Journal of Thermal Biology 124 (2024) 103943

Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

How hot is too hot? Thermal tolerance, performance, and preference in juvenile mangrove whiprays, *Urogymnus granulatus*

Emily Higgins[a,b], Ian A. Bouyoucos[a,c,*], Adam T. Downie[a], Björn Illing[a], Ana P.B. Martins[b,d], Colin A. Simpfendorfer[b,d], Jodie L. Rummer[a,d]

[a] *Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, Australia*
[b] *Centre for Sustainable Tropical Fisheries and Aquaculture, James Cook University, Townsville, QLD, Australia*
[c] *PSL Research University, EPHE-UPVD-CNRS, USR 3278 CRIOBE, Université de Perpignan, Perpignan, France*
[d] *College of Science and Engineering, James Cook University, Townsville, QLD, Australia*

ARTICLE INFO

Original content: Data from: Thermal tolerance, performance, and preference in juvenile mangrove whiprays (Original data)

Keywords:
Batoid nursery area
Biologging
Critical thermal maximum
Critical thermal minimum
Elasmobranch
Metabolic rate

ABSTRACT

Mangrove habitats can serve as nursery areas for sharks and rays. Such environments can be thermally dynamic and extreme; yet, the physiological and behavioural mechanisms sharks and rays use to exploit such habitats are understudied. This study aimed to define the thermal niche of juvenile mangrove whiprays, *Urogymnus granulatus*. First, temperature tolerance limits were determined via the critical thermal maximum (CT_{Max}) and minimum (CT_{Min}) of mangrove whiprays at summer acclimation temperatures (28 °C), which were 17.5 °C and 39.9 °C, respectively. Then, maximum and routine oxygen uptake rates ($\dot{M}O_{2max}$ and $\dot{M}O_{2routine}$, respectively), post-exercise oxygen debt, and recovery were estimated at current (28 °C) and heatwave (32 °C) temperatures, revealing moderate temperature sensitivities (i.e., Q_{10}) of 2.4 ($\dot{M}O_{2max}$) and 1.6 ($\dot{M}O_{2routine}$), but opposing effects on post-exercise oxygen uptake. Finally, body temperatures (T_b) of mangrove whiprays were recorded using external temperature loggers, and environmental temperatures (T_e) were recorded using stationary temperature loggers moored in three habitat zones (mangrove, reef flat, and reef crest). As expected, environmental temperatures varied between sites depending on depth. Individual mangrove whiprays presented significantly lower T_b relative to T_e during the hottest times of the day. Electivity analysis showed tagged individuals selected temperatures from 24.0 to 37.0 °C in habitats that ranged from 21.1 to 43.5 °C. These data demonstrate that mangrove whiprays employ thermotaxic behaviours and a thermally insensitive aerobic metabolism to thrive in thermally dynamic and extreme habitats. Tropical nursery areas may, therefore, offer important thermal refugia for young rays. However, these tropical nursery areas could become threatened by mangrove and coral habitat loss, and climate change.

1. Introduction

The optimal functioning and performance of many ectothermic organisms in marine ecosystems are influenced by their external environment (Fry, 1971). Temperature is one of the most widely studied abiotic factors affecting the physiology and behaviour of marine ectotherms; it sets the lethal thresholds of life (McKenzie et al., 2021), governs rates of development (Marshall et al., 2020), limits distribution (Twiname et al., 2020), and affects metabolic processes (Little et al., 2020). Because of the pervasive effect temperature has on the physiology of marine ectotherms, there is interest in describing organisms' thermal niche for understanding species' biogeography and predicting effects of global climate change on species' distributions (e.g., potential shifts to habitat ranges; Collin et al., 2021; Figueira and Booth, 2010; Stuart-Smith et al., 2017).

