A surgical procedure where cannula is placed inside the aorta to provide access to blood. Both dorsal and ventral aorta cannulation was reported.
Cannulation and Flow Probe	4 (22)	25, 26, 48, 95	A surgical instrumentation of blood flow probes around the dorsal aorta.
EMG tag	23 (386)	5, 8, 20, 21, 29, 36, 35, 37, 38, 39, 41, 42, 43, 44, 57, 62, 65, 66, 69, 70, 87, 88, 33	Both procedures, cannulation, and insertion of blood flow probe, were performed.
Flow Probe	3 (69)	24, 83, 96	Electromyogram tag. Surgically implanted tag with electrodes directly inserted in red and/or white muscle to measure muscular activity.
Ligation	2 (3)	4, 73	A surgical procedure of closing off coronary artery.
Magnetic Ring	1 (2)	63	An instrumentation with a magnetic ring for field tracking, tag is attached to the body of fish.
Radio Tag	2 (21)	56, 60	An instrumentation with radio transmitter, tag is attached to the body of fish.
Optode implant	1 (4)	92	Implantation of a sensor into the sinus venosus of the heart

DST - HRT ACT bio-logger	2 (14)	100, 102	An instrumentation with implantable leadless heart rate, activity, and temperature logger.
NA	N = 56 (n = 839)	1, 2, 3, 4, 6, 9, 10, 13, 14, 18, 24, 25, 27, 28, 30, 31, 37, 39, 41, 42, 44, 45, 50, 53, 54, 55, 57, 40, 58, 60, 65, 69, 70, 71, 73, 75, 76, 77, 78, 81, 82, 84, 85, 86, 87, 89, 61, 90, 12, 102,91, 93, 94, 102, 104, 105	

Appendix 3, Table 7. The summary of surgery and instrumentation procedures defined in the data.

The table contains the main category (the largest grouping that was used for analysis and data presentation, the reference number of all corresponding studies, and description of the categories.

Condition	N	Swim speed (cm/s)	Fish Length (cm)	Temperature (ºC)
Diet	10	70.4 (65, 79)	37.04 (36.8, 37.4)	9
Exercise trained	3	76.867 (73.4, 81.4)	38.685 (38.5, 38.81)	12
Fallback	10	188.71 (68.89, 290)	66.362 (58.67, 77.9)	13.6 (10, 16)
Infection	12	121.433 (93.7, 142.6)	55.3 (55.3, 55.3)	12
Mature	109	150.508 (89.8, 406)	57.522 (49.8, 71.4)	12.055 (5, 18)
Pass	10	199.224 (92.07, 292.7)	64.068 (58.14, 77.9)	14.2 (10, 16)
Toxicant	2	83.13 (79.97, 86.29)	56.76 (56.76, 56.76)	20
Unhealthy	7	125.704 (40.11, 168)	64.92 (62.22, 66)	15.714 (14, 20)

Appendix 3, Table 8. Swim performance (cm/s) measured in fish with various intrinsic conditions.

