RESEARCH ARTICLE

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Endothermy makes fishes faster but does not expand their thermal niche

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Abstract

1. Regional endothermy has evolved several times in marine fishes, and two competing hypotheses are generally proposed to explain the evolutionary drivers behind this trait: thermal niche expansion and elevated cruising speeds. Evidence to support either hypothesis is equivocal, and the ecological advantages conferred by endothermy in fishes remain debated.

2. By compiling published biologging data and collecting precise speed measurements from free-swimming fishes in the wild, we directly test whether endothermic fishes encounter broader temperature ranges, swim faster or both. Our analyses avoid several complications associated with earlier tests of these hypotheses, as we use precise measurements of the thermal experience and speed of individual fish.

3. Phylogenetically-informed analyses of 89 studies reporting temperature ranges encountered by tagged fishes reveal that endotherms do not encounter broader temperature ranges than their ectothermic counterparts. In contrast, speed measurements from 45 individuals (16 species, of which four were regional endotherms) show that endothermic fishes cruise ~1.6 times faster than ectotherms, after accounting for the influence of body temperature and body mass on speed.

4. Our study shows that regionally endothermic fishes—those with the ability to conserve metabolically derived heat through vascular countercurrent heat exchangers and elevate the temperature of internal tissues—swim at elevated cruising speeds, although not as fast as previously thought. Contrary to previous studies of endothermy's role in thermal niche expansion, our results suggest the significance of endothermy in fishes lies in the advantages it confers to swimming performance rather than facilitating the occupation of broader thermal niches. Given speed's

major influence on metabolic rate, our updated speed estimates imply endotherms have lower routine energy requirements than current estimates.

5. Our findings shed light on the evolutionary drivers of regional endothermy in fishes and question the view that the trait confers resilience to climate change through broader thermal tolerance than that of ectotherms.

1 | INTRODUCTION

Temperature has pervasive impacts on the physiology, behaviour and distribution of organisms (Payne et al., 2018; Payne, Smith, et al., 2016; Pinsky et al., 2019; Pörtner & Knust, 2007; Reynolds & Casterlin, 1980; Stevens et al., 2010). Ocean temperature strongly regulates the movement and distributions of marine fish (Hazen et al., 2013; Hiddink & ter Hofstede, 2008; Kleisner et al., 2017) and is a key consideration for forecasting their responses to climate change (Pörtner & Farrell, 2008). However, the influence of temperature on fish behaviour and distribution varies across species. One major factor influencing this is the role of endothermy. Most fishes are ectothermic (Wegner et al., 2015); however, regional endothermy has evolved independently in several lineages of marine fishes, including lamnid sharks, tunas and billfishes. Regional endothermy is the ability to conserve metabolically derived heat through vascular countercurrent heat exchangers, and elevate the temperature of specific internal tissues, such as muscle, eyes, brain and viscera—the term 'regional' referring to this localised warming. About 35 species of marine fishes are known to exhibit regional endothermy (Dickson & Graham, 2004), accounting for less than 0.1% of all described fishes (Wegner et al., 2015). Currently, regional endothermy in fishes has been identified in marine species only (Bernal et al., 2001; Block et al., 1993; Carey et al., 1971; Dickson & Graham, 2004) with no evidence for this trait in freshwater fishes. The convergent evolution of regional endothermy across multiple lineages, coupled with the significant energetic cost of the strategy (Bernal et al., 2001; Payne et al., 2015; Watanabe et al., 2015), implies strong ecological benefits. Various hypotheses have been put forward to explain the ultimate driver of endothermy in fishes. These include that endothermy (a) enables thermal niche expansion (Block, 1991; Block et al., 1993; Carey & Lawson, 1973; Dickson & Graham, 2004; Dickson et al., 2000), (b) facilitates elevated cruising speeds (Dickson & Graham, 2004; Watanabe et al., 2015), (c) allows for more effective perception of thermal gradients (Neill et al., 1976), (d) increases metabolic rates (Brill, 1996; Stevens & Neill, 1978), (e) facilitates increased rates of somatic and gonadal growth (Brill, 1996) and (f) that it is simply

an evolutionary by-product (Seebacher, 2020). The 'thermal niche expansion' and 'elevated cruising speeds' hypotheses are arguably the most widely discussed hypotheses at present, so we focused on them in this study.