An organism's thermal niche is defined by characterising its thermal limits, thermal performance, and thermal preference, with thermal limits reflecting the minimum and maximum temperatures under which biological fitness is supported. Thermal limits are commonly investigated at the level of the whole organism by using critical thermal methodology (CTM), which was originally described by Cowles and Bogert (1944) and later adapted for ectotherms, such as fishes (Beitinger et al., 2000; Dabruzzi et al., 2013; Illing et al., 2020) and crustaceans (Ern et al., 2020; Vinagre et al., 2018). Briefly, CTM estimates thermal

---

* Corresponding author. Department of Zoology, University of British Columbia, Vancouver, BC, V6T 1Z4, Canada.
E-mail address: ian.bouyoucos@zoology.ubc.ca (I.A. Bouyoucos).

https://doi.org/10.1016/j.jtherbio.2024.103943
Received 18 January 2024; Received in revised form 1 August 2024; Accepted 3 August 2024

tolerance by exposing an organism to a constant rate of temperature change that is slow enough to track body temperature, but fast enough to prevent thermal acclimation during experimental trials (Lutterschmidt and Hutchison, 1997). Temperature change proceeds until a predefined, repeatable, sub-lethal upper (critical thermal maximum, CT_{Max}) or lower (critical thermal minimum, CT_{Min}) endpoint is reached (Morgan et al., 2018). CTM is often implemented alongside estimates of metabolic rate, because metabolic rate is an informative temperature sensitive performance trait that represents the sum of aerobic energy expenditure (Clark et al., 2013). The thermal sensitivity of these performance traits – or the biological rates underpinning them – can be characterised using a thermal coefficient (Q_{10}) that, in fishes, is generally assumed to fall between 2 and 3 for metabolism (Watanabe and Payne, 2023). Values outside of this range are thought to represent physiological processes like acclimation (Sandblom et al., 2014) or metabolic depression (Speers-Roesch et al., 2018). Using CTM in conjunction with defining thermal performance of metabolic rate can be useful for predicting an organism's preferred temperatures, as the temperature range where aerobic scope (i.e., the capacity to elevate metabolic rate above homeostatic maintenance) is maximised (Christensen et al., 2021b; Norin et al., 2014).

An organism's thermal preference is indicative of its thermal niche, defined as the range of temperatures within which it can optimally perform and survive. Conventionally, thermal preference of marine organisms is determined via laboratory studies using a shuttle-box system (Christensen et al., 2021a). Such systems are ideal for small-bodied, active organisms (e.g., coral reef fishes; Nay et al., 2015), but are scalable to accommodate larger organisms (e.g., small-bodied sharks; Nay et al., 2021). For even larger-bodied species, thermal preference is characterised from temperature loggers deployed on wild animals (e.g., Bouyoucos et al., 2020), where logged temperatures are often used as proxies for body temperatures (Gleiss et al., 2019; Hight and Lowe, 2007). Temperature loggers are also deployed in the environment to characterise habitat temperatures for reference against body temperatures (e.g., Bouyoucos et al., 2020; Dubois et al., 2009; Nay et al., 2021). Together, logged body and habitat temperatures allow researchers to characterise an organism's realised thermal niche (i.e., the range of temperatures experienced by the animal) and preferred temperatures based on analysis techniques such as electivity analysis (Huey, 1991).

Sharks and rays (i.e., chondrichthyans) comprise a group of large-bodied, mobile animals, whose thermal niches have largely been characterised using temperature loggers deployed on wild animals (e.g., Andrzejaczek et al., 2018; Papastamatiou et al., 2015; Speed et al., 2012). Studies examining shark and ray movement have shown that water temperature is highly correlated with movements of individually tracked animals (Andrzejaczek et al., 2019; Schlaff et al., 2014). For example, female leopard sharks, *Triakis semifasciata*, select different water temperatures throughout the day to increase core body temperature and potentially metabolic rate (Hight and Lowe, 2007; Miklos et al., 2003). Similarly, female round stingrays, *Urobatis halleri*, inhabit warm, shallow habitats during gestation, suggesting they may utilise specific habitats for reproductive success (Jirik and Lowe, 2012). Further, tiger sharks, *Galeocerdo cuvier*, have demonstrated shifts in their abundance associated with climate change-driven ocean warming (Hammerschlag et al., 2022; Niella et al., 2021; Payne et al., 2018). Whilst investigating shark and ray thermal niches using telemetry devices (e.g., temperature loggers) alone provides a wealth of information, descriptive data regarding thermal limits of performance are often absent (Santos et al., 2021), largely due to the inaccessibility of large-bodied animals for laboratory-based physiology experiments (Lawson et al., 2019). Indeed, there is a growing body of research on the thermal niche (i.e., limits, performance, and preference) of juvenile sharks (e.g., Crear et al., 2020; Lear et al., 2019); however, relative to sharks, there is a conspicuous knowledge gap concerning thermal niches of rays (Dabruzzi et al., 2013).