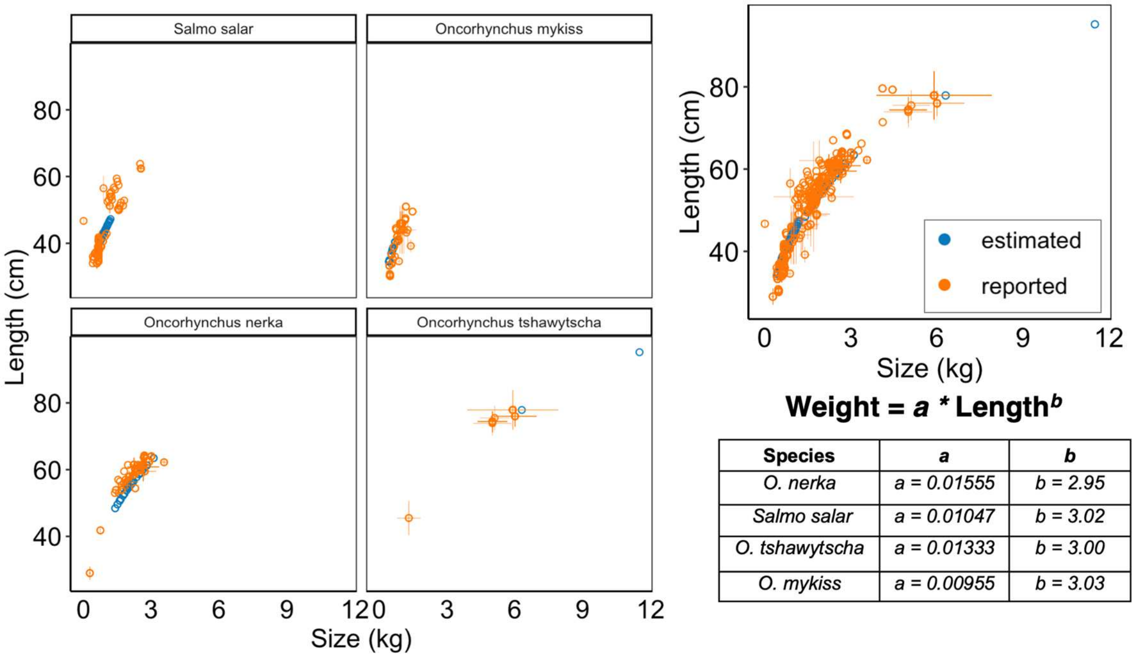
Condition	N	Swim speed (BL/s)	Fish Length (cm)	Temperature (ºC)
Density	2	1.755 (1.73, 1.78)	30.4 (30.3, 30.5)	19
Density exercise trained	2	1.445 (1.17, 1.72)	30.45 (30.1, 30.8)	19
Diet	18	2.103 (1.75, 2.62)	37.989 (36.8, 40.6)	9.444 (9, 10)
Exercise trained	6	2.609 (2.3, 2.85)	*NA*	12
Fallback	8	9.355 (2.86, 13.48)	60.067 (59, 60.6)	15.75 (12, 17)
Infection	23	2.103 (1.4, 2.77)	50.532 (34, 60.55)	12.609 (10, 16)
Mature	121	2.68 (0.9, 7.91)	56.217 (46.1, 71.4)	13.653 (9, 20)
Pass	7	5.693 (1.85, 10.93)	60.067 (59, 60.6)	15.571 (12, 17)
Prior anesthetic	10	2.384 (1.25, 3.53)	49.625 (36.6, 62.65)	12 (11, 13)
Spawned	2	1.93 (1.73, 2.13)	47.2 (47.2, 47.2)	15
Toxicant	9	1.337 (1.19, 1.61)	53.047 (33.9, 57)	19.556 (16, 20)
Unhealthy	59	2.016 (0.64, 2.58)	64.92 (62.22, 66)	17.339 (11, 22)

Appendix 3, Table 9. Swim performance (BL/s) measured in fish with various intrinsic conditions.

Data Subgroup	***N (data)***	***N (sp.)***	***Intercept (ß, SE)***	***Slope (ß, SE)***	***Chi^2 (slope)***	***P value (slope)***
Ucrit and Umax	928	8	-37.175 (13.705)	2.859 (0.184)	240.55	< 0.001
Field (all data)	346	7	78.746 (79.144)	1.914 (1.127)	2.885	0.089
Field (> 250 cm/s)	54	5	415.896 (174.997)	0.731 (2.66)	0.076	0.784
Field (< 250 cm/s)	292	6	197.037 (40.42)	-1.645 (0.56)	8.625	0.003

Appendix 3, Table 10. Body size scaling relationships between species specific swimming performances.

