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RESEARCH ARTICLE

Thermal limitation of performance and biogeography in a free-ranging ectotherm: insights from accelerometry

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ABSTRACT

Theoretical and laboratory studies generally show that ectotherm performance increases with temperature to an optimum, and subsequently declines. Several physiological mechanisms probably shape thermal performance curves, but responses of free-ranging animals to temperature variation will represent a compromise between these mechanisms and ecological constraints. Thermal performance data from wild animals balancing physiology and ecology are rare, and this represents a hindrance for predicting population impacts of future temperature change. We used internally implanted accelerometers near the middle of a species' geographical distribution and gill-net catch data near the species' latitudinal extremes to quantify temperature-related activity levels of a wild predatory fish (*Platycephalus fuscus*). We examined our data in the context of established models of thermal performance, and the relationship between thermal performance thresholds and biogeography. Acceleration data approximated a thermal performance curve, with activity peaking at 23°C but declining rapidly at higher temperatures. Gill-net catch data displayed a similar trend, with a temperature-associated increase and decrease in catch rates in temperate and tropical regions, respectively. Extrapolated estimates of zero activity (CT_{min} and CT_{max}) from the accelerometers were similar to the minimum and maximum mean monthly water temperatures experienced at the southern and northern (respectively) limits of the species distribution, consistent with performance-limited biogeography in this species. These data highlight the fundamental influence of temperature on ectotherm performance, and how thermal performance limits may shape biogeography. Biologging approaches are rarely used to examine thermal performance curves in free-ranging animals, but these may be central to understanding the trade-offs between physiology and ecology that constrain species' biogeographies and determine the susceptibility of ectotherms to future increases in temperature.

KEY WORDS: Climate change, Pejus, Range contraction, Tagging, Telemetry, Thermal tolerance

INTRODUCTION

Ectotherms are particularly vulnerable to global warming because their fundamental physiological functions such as locomotion, growth and reproduction are strongly influenced by temperature (Huey and Kingsolver, 1989; Deutsch et al., 2008; Kingsolver, 2009). The influence of temperature on ectotherm function is often described by a thermal performance curve, with relative performance, growth or fitness increasing to an optimum temperature (T_{opt}), and declining rapidly thereafter (Fry, 1947; Huey and Kingsolver, 1989; Pörtner, 2001; Deutsch et al., 2008; Kingsolver, 2009; Pörtner, 2010). Thermal performance models quantify the effect of temperature on organism fitness, thereby representing a framework for understanding how ectotherms are likely to respond to future changes to temperature regimes (Deutsch et al., 2008; Pörtner, 2010; Buckley et al., 2012).

For thermal performance curves in fish, T_{opt} is often defined as the temperature at which aerobic scope (the difference between minimum and maximum rates of oxygen uptake) is maximised (Fry and Hart, 1948; Brett, 1971; Pörtner, 2001; Pörtner, 2002; Farrell, 2009), and critical temperature (T_{crit}; often called CT_{min} and CT_{max} for lower and upper critical temperatures, respectively) as that where aerobic scope declines to zero and mitochondrial metabolism proceeds anaerobically (Pörtner et al., 1998; Pörtner, 2001; Farrell, 2009). As critical functions such as growth, reproduction and locomotion require an increase in oxygen uptake beyond the maintenance rate (Farrell, 2009), an animal's thermal niche should lie between the lower and upper values of T_{crit}. Temperature has long been thought to constrain species' geographic distributions (e.g. Shelford, 1931), and while T_{opt} for aerobic scope does not necessarily correspond to the preferred temperature of a species (Clark et al., 2013; Farrell, 2013; Pörtner and Giomi, 2013), physiological performance metrics such as T_{crit} or lethal thermal limits have recently been used to interpret ectotherm range boundaries (Sunday et al., 2011; Sunday et al., 2012). Such approaches are also providing insight into the role of global temperature increases in the recent range shifts of several aquatic animals (Perry et al., 2005; Pörtner and Knust, 2007; Farrell et al., 2008). However, long-term persistence requires at least some scope for activity, growth and reproduction, so an animal's functional thermal niche should be narrower than that bounded by T_{crit} values (Farrell, 2009), and may instead be delimited by other performance thresholds (e.g. 'pejus' thresholds – temperatures coinciding with the onset of performance limitation (Frederich and Pörtner, 2000; Pörtner, 2001; Pörtner, 2002). Indeed, T_{crit} and lethal temperatures were recently shown to be somewhat unreliable predictors of ectotherm range limits (Sunday et al., 2012). Understanding the mechanisms by which temperature restricts animals' geographic distribution has long been identified as a critical pursuit (Shelford, 1931; Pörtner, 2001), yet remains a major challenge for biologists (Seebacher and Franklin, 2012; Sunday et al., 2012; Brown, 2014). Much of this difficulty probably arises from complexities associated with scaling up laboratory data to biogeography, because a species' functional thermal niche can be affected by a variety of