Relative to sharks, the biology and ecology of rays is considerably less well studied (Flowers et al., 2021). Rays are the most diverse taxonomic group of chondrichthyans (Last et al., 2016), as well as one of the most threatened groups, where proportionally more rays are threatened than sharks (31 % vs 36 % of all sharks and rays, respectively; Dulvy et al., 2021). In general, rays are thought to play important roles in ecosystems not only as mesopredators (Flowers et al., 2021; Sherman et al., 2020), but in affecting biogeochemical processes in the benthos via bioturbation (O'Shea et al., 2012). Like sharks, rays' life histories are characterised by late ages at maturation and low fecundity (Frisk et al., 2001), which underscores rays' vulnerability to extinction through exploitation and habitat loss (Stevens et al., 2000). Of all sharks and rays, coral reef associated species are among the most threatened (47 % and 57 % of coral reef sharks and rays, respectively). Overfishing is the main anthropogenic threat to coral reef sharks and rays; however, water temperature was also found to have a strong association with extinction risk in coral reef sharks and rays (Sherman et al., 2023).

Nursery areas are important habitats for young rays (Martins et al., 2018). In general, nursery areas for fishes and invertebrates are hypothesised to increase the recruitment of reproducing adults to a population (Beck et al., 2001). Whilst relatively more is understood about nursery areas for sharks than for rays (Heupel et al., 2019), nursery areas for ray species are increasingly being identified. As is the case for sharks, nursery areas for rays are habitats with proportionally high neonate and juvenile abundance that is stable over time, where young individuals remain for extended periods (Heupel et al., 2007; Martins et al., 2018). Because a large number of ray species lay eggs (Wheeler et al., 2020), nursery areas for rays are also defined as habitats with proportionally high egg abundance, where the habitat is used repeatedly across time and newly hatched rays leave the area (Martins et al., 2018). Studies to date (*c.* 2023) have demonstrated the importance of mangrove habitats as nursery areas for coral reef associated rays (Kanno et al., 2023). A potential constraint on tropical nursery areas is the dynamic and often extreme temperatures associated with mangrove habitats (Kanno et al., 2023); however, selecting for thermally extreme habitats may benefit young rays by accelerating physiological processes associated with growth and excluding less thermally tolerant predators (Davy et al., 2015; Martins et al., 2018).

The present study examines the thermal performance and behaviour of juveniles of a coral reef associated ray, the mangrove whipray, *Urogymnus granulatus*, in a highly thermally variable nearshore nursery area at Orpheus Island, Australia. Specifically, this study aimed to: 1) determine the upper and lower thermal thresholds for juvenile mangrove whiprays; 2) estimate metabolic rates from measured oxygen uptake rates at current-day mean (28 °C) and predicted heatwave (32 °C) temperatures to assess the effects of elevated temperatures on performance; and 3) determine the temperature preferences of juvenile mangrove whiprays in the wild. Limited studies on tropical sharks and rays in nursery areas suggest that juveniles must reflect traits of hyperthermic specialists to exploit tropical mangrove habitats (Bouyoucos et al., 2022; Dabruzzi et al., 2013; Lear et al., 2019). Therefore, mangrove whiprays were predicted to exhibit characteristics of hyperthermic specialists, possessing high thermal limits, a metabolic rate with low sensitivity to temperature changes, and a preference for warmer temperatures in order to exploit a thermally variable habitat as a nursery area. Together, these data offer insight into the role that nursery areas may play as thermal refugia for juvenile rays. Further defining the thermal niche of tropical rays can also provide context for understanding the risks that climate change and ocean warming pose for young rays in nursery areas.