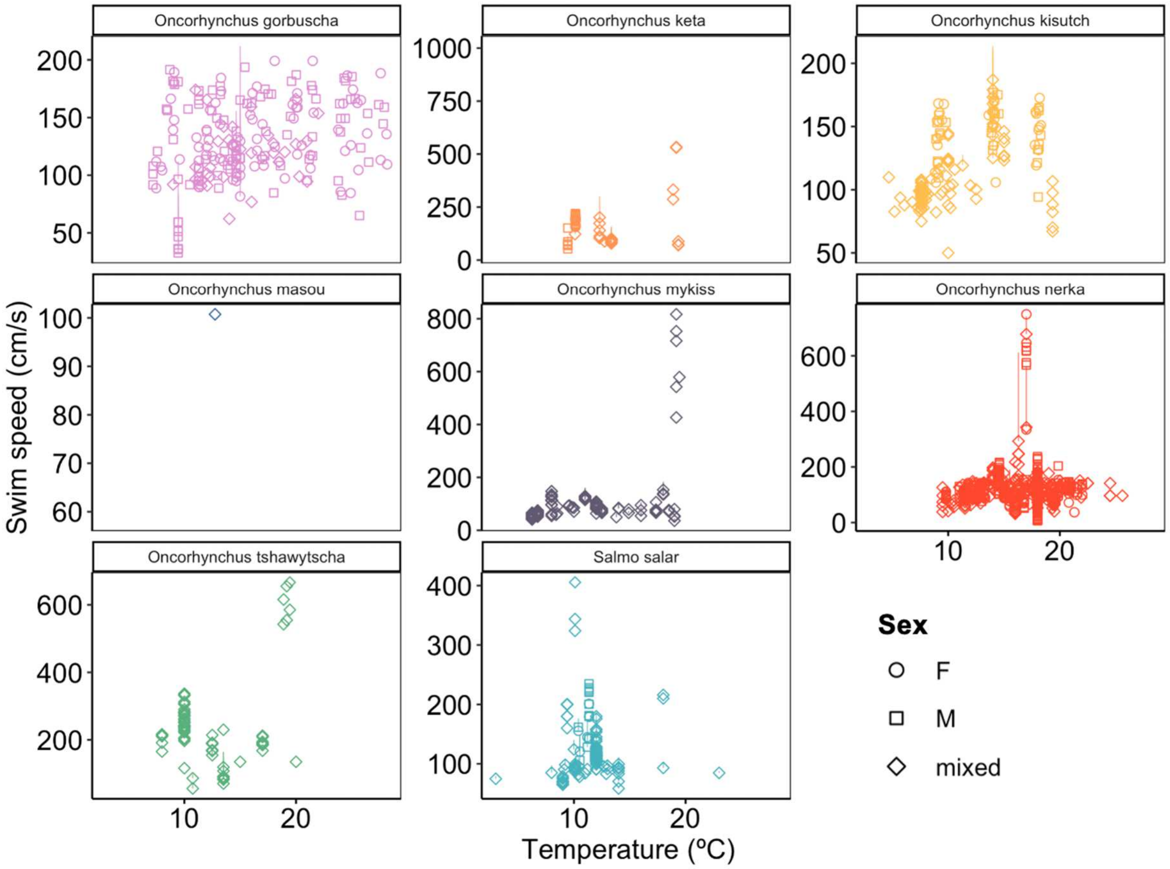
Mixed effect model results are presented. Species was added as a random effect (best model BIC model selection). Models with species as a fixed effect were evaluated, but these models were not best fit models. Size was in body lengths, cm.