The thermal niche expansion hypothesis predicts that regionally endothermic fishes can tolerate a broader range of environmental temperatures, enabling them to expand their geographic range or niche. Although it remains formally untested, this hypothesis is widely accepted and underpins several long-standing hypotheses about the thermal niches of fishes, such as the latitudinal diversity gradient (Stevens, 1989). The ideas underlying the thermal niche expansion hypothesis were first formed during work undertaken in the 1970s by Carey and Lawson (1973) on Atlantic bluefin tuna *Thunnus thynnus* when it was postulated that by warming their red muscle the species could 'greatly expand [its] range'. This idea was then formalised by Block (Block, 1991; Block et al., 1993), supported further by Dickson et al. (2000), and remains one of the most widely accepted hypotheses (Madigan et al., 2015; Weng et al., 2005). Alternatively, the elevated cruising speeds hypothesis focuses on how slow-twitch, oxidative myotomal muscle fibres, within the centralised red muscle, power sustained (aerobic) swimming and how the output of these muscle fibres increases with elevated temperature (Dickson & Graham, 2004; Watanabe et al., 2015), thereby allowing increased cruising speed of the fish. Furthermore, temperature's influence on basal metabolic rate (which will increase under elevated temperature) increases the speed at which cost of transport is minimised (Iosilevskii & Papastamatiou, 2016), which may represent preferred speed for many fishes (i.e. COT_{min}).

Here, we simultaneously test the 'thermal niche expansion' and 'elevated cruising speeds' hypotheses using both collated and published animal-borne sensor data (i.e. biologging data) and by measuring speed and temperature experiences of individual fish of multiple species swimming in the wild. Specifically, we test whether regionally endothermic fishes encounter broader temperature ranges than ectothermic fishes and/or whether they swim at elevated cruising speeds. By using individual-level data, we can better examine the factors influencing thermal niche formation and adaptation, as well as intraspecific

individual variation in thermal ranges, and gain a more detailed measure of the extent and variability of thermal ranges of fishes.

Evidence supporting either hypothesis is rare; however, past studies have attempted to decipher the driving cause of endothermy in fishes and found mixed results. Dickson and Graham (2004) found evidence to support the thermal niche expansion hypothesis but could not provide direct support for the elevated cruising speeds hypothesis. Although Watanabe et al. (2015) showed support for the elevated cruising speeds hypothesis, some of the early endothermic speed values have since been shown to be overestimates (Watanabe et al., 2019b). By improving consistency within our speed dataset, we avoid several complications associated with these earlier tests. We accomplished this by exclusively using propeller-style speed loggers (from one manufacturer; Little Leonardo) for all speed measurements. This increases consistency in measurements and reduces the likelihood of overestimates. Furthermore, our dataset includes more endothermic species, tagged with speed propellers, ($n = 4$) than Watanabe et al. (2015; $n = 1$; Salmon shark *Lamna ditropis*) thereby reducing the impact of overestimates on the data as a whole. This novel approach allows us to directly test the elevated cruising speeds hypothesis without complications seen in previous studies.

2 | MATERIALS AND METHODS

2.1 | Data collation: Thermal niche expansion dataset

Data collection for this study consisted of an extensive literature review of peer-reviewed published sources. Library and electronic database searches were carried out across multiple platforms, such as JSTOR, Web of Science, ScienceDirect, Research Gate, among others. Title searchers and keywords included 'biologging', 'thermoregulation', 'endothermy', 'regional endothermy' 'tagging', 'shark(s)', 'teleost(s)', 'ectothermic', 'internal temperature', 'body temperature', 'thermal ecology', 'thermal niche expansion', 'elevated cruising speeds' and/or 'shark tagging'. In addition, studies cited in papers found during these searches, but not identified directly by the search, were also included. Papers for this study were chosen based on a number of selection criteria: (a) species tagged (e.g. marine species only), (b) tag type (e.g. Pop-up Archival Tag; PAT), (c) location of animal at the time of tagging (e.g. only wild fishes in their natural habitat were utilised), (d) frequency of data collection/recording, (e) duration of recording, (f) type of publication (e.g. peer-reviewed journal articles only), (g) recorded parameters (e.g. depth, ambient temperature, internal temperature) and (h) availability and reliability of the data (e.g. robustness of methodologies and technologies used). We chose several data parameters to extract during this review: species common name, species scientific name, thermoregulatory ability, tag type, body size, number of individuals, ambient and body temperature (min., max., mean, 10% upper and lower percentiles), recording duration, depth (min., max., mean, 10% upper and lower percentiles) and latitude (if available).