2. Material and methods

2.1. Study site and species

Orpheus Island (18°37′S, 146°30′E) is one of four main islands constituting the Palm Island Group in the central Great Barrier Reef

(GBR) in Australia (Fig. 1). It is located 17 km off the coast of northern Queensland. The island is bordered by a fringing coral reef and comprises several bays containing coral rubble and sandy intertidal flats. These bays support stands of non-estuarine mangroves (*Rhizophora* spp.) and are subject to ~4 m tidal ranges with some flats completely exposed during extremely low tides. The mangrove stands occupy a combination of sandy and rocky substrates and are inundated at tidal heights above 1.8 m.

Urogymnus granulatus is a small-bodied whipray distributed throughout the Indo-Pacific. Around Orpheus Island, juvenile mangrove whiprays occur in Pioneer Bay (Fig. 1), using the bay as a nursery area (Davy et al., 2015; Martins et al., 2018). Within Pioneer Bay, juvenile mangrove whiprays tend to remain in shallow water, where movement is tidally driven (Davy et al., 2015; Kanno et al., 2019; Martins et al., 2021). Mangrove whiprays show a strong reliance on mangrove stands for evading predators (Davy et al., 2015; Kanno et al., 2019). Furthermore, it has been hypothesised that juvenile mangrove whiprays utilise high temperature habitats like mangrove stands as thermal refugia, which may offer physiological benefits like increased digestive performance and growth (Davy et al., 2015), or general survival benefits like exclusion of less thermally tolerant predators (Martins et al., 2018).

2.2. *Animal capture and handling*

Juvenile mangrove whiprays were captured in Pioneer Bay, Orpheus Island (Fig. 1), during the peak austral summer months (February to March) in 2018. A 10 m monofilament seine net (2 × 2 cm mesh) and hand-held landing nets were used for capture. Upon capture, disc width was measured (DW; to nearest cm), and individuals were sexed and tagged through the spiracle with an identification tag (Self-locking loop tags, Hallprint, Hindmarsh Valley, South Australia). Male mangrove whiprays were classified as mature or immature depending on the degree of clasper calcification, and females were classified as immature if they were smaller than 50 cm DW (Last et al., 2016). Handling time did not exceed 10 min, and all mangrove whiprays captured were used either for laboratory experiments or field studies, but not for both.

2.3. *Laboratory experiments*

A total of 12 juvenile mangrove whiprays (4 males, 8 females; 30–35 cm DW) were captured and transported in seawater-filled containers from the capture site to holding tanks at the Orpheus Island Research Station (OIRS) in Pioneer Bay. Mangrove whiprays were maintained in flow-through holding tanks that were partially shaded, maintained under a natural photoperiod, and continually aerated. While in captivity, whiprays were fed daily to satiation with defrosted, commercially available school prawns (*Metapenaeus bennettae*).

2.3.1. *Critical thermal limits*

Summer thermal tolerance limits for juvenile mangrove whiprays were determined using critical thermal methodology (CTM) with approaches similar to previous studies on rays (Dabruzzi et al., 2013; Fangue and Bennett, 2003). First, mangrove whiprays were habituated to holding conditions (i.e., 28 °C, 35 ppt salinity, natural photoperiod) for two weeks prior to experimentation and then randomly selected for either a CT_{Max} ($n = 6$) or CT_{Min} ($n = 6$) experiment. Individual mangrove whiprays were only tested for one CTM. For each CTM, a mangrove whipray was placed into a black round tank (110 × 40 cm) for a 1-h habituation period. The experimental tank was connected to an external seawater bath (110 × 60 cm) that could be heated (using a 3 KM submersible seawater heater) or chilled (using three Hailea, HC Series Chillers, 1/15 horsepower) from a starting temperature of 28 °C at a rate of 0.07 ± 0.01 °C min^{-1}. Water temperature change continued until muscle spasms (MS) occurred or until spiracle contraction cessation (SCC) of more than 1 min, at which point the individual was inverted to test for loss of equilibrium (LOE). This process ensured a repeatable, non-lethal endpoint at high and low temperatures (Dabruzzi et al., 2013; Fangue and Bennett, 2003). Importantly, preliminary tests demonstrated that MS and SCC occurred at the same temperature. Following each trial, mangrove whiprays were returned to pre-experiment temperatures to recover. For each mangrove whipray, CT_{Max} and CT_{Min} were defined as the temperature at which LOE occurred.