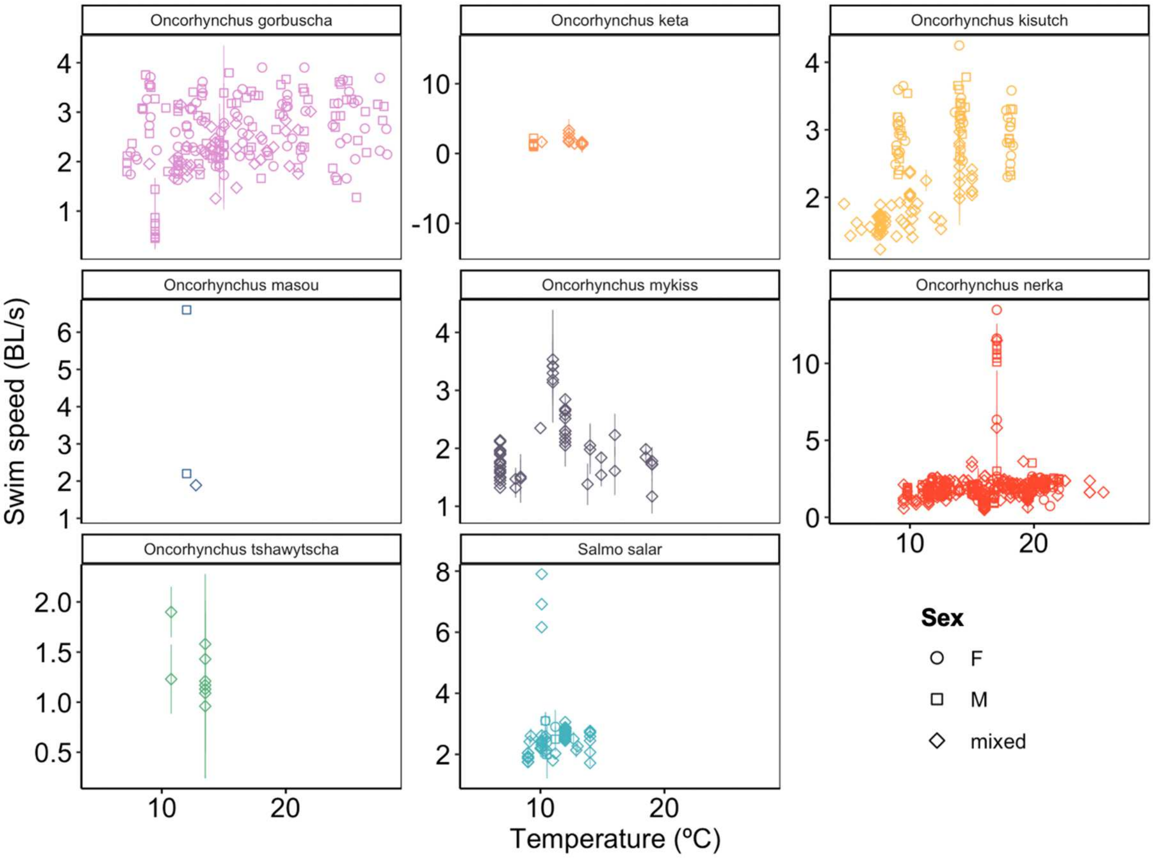
Species	*a*	*b*
O. nerka	*a* = 0.01555	*b* = 2.95
Salmo salar	*a* = 0.01047	*b* = 3.02
O. tshawytscha	*a* = 0.01333	*b* = 3.00
O. mykiss	*a* = 0.00955	*b* = 3.03

Appendix 3, Figure 1. Length-mass relationships and estimated values.