environmental factors (Helmuth et al., 2005; Farrell, 2009) and ontogeny (Pörtner and Farrell, 2008).

Many theoretical and laboratory studies have examined the influence of temperature on fish performance (e.g. Fry, 1947; Fry and Hart, 1948; Brett, 1971; Graham and Farrell, 1989; Lee et al., 2003; Farrell, 2009; Pörtner, 2010; Brownscombe et al., 2014), and some have matched laboratory-based performance data to fish distributions and abundance (Pörtner and Knust, 2007; Farrell et al., 2008) or growth rates (Neuheimer et al., 2011). However, there remains a paucity of data on how temperature influences locomotory performance in free-ranging animals [but see Righton et al. for seasonal changes in cod *Gadus morhua* activity that may have been driven by temperature (Righton et al., 2001)]. This represents a significant shortcoming, as the response of animals to future temperature changes may be largely influenced by behaviour and ecology (Huey and Stevenson, 1979; Kearney et al., 2009), which will affect the accuracy of predictions based solely on physiological performance models. Quantifying thermal performance curves in free-ranging animals may become increasingly important given emerging evidence that regional adaptation of thermal thresholds in ectotherms is heavily constrained by evolutionary history (Araújo et al., 2013; Grigg and Buckley, 2013).

Biologging approaches have emerged as powerful tools for addressing remarkably diverse objectives (Payne et al., 2014), and accelerometers in particular hold significant potential for examining thermal performance curves in free-ranging ectotherms. Despite this potential, we are not aware of any studies that have used biologging to test for thermal performance curves in the activity levels of free-ranging ectotherms.

In this study, we used accelerometer transmitters and commercial gill net (a passive gear type that relies on fish movement for capture) catch data to quantify the effects of temperature on locomotory performance of a free-ranging estuarine fish – the dusky flathead *Platycephalus fuscus* G. Cuvier 1829. This species is a benthic ambush predator inhabiting estuarine and near-shore coastal ecosystems across almost 21° of latitude along Australia's east coast [from Gippsland Lakes in the south to Cairns in the north (Gray et al., 2002)], and is therefore exposed to large spatial and temporal fluctuations in temperature. We used our biologging data to create a thermal performance (voluntary activity) curve for flathead near the middle of the species' geographical distribution, and the catch data to examine thermal performance trends near the northern (tropical) and southern (temperate) extremes of the species' range. In doing so, we explored the relationship between thermal performance and biogeography, and interpret our data in the context of a warming climate.

RESULTS

Between 900 and 10,774 activity data were collected for each tagged fish, with a total of 23,169 data recordings over 66 days in winter/spring, and 28,456 data recordings over 89 days in summer/autumn. Activity of tagged flathead increased with temperature to ~23°C, at which point activity levels declined rapidly (Fig. 1A; all parameters $P<0.001$, d.f.=99, R^2=0.58). The two-part