2.3.2. *Respirometry*

Maximum metabolic rates (MMR; the upper limit of aerobic metabolism estimated via oxygen uptake), routine metabolic rates (RMR; the average metabolic rate), and excess post-exercise oxygen consumption (EPOC; elevated oxygen uptake during recovery from exercise) were estimated to define the sensitivity of whole-organism performance in mangrove whiprays. The same individuals that were used to estimate CT_{Max} and CT_{Min} were used to estimate metabolic rates after at least two weeks of recovery. After this recovery period, five mangrove whiprays were acclimated to 28 °C (average summer water temperature), and another five were acclimated to 32 °C (predicted summer heatwave

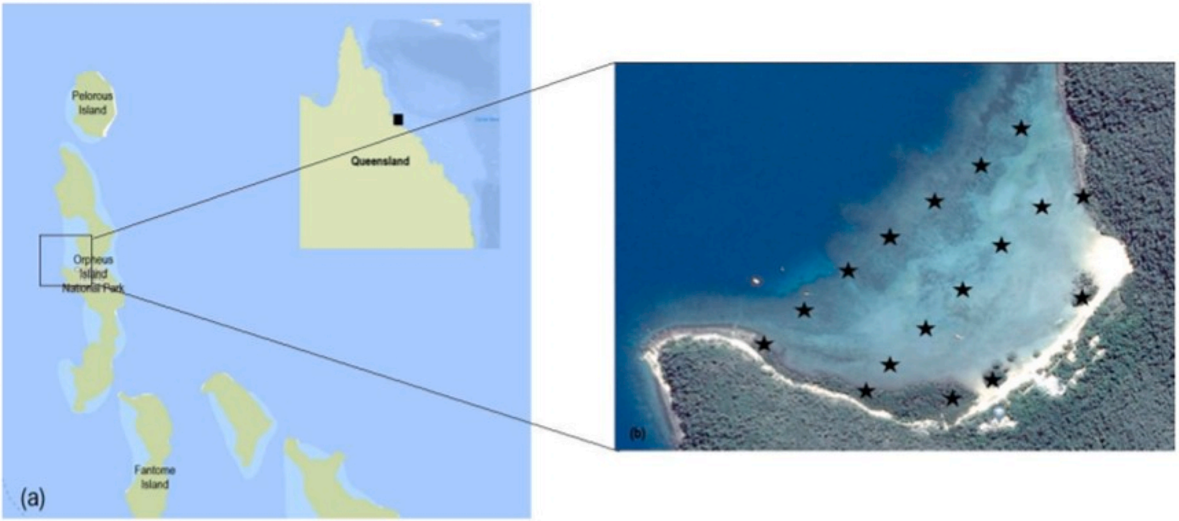

Fig. 1. Map of the study site at Orpheus Island located in the Palm Island group in the Great Barrier Reef World Heritage Area (QLD). Pioneer Bay is shown in the inset figure, with stars representing locations of HOBO temperature data-loggers (adapted from Davy et al., 2015 and George et al., 2019).

temperature). Acclimation to elevated temperatures consisted of a daily temperature increase of 1 °C, until the appropriate treatment temperature (32 °C) was reached (Dabruzzi et al., 2013). Mangrove whiprays were then maintained at acclimation temperatures for an additional 14 d prior to undergoing respirometry experiments.