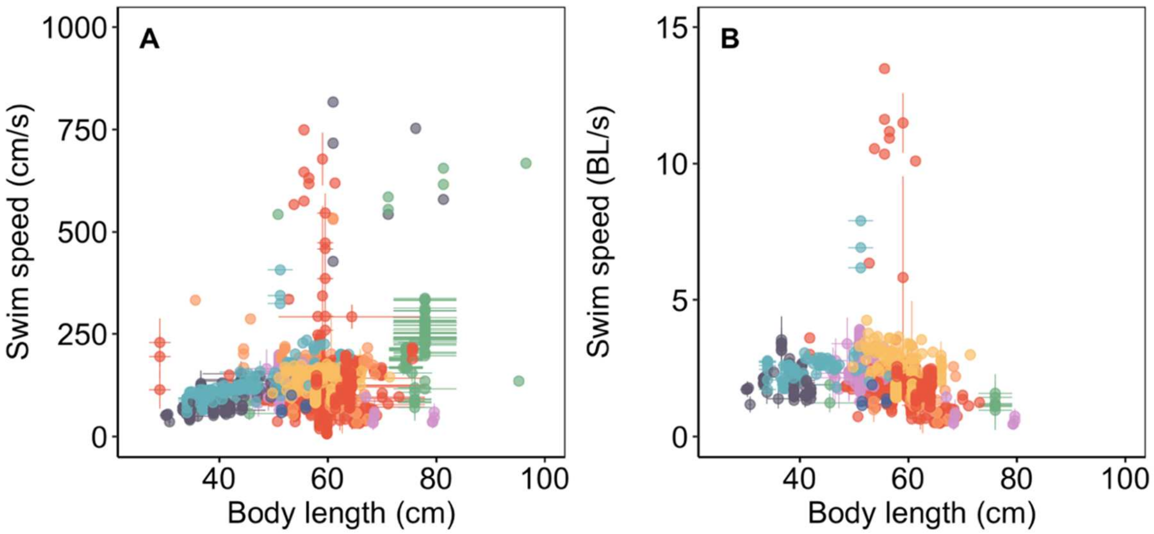
Estimation of body length (cm) of fish, when only mass (kg) was available. The error is SD for entries representing swim performance of n > 1 fish. Blue dots are estimated/calculated lengths of fish (cm) and orange are reported lengths. Lengths (both estimated or reported) were then used to calculate swim speeds in cm/s if only BL/s was available.



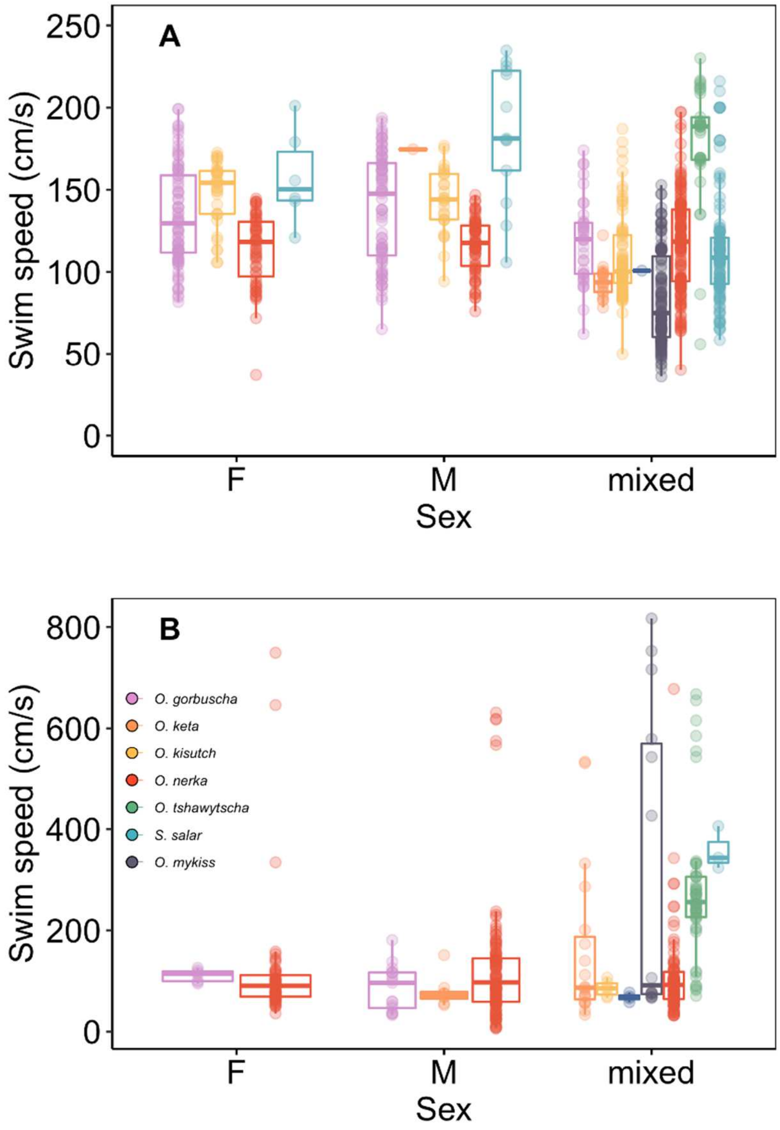
Appendix 3, Figure 2. Species specific absolute swim performance (cm/s). Symbols indicate sex (M = male, F = female, mixed = not specified or specified mixed sex). The error is SD (only positive error is displayed to maintain positive y axis). Y axis range varies for each species.