2.2 | Speed measurements: Elevated cruising speeds dataset

The elevated cruising speeds hypothesis has been tested previously primarily using data from accelerometers, time depth recorder's and pop-off satellite archival tag data, none of which directly record the swimming speed of free-swimming fish in the wild, and could therefore provide inaccurate speed estimates (Bidder et al., 2012; Cade et al., 2018). Furthermore, studies that did use speed propeller sensors (Watanabe et al., 2015) combined multiple sensor manufacturers, several logger types and other speed estimation methods. This resulted in inconsistent estimates with large variation among individuals and may introduce methodological biases. Therefore, we confined our data collection to speed propellers of the same type, from the same manufacturer, to directly collect precise speed measurements of fishes free-swimming in the wild, while simultaneously recording the ambient temperature, along with several other parameters.

We captured fish by drum lines, long lines, or by angling. Biologging packages were fitted to dorsal or pectoral fins of each animal, which were then immediately released; associated methods detailed further in published sources (Huveneers et al., 2018; Nakamura et al., 2011; Papastamatiou et al., 2018; Watanabe et al., 2015, 2019a, 2019b). Biologging packages varied slightly among species but all packages included accelerometers (recording tri-axial acceleration at 25 Hz and depth at 1 Hz; Techno-Smart AGM-1), temperature loggers (recording ambient temperature at 1 Hz) and propeller-based speed sensors (all manufactured by Little Leonardo Corp.) of similar models (PD3GT logger, maximum dimensions 115 × 21 mm, 60 g in air; W1000-PD3GT logger, 22 × 123 mm, 90 g in air; and ORI400/1300-PD3GT logger, 16 mm × 74 mm, 37 g in air), measuring speed in m/s (accuracy of 0.03–0.05 m/s), recording at 1 Hz (Nakamura et al., 2011; Payne, Iosilevskii, et al., 2016; Watanabe et al., 2015). To enable retrieval, tag packages also included a VHF transmitter (Advanced Telemetry Systems, MM100), satellite position only tag (Wildlife Computers Model 258; ARGOS enabled) and a time-release mechanism. Once detached from the animal, packages floated to the surface as they were constructed of a positively buoyant material (Diab Syntactic © non-compressible foam). Packages were then located using the ARGOS system and a VHF receiver and retrieved from the ocean surface by boat. A total of 16 species (four regional endotherms and 12 ectotherms) were tagged, ranging between 8.2 and 807.5 kg body mass and having encountered a range of water temperatures (12–28.2℃).

2.3 | Data analyses

Data handling and statistical analyses were carried out in R Version 4.0.2 (R Core Team, 2020), with similar methodologies implemented for the analyses of both collated (thermal niche expansion hypothesis) and measured (elevated cruising speeds hypothesis) data. Several parameters had to be estimated using source data (e.g. total length,

body mass) and published conversion factors or equations (see Table S1A,B) when not reported or directly recorded. Additionally, several studies compiled as part of the thermal niche expansion dataset reported data in the form of figures but did not provide the raw dataset. In this instance, we used plot digitizer software (Rohatgi, 2019) to extract data for analysis. For the elevated cruising speeds dataset, as each individual displayed strongly unimodal ambient temperature experiences and spent most time in a small range (2–3℃) of temperatures throughout sensor deployment, we used mean ambient temperature for each individual (to the nearest °C) in subsequent analyses. As body temperature was not directly recorded, for ectotherms, it was set at the same value as the mean ambient temperature (Watanabe et al., 2015). For endotherms, body temperature (T_b) was estimated from published relationships with ambient temperature (T_a); for Atlantic bluefin tuna *T. thynnus*, Addis et al. (2009) used $T_b = 0.5531T_a + 17.2365$; for salmon sharks *L. ditropis*, Goldman et al. (2004) used $T_b = 0.2047T_a + 23.156$; and for white sharks *Carcharodon carcharias* and striped marlin *Kajikia audax*, T_b was extrapolated from figures in the studies by Goldman (1997) and Morrow and Mauro (1950) respectively. As our speed measurements were strongly unimodal and right-skewed, the modal speed was used in the models to represent the cruising speed of the animal, as opposed to burst events. Cruising speed was chosen specifically for analysis as it is aerobically powered, can be sustained for prolonged periods of time (Gioanni, 1988; Ryan et al., 2015; Ware, 1978; Watanabe et al., 2012) and is the most common speed at which the animals travel as we have defined it (i.e. modal swimming speed).