Standard, whole-tank respirometry techniques (*sensu* Crear et al., 2019) were used to measure maximum oxygen uptake rate ($\dot{M}O_{2max}$) as an estimate of MMR and routine oxygen uptake rate ($\dot{M}O_{2routine}$) as an estimate of RMR. Because mangrove whiprays are a predominantly benthic fish, an exhaustive exercise protocol using a standard chasing duration was assumed to be most ecologically relevant (Rees et al., 2024). For each trial, an individual mangrove whipray was chased continuously for 3 min, using a fibreglass rod to initiate movement if the individual decreased their activity level. Individuals were then held out of water for 1 min using a hand-held landing net to achieve $\dot{M}O_{2max}$ (Clark et al., 2012). Individual mangrove whiprays were then placed into a circular respirometer constructed from a modified 400 L tank with a polypropylene vinyl acetate (EVA) sheet stretched across the water surface and taped to the side of the tank (Byrnes et al., 2020), resulting in a respirometer with a total volume of 75 L. Dissolved oxygen (DO) levels were measured using fibre optic oxygen sensor dipping probes (Firesting, PyroScience, Germany), which were fitted inside the respirometry tank and set to take readings every 5 s. Before any mangrove whiprays were introduced to the chambers all oxygen probes were calibrated to 100% air saturation by placing the probe in a constantly aerated beaker of seawater. Similarly, oxygen probes were calibrated to 0% using an anhydrous sodium sulphite solution (Sigma, Germany). To ensure even water mixing in the respirometry tank, a recirculation pump (600 L h^{-1}) was set up inside the tank alongside an outflow pump to allow water to flow out of the tank during flush cycles. A one-way valve was fitted to the area of the flush pump circuit entering each chamber to prevent water from siphoning from the respirometry tank back into the reservoir tank during measurement cycles. Each respirometry tank was connected to an aerated 300 L seawater filled reservoir that maintained water temperature, air saturation, and the flow through of clean seawater into the respirometry tanks.

Oxygen uptake rate ($\dot{M}O_2$) measurement periods commenced within 10 s of placing the mangrove whiprays into the respirometer and consisted of 10 min to measure a decline in oxygen followed by a 20 min flush period. The measurement period of 10 min was short enough to ensure that oxygen within the chambers always remained above 70% air saturation. This is important to ensure that oxygen uptake rates do not become dependent on ambient oxygen (Rummer et al., 2016). Each trial lasted 5 h, yielding 10 $\dot{M}O_2$ measurements. At the end of each trial, mangrove whiprays were removed from their respirometers and returned to their holding tanks. A blank respirometry trial was run for 1 h before and after each trial to measure background respiration (Rodgers et al., 2016).

Oxygen data recorded during respirometry trials were analysed using the program LabChart (AD Instruments, 2017). $\dot{M}O_{2Max}$ (in mg O_2 kg^{-1} h^{-1}) was calculated from the steepest slope (mg O_2 h^{-1}) with an $R^2 > 0.95$ calculated over successive 30-s bins during the first 10-min measurement, multiplied by the respirometer volume and divided by animal mass (Bouyoucos et al., 2018). $\dot{M}O_{2routine}$ was calculated as the average of all $\dot{M}O_2$ values calculated over each 10-min measurement (with an $R^2 > 0.95$) during the entire trial (Killen et al., 2021). All values were corrected for non-whipray respiration by subtracting the trial background respiration from the total. All animals were released to Pioneer Bay following respirometry experiments.

2.4. *Field experiments*

2.4.1. *Characterisation of Pioneer Bay temperature regime*

To investigate the temperature regime across the mangrove whiprays' habitat, a survey of Pioneer Bay was conducted for the entire month of February 2018. Seventeen HOBO temperature loggers (UA-002-64, Onset HOBO Data Loggers, Adelaide, Australia) were deployed in Pioneer Bay across the reef crest, reef flat, and mangrove stands (Fig. 1). These loggers were positioned 100 m apart or within habitats known to be utilised by mangrove whiprays (Davy et al., 2015) and secured onto mangrove prop roots or coral heads using cable ties. Temperature was recorded every 5 min at a resolution of ±0.5 °C. Temperature data generated from the loggers were then used to determine the diel and tide related temperature fluctuations across three habitat zones. Thirteen HOBO temperature loggers were retrieved from the bay at the end of this study (Fig. 1). Four loggers were lost due to flooding or uprooting during storms. Temperature readings were only used during times when the loggers were submerged during tidal movements, as determined by tidal data collected during the duration of deployment.