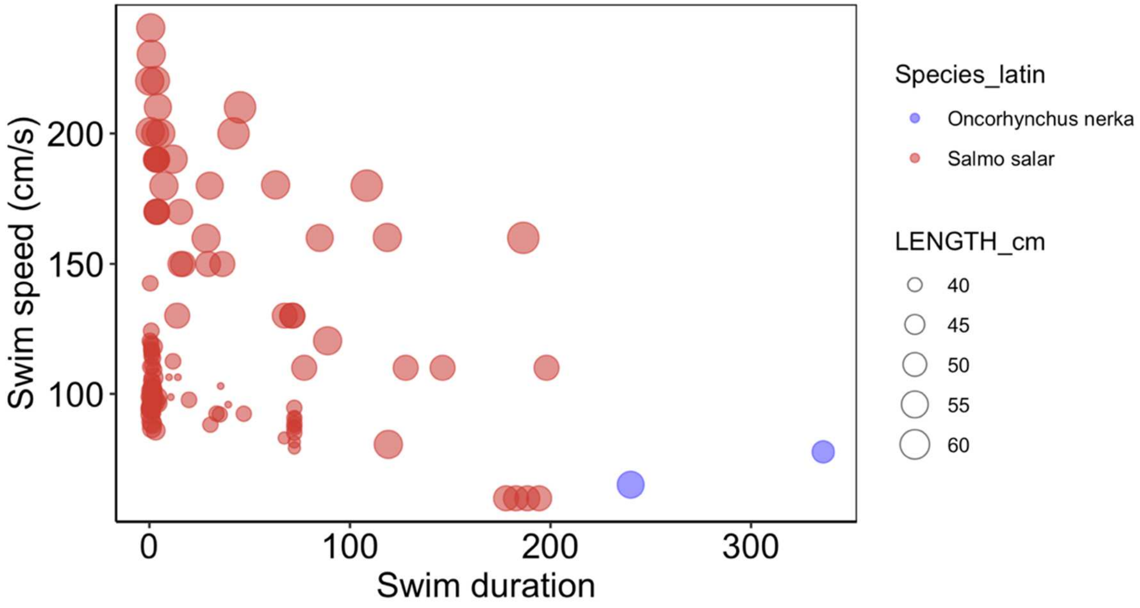
Appendix 3, Figure 3. Species specific relative swim performance (BL/s).
Symbols indicate sex (M = male, F = female, mixed = not specified or specified mixed sex). The error is SD. Y axis range varies for each species.