2.3.1 | Phylogenies and MCMCglmm

We used non-phylogenetic regression analyses, with phylogenetically informed allometry and model selection based on AIC scores, to test whether regionally endothermic fishes encounter a broader range of temperatures than ectothermic fishes and/or whether they swim at elevated cruising speeds. Phylogenetic trees were created using the Tree of Life package (Hinchliff et al., 2015; Michonneau et al., 2016; see Figures S2 and S3). The tree was then used to inform the modelling analyses using the R package 'MCMCglmm' (Hadfield, 2009). Continuous variables (i.e. 'days at liberty', body mass, speed, depth, body temperature and ambient temperature) were log_{10}-transformed to improve the linearity of relationships among variables. 'Days at liberty' and number of individuals were included in models to account for the influence of sample size on thermal range. Body mass and body temperature were included to account for the influence of thermal inertia and elevated the spatial range of large-bodied animals. Depth range was also included to account for the potential vertical niche expansion (Madigan et al., 2015). Fish thermoregulatory ability was included as a categorical variable (i.e. regional endotherm, ectotherm) and species name was included as a random factor. Thermal niche was represented by two separate measures of the individuals' thermal

experience—absolute thermal range (max. T_a – min. T_a) and the 80th percentile thermal range (90th–10th percentile T_a). The latter measure indexes a range of water temperatures that each individual spends ~5 hr per day (or 12 min/hr) outside. These individual measures were used concurrently to account for the absolute maximum and minimum temperature each individual experienced, while also accounting for the thermal range they spent most time in (i.e. 80% of their time). This allows us to more accurately represent the realised thermal niche of these animals and mitigates issues presented by thermal inertia effects. The measure chosen to evaluate depth range was the 80th percentile depth range (i.e. 90th–10th percentile depth). This measure indexes a range of depths that each individual spends ~5 hr per day (or 12 min/hr) outside. This represents the depth range the individuals spend most time in (i.e. 80% of their time). Alternate models were constructed to test the opposing hypotheses (see Tables S2 and S3).

## 3 | RESULTS

3.1 | Thermal niche expansion

To test if regionally endothermic fishes encounter broader temperature ranges than their ectothermic counterparts, we compiled 89 published studies reporting temperature ranges encountered by tagged fishes of 41 species, 14 of which were regional endotherms. Non-phylogenetic regression analyses (see Table S2), followed by phylogenetically informed GLMMs, MCMCglmm (Hadfield, 2009), show that endothermy does not have an influence on absolute thermal range (posterior mean = 3.5, pMCMC = 0.08, λ_{mode} = 0.002). Endothermy does not affect the 80th percentile thermal range (posterior mean = 1.4, pMCMC = 0.4, λ_{mode} = 0.00068).

In addition to thermal range, we investigated the significance of endothermy on depth range in order to address vertical niche expansion (Madigan et al., 2015). Phylogenetically informed GLMMs, MCMCglmm (Hadfield, 2009), show that endothermy does not have an influence on 80th percentile depth range (posterior mean = 33.3, pMCMC = 0.6, λ_{mode} = −0.0001).

These results indicate that endothermic fishes do not encounter broader temperature ranges than their ectothermic counterparts. Larger bodied animals have greater absolute thermal ranges (Figure 1a; posterior mean = 3.2, pMCMC = 0.003), but no such relationship was found for the 80th percentile thermal range (Figure 1b; posterior mean = 1.1, pMCMC = 0.374). Furthermore, larger bodied animals do not encounter broader depth ranges (Figure 1c: posterior mean = 67.1, pMCMC = 0.2).