model returned parameter estimates (and lower and upper 95% confidence interval, CI) of: T_{opt}=22.96°C (22.27 and 23.63°C), σ=2.37°C (1.89 and 2.92°C), CT_{max}=27.49°C (26.91 and 28.54°C) and S=0.16 (0.15 and 0.17), and we estimated CT_{min}=13.46°C (10.58 and 16.01°C). A very similar trend was seen for the 95th percentile data (supplementary material Fig. S1), with parameter estimates of: T_{opt}=22.95°C (22.09 and 23.73°C), σ=2.55°C (2.01 and 3.16°C), CT_{max}=27.96°C (27.16 and 29.65°C) and S=0.70 (0.65 and 0.76), and we estimated CT_{min}=12.74°C (9.45 and 15.68°C). Commercial gill net catch per unit effort (CPUE) appeared to increase with temperature near the southern limits of their distribution (Victoria; Fig. 1B, circles), and decrease with temperature near their northern limits (Queensland; Fig. 1B, triangles). The range of temperatures was greater for estuarine (Fig. 1B, filled symbols) than coastal habitats (open symbols) in both regions, and the minimum and maximum mean monthly temperatures recorded were 11.24 and 28.7°C for Lake Tyers and Cairns, respectively.

DISCUSSION

This study suggests the voluntary performance of free-ranging *P. fuscus* is heavily influenced by environmental temperature, with activity distributions that are consistent with established models of thermal performance (Huey and Kingsolver, 1989; Pörtner, 2001; Pörtner and Farrell, 2008). This represents one of the first examples of a thermal performance curve for an animal balancing physiological and ecological constraints in the wild, and provides insight into how thermal performance may be linked to species' biogeography.