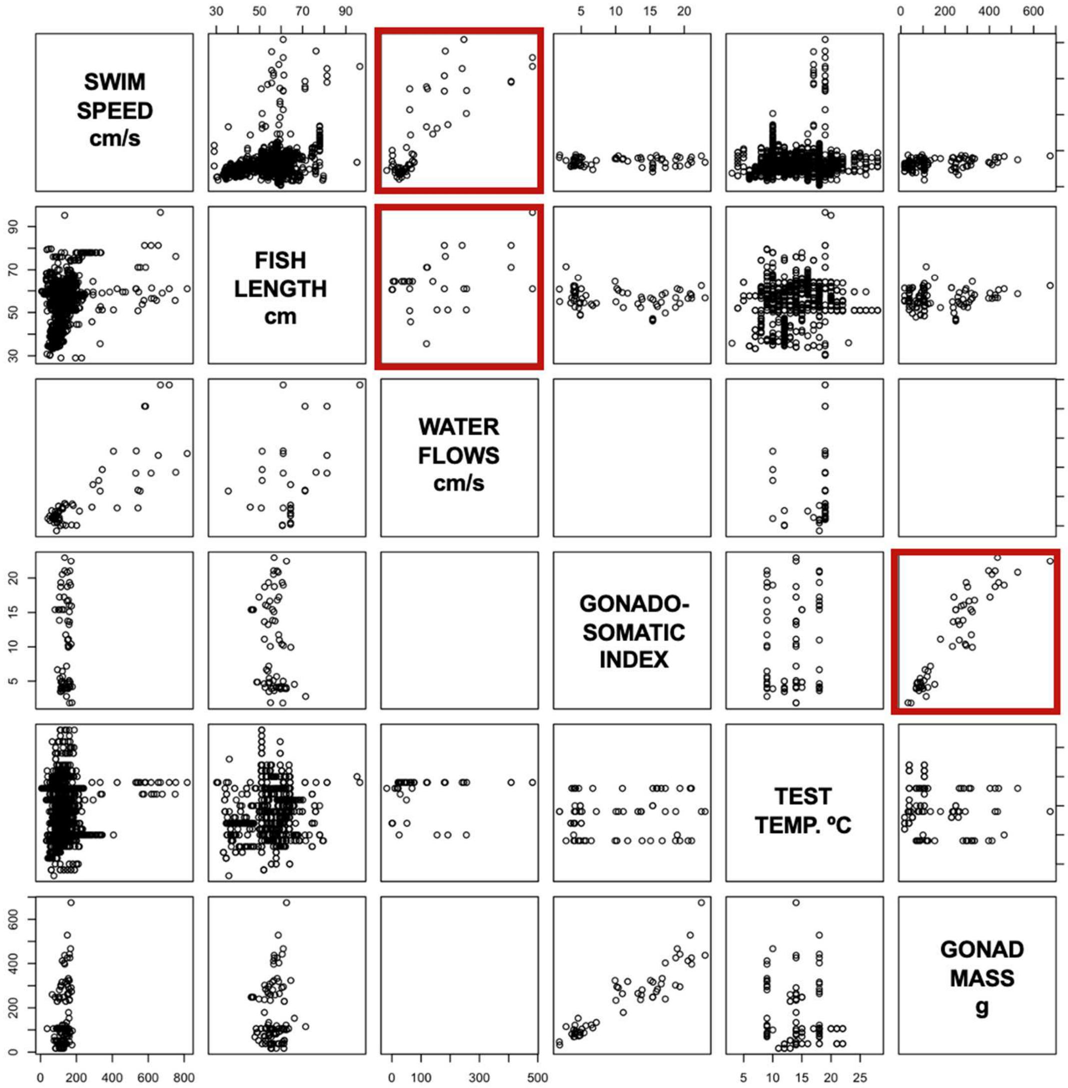
Appendix 3, Figure 4. Body length scaling relationships of swim performance.
Scaling of swim performance in classic swim tunnel experiments (U_{crit} and U_{max}) (A), and in adult salmon in the wild (B). Estimated statistical relationships are described in Appendix 3, Table 10.



Appendix 3, Figure 5. Swim performance by species and sex.
Swimming performance classified by sexes (x-axis) and species (colors) measured in classic swim tunnel experiments (U_{crit} and U_{max}) (A), and in the field (B). M = male, F = female, mixed = mixed sex, or not specified.



Appendix 3, Figure 6. Time to fatigue and swim speeds.
The data from time to fatigue studies, predominantly performed on Atlantic Salmon, *Salmo salar*. The size of the symbol is representative of fish size.



Appendix 3, Figure 7. Correlation matrix showing all continuous metrics.
Red boxes indicate significant relationships ($p < 0.05$)

SECTION 3: REFERENCE LIST OF STUDIES COLLATED FOR THIS REVIEW

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