3.2 | Elevated cruising speeds

To test if endothermy facilitates elevated cruising speeds in fishes, we directly collected biologging data for 45 individual fish in the wild, from 16 species including four regionally endothermic species,
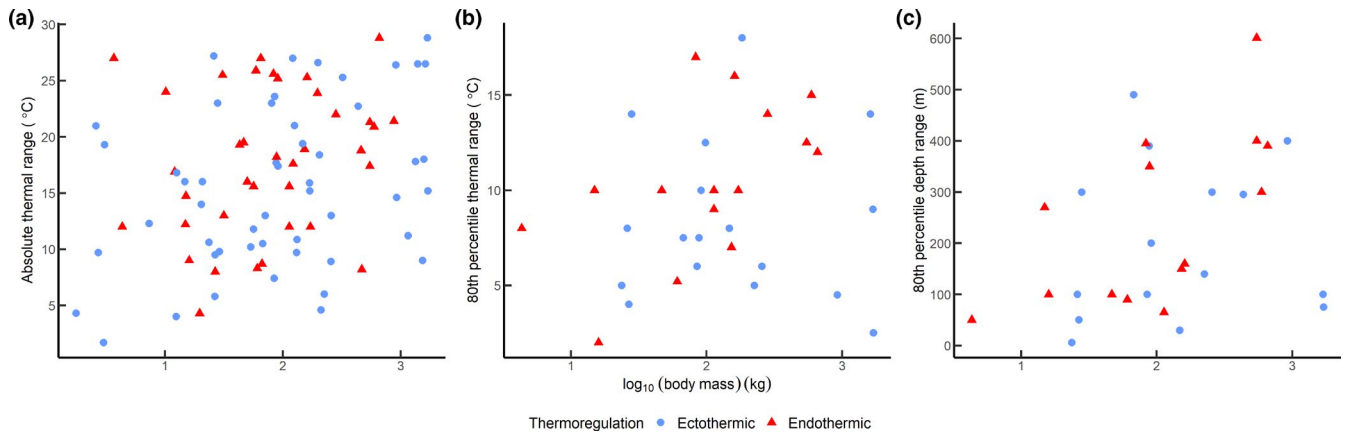
FIGURE 1 (a) Absolute thermal range (max. T_a – min. T_a) as a function of body mass ($\log_{10}$-transformed; kg), taken from thermal niche expansion dataset: thermal range of fishes with regional endothermy (red triangles) and fishes without it (light blue circles). (b) The 80th percentile thermal range (90th–10th percentile T_a) as a function of body mass ($\log_{10}$-transformed; kg): thermal range of fishes with regional endothermy (red triangles) and fishes without it (light blue circles) recorded in the wild. Endothermy does not have an influence on the thermal range individuals spent 80% of their time in. (c) The 80th percentile depth range (90th–10th percentile depth) as a function of body mass ($\log_{10}$-transformed; kg): depth range of fishes with regional endothermy (red triangles) and fishes without it (light blue circles) recorded in the wild. Endothermy does not have an influence on the depth range individuals spent 80% of their time in
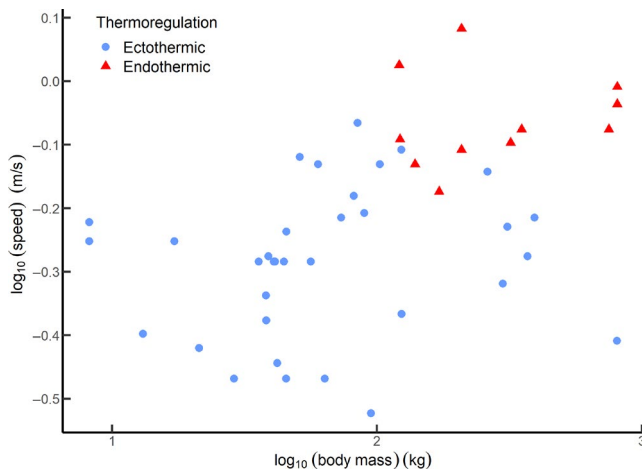
FIGURE 2 Cruising speed ($\log_{10}$-transformed; m/s) as a function of body mass ($\log_{10}$-transformed; kg): cruising speed of fishes with regional endothermy (red triangles) and fishes without it (light blue circles) recorded in the wild. Fishes with regional endothermy have higher cruising speeds (pMCMC = 0.016)