Laboratory-derived physiological thresholds (e.g. T_{crit}, pejus thresholds or lethal limits) are often used to explore range boundaries or changes in relative abundance of ectotherms (Pörtner and Knust, 2007; Farrell et al., 2008; Sunday et al., 2011; Sunday et al., 2012), yet such metrics can fail to fully explain the limits of species' distributions (Addo-Bediako et al., 2000; Sunday et al., 2012). For example, aerobic scope in pink salmon *Oncorhynchus gorbuscha* is maximised around 21°C and approaches zero (CT_{max}) at ~30°C [under extrapolation of data in fig. 3 of Clark et al. (Clark et al., 2011)], yet individuals of that same population rarely encounter river temperatures as high as T_{opt}, let alone CT_{max} (Clark et al., 2011). Such an example highlights the difficulties associated with identifying single physiological bases for species' range limits (Helmuth et al., 2005; Pörtner and Farrell, 2008; Farrell, 2009). Voluntary performance data from free-ranging animals may be very informative in this respect, and our biologging data are suggestive of performance-limited biogeography, with extrapolated estimates of zero activity (CT_{min} and CT_{max}) close to the minimum and maximum mean monthly temperatures experienced in the southern and northern (respectively) limits of the *P. fuscus* range (95% CIs for CT_{min} overlap the minimum monthly temperatures experienced at the southern geographical limit, and the CIs for CT_{max} are within 0.2°C of the maximum temperatures at the northern limit; Fig. 1A). Given our biologging data were collected near the middle of the species' range, tagged flathead did not experience the extreme temperatures that occur at the latitudinal limits of their distribution (monthly means of ~11 and 29°C in the south and north, respectively), so our confidence limits for CT values are rather broad, particularly for CT_{min} (Fig. 1A). However, if limits of voluntary activity do indeed delineate the thermal niche of this species, the congruence between CT estimates derived from the middle of the species' distribution and temperature extremes at the northern and southern range limits would indicate a low degree of
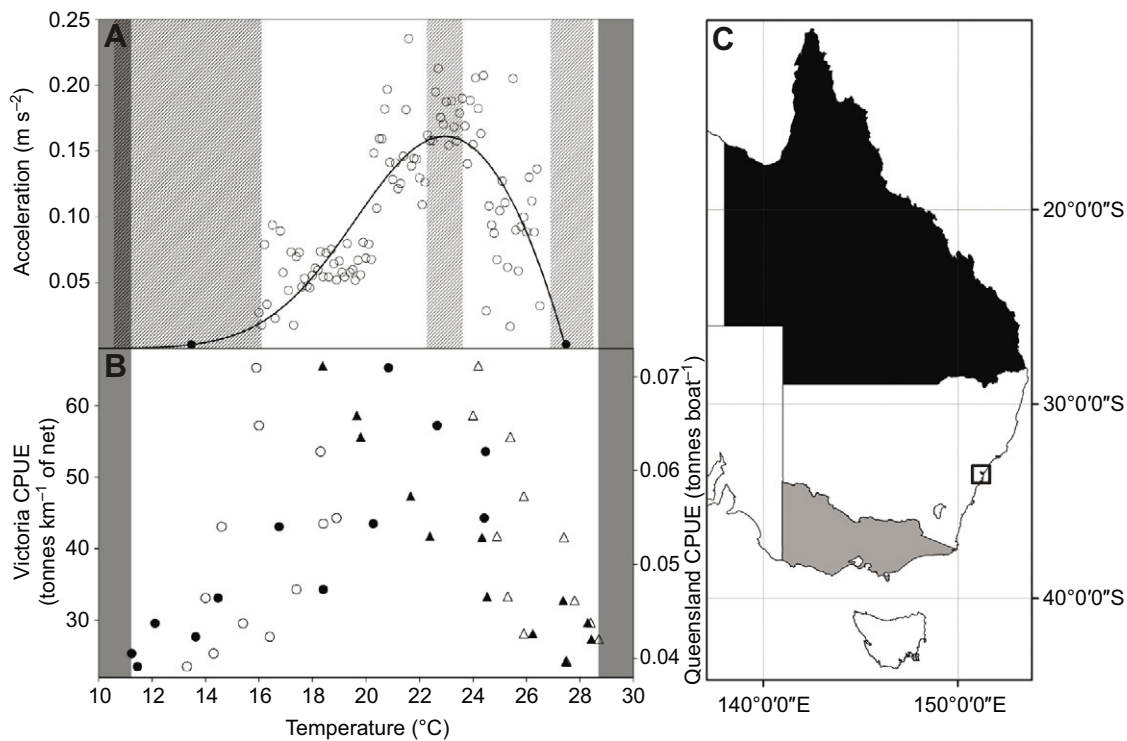
Fig. 1. *Platycephalus* thermal performance. (A) Relative activity rates of fish tagged in the Georges River, NSW, with activity (acceleration) data averaged for each 0.1°C increment in water temperature. Shaded areas indicate the minimum and maximum mean monthly temperatures experienced at the southern and northern limits of the species' geographical distribution, respectively, and hatching indicates 95% confidence intervals for the lower critical temperature (CT_{min}, left filled circle), optimum temperature (T_{opt}) and upper critical temperature (CT_{max}, right filled circle). (B,C) Mean monthly commercial gill net catch rates of *Platycephalus* spp. from two thermally distinct regions of Australia's eastern coastline – Victoria: circles (B) and grey region (C), and Queensland: triangles (B) and black region (C). Filled data indicate estuarine temperatures and open circles indicate coastal sea surface temperatures. The location of accelerometer data collection within NSW is indicated by the box in C.

regional adaptation in this species. Unfortunately, we cannot directly compare the biologging and catch data (given the different units between regions, low spatial resolution of capture locations and the lack of zero-reporting for catch data). However, catches do peak at intermediate temperatures when data from the southern and northern extent of the species' range are combined (Fig. 1B), which is in line with the biologging data (Fig. 1A). Recent meta-analyses suggest regional adaptation of ectotherm thermal thresholds is highly conserved within species (Araújo et al., 2013; Grigg and Buckley, 2013), but flathead accelerometer data from cooler and warmer regions would allow for the quantitative test required to determine whether populations of this species have adapted their activity thresholds to local temperature regimes.

The proximate mechanisms driving the temperature-associated voluntary performance curve are uncertain, and may be a combination of physiological factors [e.g. limits to cardiac function and/or oxygen supply (Pörtner, 2001; Farrell, 2009)] and ecological factors (e.g. relative abundance of predators and prey or reproductive behaviours). Further, while the sit-and-wait ambush predation strategy of *P. fuscus* suggests much of the variation in acceleration data is driven by changes in the frequency of swimming events, the transmitters we used provide a single relative activity value averaged over ~2 min of recording, so discriminating between changes in burst-event frequency, routine swimming speeds or the proportion of time spent swimming was not possible. Other biologging devices allow identification of such behaviours, but represent a variety of trade-offs [e.g. size, battery life and the need to retrieve devices (Payne et al., 2014)]. Future biologging research on thermal performance should aim to increase understanding of the

mechanisms underlying thermal performance curves in wild animals, and a variety of tools are available for this pursuit. For example, accelerometers that log high frequency data could reveal whether temperature-dependent variation in activity levels is driven by a change in mean stroke frequency, prevalence of burst (e.g. predation) events, or overall time spent active. Swim-speed sensors could reveal similar information for aquatic animals, albeit without the level of biomechanical insight obtained with accelerometers. High resolution data from those tools can quantify ecological proxies of performance such as predation frequency and foraging success or predator avoidance, particularly if coupled with video recordings (Watanabe and Takahashi, 2013). Combining field approaches like these with laboratory evaluations of temperature-associated physiological changes and other performance metrics in wild animals [e.g. growth rates (Neuheimer et al., 2011); relative feeding success (Watanabe and Takahashi, 2013)] will provide a more complete picture of how temperature affects animal fitness, and this could represent a major step toward understanding the influence of temperature on biogeography. Particularly powerful studies may be those that simultaneously identify physiological (e.g. reactive rates, cardiac function or aerobic scope) and ecological (e.g. voluntary activity or foraging success) thresholds and link those to species' range boundaries. Such an approach would help to reconcile the relative influences of physiological and ecological limitations on performance and this would provide significant mechanistic insight into the factors that determine the limits of animal distributions.

The thermal tolerance of many organisms is proportional to the magnitude of temperature variation they experience (Deutsch et al., 2008), so animals in temperate regions are thought to be more

tolerant of increasing temperatures than those in the tropics (Deutsch et al., 2008; Huey et al., 2009). Further, the optimum temperature for *P. fuscus* performance appears close to, or below, the minimum temperature they experience in coastal regions in the tropics [Fig. 1A,B (open triangles)]. Taken with the apparently limited degree of regional adaptation in this species, it could be expected that *P. fuscus* populations at lower latitudes are particularly vulnerable to increases in local water temperatures. Further warming of Australia's tropics may lead to a contraction in the distribution of this species from the tropics.

This study is one of the first to use biologging to document locomotory function approximating a thermal performance curve in a free-ranging animal. Biologging tools similar to the ones we used can be employed on a broad range of ectothermic taxa, and such applications may play a large part in understanding how ectotherms balance physiology and ecology to deal with fluctuating temperatures. This will facilitate a greater predictive capacity (with respect to stressors such as climate change) than a reliance on physiological models alone.

MATERIALS AND METHODS
Work with animals in this study was permitted under University of NSW Animal Research permit 11/30A. Twelve *P. fuscus* (400–500 mm total length) were angled ~15 km upstream of the mouth of the Georges River estuary in NSW, Australia (34.0°S, 151.0°E) during two periods: winter/spring 2011 and summer/autumn 2012. Accelerometers (Vemco, Halifax, NS, Canada; model V9A-2L, representing ≤1.5% fish mass) were surgically implanted (see Walsh et al., 2012), with the length of each transmitter lying parallel with each fish body, within the peritoneal cavity. Each tag recorded acceleration on *x*-, *y*- (dorsoventral and lateral) and *z*-axes (forwards–backwards). Acceleration was sampled at 5 Hz for 120 s on each axis, with a measurement range of ±3.34 m s^2. Acceleration was calculated as a root mean square value from each axis, and recorded data were transmitted every 190–290 s. Averaging acceleration (over 2 min) in this way precludes identification of the absolute frequency of specific behaviours, so our biologging data represent relative, voluntary activity levels across the temperatures the fish experienced (after Payne et al., 2011; Payne et al., 2013), and we refer to these data as 'activity' hereafter. Five Vemco VR2W receivers recorded activity data from the transmitters within the study site, and these were spaced ~500 m apart. Two Odyssey temperature and salinity (Dataflow Systems Pty Ltd) loggers were attached to two of the receivers (in 4–6 m water depth) to continuously record water temperature.