ranging 8.2–807.5 kg body mass and a mean recording duration of 49.34 hr (see Table S4). Non-phylogenetic regression analyses (see Table S3), followed by phylogenetically informed GLMMs, MCMCglmm (Hadfield, 2009), show that endothermy has a significant influence on speed (posterior mean = 0.20, pMCMC = 0.016, λ_{mode} = 0.10). Even after accounting for the influence of body temperature on speed, regional endotherms of given mass cruise faster than ectotherms (pMCMC = 0.016; see Figure 2). A significant effect of endothermy, after also accounting for body temperature, suggests other traits of endotherms are involved with faster swimming in addition to temperature effects. Further, on average, for a given body mass across the range given here, regional endotherms swim ~1.6 times faster than ectotherms. Although body mass has a

positive slope (posterior mean = 0.019) with speed, it is not significant (pMCMC = 0.7; see Figure 2).

4 | DISCUSSION

Our study shows that regionally endothermic fishes do not encounter broader temperature ranges than their ectothermic counterparts, but that they swim at elevated cruising speeds. Contrary to previous studies of endothermy's role in thermal niche expansion (Block et al., 2001; Carey & Lawson, 1973; Dickson & Graham, 2004; Weng et al., 2005), our results therefore suggest that the significance of endothermy lies in the competitive advantages it confers to swimming performance rather than facilitating occupation of broader thermal niches.

It has been shown previously that elevated body temperature positively influences swimming speed in many fish species (Dickson & Graham, 2004; Kieffer et al., 1998; Rome et al., 1984; Sisson & Sidell, 1987; Whitney et al., 2016), primarily through the mechanism of increased aerobic capacity of red muscle. Building upon this understanding, our study accounted for the effect of body temperature on speed and showed evidence for an additional influence of endothermy on cruising speed. Interestingly, while the eyes and brain of striped marlin are maintained at elevated temperatures, their medially positioned red muscle is not (Dickson & Graham, 2004); yet they swim at relatively high speeds. Medial red muscle and regional endothermy are often conflated with one another because the traits are highly correlated. However, it is possible mechanical advantages of medial red muscle alone, such as restriction of body undulations towards the tail and associated drag reductions (Donley et al., 2004), are largely responsible for higher speeds in species with that trait, most of which also maintain the red muscle at higher temperatures. More swimming speed

data from species with medial and unheated red muscle would help address this question.

Taken together, our data remain in support of the general conclusions of Watanabe et al. (2015) that regional endotherms swim faster than ectotherms. However, we found a far smaller difference—1.6 times faster than ectotherms, compared to 2.7 times faster in Watanabe et al. (2015)—likely attributable to our use of consistent measurement methodology (speed propellers), increased sample size and lack of extrapolated speed measurements culminating in a more accurate estimate of speed. This finding has important consequences for our understanding of fish energetics, particularly given speed's strong influence on rates of energy expenditure; as energy expenditure increases approximately to the cube of speed (Bernal et al., 2012; Carlson et al., 2004), routine metabolic rates (and therefore daily energy budgets) of regionally endothermic fishes would therefore be considerably lower than currently thought (e.g. Semmens et al., 2013; Watanabe et al., 2019b). The overestimation of energy requirements for regionally endothermic fishes, most of which are high-level predators (e.g. white sharks, mako sharks, Atlantic bluefin tuna), is problematic for accurately predicting changes throughout lower trophic levels following changing abundances of such predators. These results highlight the significant uncertainties that remain in our understanding of the energetics of large marine fishes, many of which are too difficult to study in metabolic chambers (Bernal et al., 2012; Payne et al., 2015).

The potential advantages conferred by elevated cruising speeds include the ability to perform further annual migrations than ectothermic species (Watanabe et al., 2015), increased predator–prey encounter rates (Jacoby et al., 2015) and enhanced ability to identify and capture prey (Fritsches et al., 2005; Ryan et al., 2015; Schieber et al., 2012) due to the higher temporal resolution in the visual system achieved under faster locomotion speeds; speed of locomotion determines the rate at which sensory information is encountered and processed by an animal as it moves through its natural environment (Ryan et al., 2015). Taken in the context of the visual system, the higher the swimming speed, the faster the rate at which an image moves across the animal's eye (Eckert & Zeil, 2001), such that animals exhibiting higher swimming speeds tend to have higher temporal resolution and therefore process visual information faster (Autrum, 1958; Lisney et al., 2011; McFarland & Loew, 1983; Ryan et al., 2015). Although studies like ours have been conducted in the past, the novelty of our study lies in our methodology. Previous studies have been limited by the resolution of their data, the unattainability of multiple, simultaneous measurements of environmental parameters and small sample sizes (especially for endothermic species). Our study overcame some of these limitations using cutting-edge technology that provides speed estimates of high precision and accuracy, and so provides the most representative speed information for this group of animals. Further refinements could come from directly measuring core body temperatures of each animal rather than estimating it from the environment or other studies (as we did). Technological developments are starting to facilitate such future work.

Our findings for the thermal niche expansion hypothesis contrast with those of numerous previous studies (Block, 1991; Block et al., 1993; Carey & Lawson, 1973; Carey et al., 1971; Dickson & Graham, 2004; Watanabe et al., 2015). This may be because ours is the first to compare the thermal experience of a large number of species from both regional endotherms and ectotherms, at the individual level. Species-level thermal tolerance is influenced by factors such as abundance, migration and seasonality, and may obscure the temperature experience of individuals, with the individual level being that at which niche expansion ought to provide benefit. Our finding that endothermy does not enhance thermal or vertical niches of individuals has broad implications, particularly in terms of climate change. It has previously been suggested that regionally endothermic fishes may be better able to deal with changing ambient temperatures by stabilising their tissue temperatures (Carey & Teal, 1969; Neill et al., 1976; Stevens & Neill, 1978; Weng & Block, 2004), a situation which would be expected under current climate change scenarios, such as global ocean warming. Taken in conjunction with the assumption of thermal niche expansion, regionally endothermic fishes are often assumed to be less susceptible to the global- and local-scale impacts of ocean warming (Block, 1991), due to their ability to escape thermal stress by expanding or shifting their distributions. That may be the case, but our results indicate that endothermy does not facilitate occupation of broader temperature or depth ranges, so the future climate resilience of such fishes may be overstated. Marine spatial planning and protection and re-introduction strategies, for conservation purposes, are largely informed by species distribution models (SDMs). SDMs are constructed from past and present distribution data of species, and then used to make spatially explicit predictions of environmental suitability for species and potential redistribution of the species (Jarvie & Svenning, 2018). This makes SDMs extremely useful tools in predicting species range shifts under climate change scenarios. While current SDMs for regionally endothermic fish species are based on current distribution data, the predictions they make for potential redistribution, under climate changes scenarios, may be susceptible to overestimation due to the long held assumption (Block, 1991; Block et al., 1993; Dickson et al., 2000; Watanabe et al., 2015; Weng et al., 2005) that regionally endothermic fishes can expand their thermal and vertical (Madigan et al., 2015) niche and therefore exploit a wider spatial niche.

In conclusion, our quantitative and comparative analyses indicate that the significance of endothermy lies in the competitive advantages it confers to swimming performance rather than facilitating occupation of broader thermal niches. Moreover, our results suggest that the magnitude of the difference in swimming speed between ectotherms and regional endotherms is not as large as estimated previously. Rather than facilitating broader thermal niches, our data imply that convergent evolution of regional endothermy is more likely linked to the advantages in ecological interactions, such as predator–prey interactions. Taken in conjunction with the fact that regional endothermy has evolved independently in the lineages

of fishes which are largely high-level predatory species, we consider the likely advantage of endothermy lies in the competitive advantage it confers to predation.

AUTHORS' CONTRIBUTIONS

L.H., N.P., A.B., A.J. and I.D. conceived the ideas and designed methodology; L.H., N.P., A.B., L.H., C.H., C.M., Y.P., J.S., E.S. and Y.W. collected the data; L.H. analysed the data and led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

DATA SOURCES

Data sources are within the Supporting Information of this manuscript.

DATA AVAILABILITY STATEMENT

Data are available within the Supporting Information of this manuscript or within the cited source material. Data are deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.hmgqnk9h2 (Harding et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.