Activity data from all tagged fish and across the entire sampling period were averaged for every 0.1°C increment of water temperature, such that 10 values were generated per 1°C across the monitoring period. As fish did not all experience the same range of temperatures (because of our staggered tagging dates and the periodical absence of individual fish from the detection range of receivers), we pooled the data across fish into our 0.1°C increments, and generated means per increment to account for the variable number of activity data collected at each temperature. Visual examination of the activity data suggested an asymmetric distribution, so we fitted a two-part 'performance' curve after Deutsch et al. (Deutsch et al., 2008), using minimum least-squares non-linear regression. This curve consists of a Gaussian function to describe the rise in performance up to T_{opt}, and a quadratic decline to zero activity, CT_{max}, at higher temperatures:

$$A = \begin{cases} S \times e^{-\left(\frac{T - T_{opt}}{2\sigma}\right)^2} & \text{for } T \leq T_{opt} \\ S\left(1 - \left(\frac{T - T_{opt}}{T_{opt} - CT_{max}}\right)^2\right) & \text{for } T > T_{opt} \end{cases}, \quad (1)$$

where T_{opt} is the temperature (*T*) at which activity is maximised, σ is the standard deviation for the normally distributed half of the curve and *S* is a

scalar. As the Gaussian function does not intersect the *x*-axis (at low temperatures), we defined the critical thermal minimum (CT_{min}) as 4σ below T_{opt} (after Deutsch et al., 2008). In this way, CT_{min} represents an estimate of activity ~1.8% of that at T_{opt}. We used 95% CIs to describe the uncertainty of our parameter estimates. For our operational estimate of CT_{min}, we calculated the lower CI as the lower 95% CI for T_{opt} minus 4× the upper 95% CI for σ, and the upper CI of CT_{min} as the upper 95% CI for T_{opt} minus 4× the lower 95% CI for σ. A Weibull curve was also fitted to the data (not shown), but this did not provide sufficient improvement in fit compared with the two-part curve. The two-part curve was preferred over the Weibull given its more mechanistic derivation (Deutsch et al., 2008). As a second metric of acceleration and to examine trends in higher activity values, we also fitted the two-part curve to 95th percentile data (rather than means) that we derived for each 0.1°C increment of water temperature.

Gill netting is a passive fishing technique that relies on fish actively swimming into nets. As such, and given the largely benthic habit of the species, an increase in fish activity (and/or relative abundance) should correlate with an increase in gill netting CPUE. Archival commercial *Platycephalus* spp. CPUE data were collected from the southern and northern (throughout Victoria and Queensland, respectively; Fig. 1C) extremes of their range for the period 2001–2005 from Fisheries Victoria and Queensland Department of Agriculture, Fisheries and Forestry, and summarised as mean monthly catch. Because of government privacy laws, the finest spatial resolution for catch locations was at the scale of State (throughout the coastline of Queensland or Victoria), so there was some uncertainty regarding the local temperatures experienced at the time of capture (e.g. *P. fuscus* are distributed across ~10° of latitude in Queensland, and in both estuaries and coastal habitats in both States). To account for this uncertainty we paired State-wide catch data to two temperature datasets: mean monthly temperatures experienced in estuaries at intermediate latitudes within each state (Lake Tyers, 37.8°S, 148.1°E, for Victoria; and Fitzroy River, 23.5°S, 15.9°E, for Queensland), and mean monthly coastal sea surface temperatures at the latitudinal extremes of the *P. fuscus* distribution (Wilson's Promontory, 38.9°S, 146.3°E for Victoria and Cairns; 16.9°S, 145.7°E for Queensland; http://www.metoc.gov.au). Because of differences in reporting protocols between States (CPUE is reported as tonnes per km of net per day in Victoria and as tonnes per boat per day for Queensland), and the fact that zero-catches are not reported in either state (undermining any estimate of CT_{min} or CT_{max} for catch data), we considered it inappropriate to estimate T_{opt} or CT values for CPUE, and instead examined catch trends visually.

Author contributions
N.L.P. conceived the study, R.G. and N.L.P. performed the experiments, and all authors analysed the data and prepared the manuscript.

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