2.4.2. *Characterisation of whipray body temperatures*

Water temperatures encountered by captured mangrove whiprays were monitored by external iButton® temperature loggers (DS 1922L, Enviroworld Technologies, Bayswater, Victoria, Australia). These loggers were waterproofed using heat shrink tubing secured to a backing plate that was attached to the mangrove whiprays' spiracle tag using a small cable tie (Fig. 2). Fourteen juvenile mangrove whiprays between 29 and 45 cm DW were captured during the study period. Temperature loggers were small (4 cm length and 0.5 cm height, ~3 g in air). Assuming that a mangrove whipray's submerged weight is ~4% of its mass (Baldridge, 1970; Lear et al., 2018) a 3 g tag package would account for less than 3% of an animal's apparent submerged weight. Loggers recorded temperature (±0.5 °C) at 10 min intervals, and data were logged for a minimum of 14 d prior to mangrove whipray recapture and tag removal. Tagging procedures did not exceed 10 min in duration, and once tag attachment was complete, mangrove whiprays were released within 10 m of their capture location.

2.5. *Statistical analyses*

All data were analysed using the statistical program R (R Core Team, 2024). Analyses were conducted using the base R stats package, *nlme* (Pinheiro et al., 2024), and *emmeans* (Lenth, 2024). Statistical significance was determined using type I error rate of 0.05.

2.5.1. *Laboratory experiments*

Welch's *t*-tests were used to compare oxygen uptake rate estimates (i.e., $\dot{M}O_{2max}$ or $\dot{M}O_{2routine}$) between 28 °C and 32 °C. Temperature effects were further quantified by calculating Q_{10} for $\dot{M}O_{2max}$ and $\dot{M}O_{2routine}$ using the following formula:

Fig. 2. A juvenile mangrove whipray, *Urogymnus granulatus*, with an external temperature data-logger attached to a spiracle tag.

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\frac{10^{\circ}C}{T_2 - T_1}}$$

where R_1 and R_2 represent $\dot{M}O_2$ measured at temperatures, T_1 and T_2, respectively. Next, excess-post-exercise oxygen consumption (EPOC) was estimated by fitting a polynomial curve to an individual ray's $\dot{M}O_2$ over time. Curves were fit following:

$$\dot{M}O_2 = a \bullet e^{time \bullet b}$$

where a and b are coefficients. After fitting curves, EPOC was calculated by integrating the area under each curve and subtracting each individual's $\dot{M}O_{2routine}$. Recovery time was estimated at the intersection of each mangrove whipray's curve and $\dot{M}O_{2routine}$. Then, EPOC and recovery time were compared between 28 °C and 32 °C using Welch's *t*-tests.

2.5.2. Field experiments

First, habitat temperature profiles were compared between mangrove, reef crest, and reef flat habitat using Kolmogorov-Smirnov tests. Next, linear mixed effects models were used to test for differences between habitat (i.e., HOBO logger data) temperatures and mangrove whipray (i.e., iButton logger data) temperatures. The natural logarithm of hourly mean temperature was fit with time of day (in 6-h bins, i.e., 00:00–06:00, 06:00–12:00, 12:00–18:00, 18:00–24:00) and logger type (i.e., habitat or mangrove whipray) as interacting fixed effects with logger ID as a random effect. From previous tracking studies of mangrove whiprays in Pioneer Bay (Davy et al., 2015; Martins et al., 2021), mangrove whiprays use mangrove habitats at > 200 cm tidal height, the reef flat between 100 cm and 200 cm, and the reef crest when tide was <100 cm. Temperature data from loggers within each habitat type (i.e., mangrove, reef flat, or reef crest) and from mangrove whiprays were filtered based on tidal height so that water temperatures within each habitat could be compared to mangrove whipray temperatures when animals were assumed to use each habitat. In summary, three linear mixed effects models were run to test for differences between habitat and mangrove whipray temperatures (i.e., one per habitat). These analyses allowed us to assess whether mangrove whiprays were selecting specific temperature ranges at certain periods of the day.

To examine the proportion of time mangrove whiprays spent at different temperatures, frequency plots of temperatures were constructed using 1.0 °C intervals. Ivlev's (1961) electivity index (*E*) was used to investigate the affinity for specific temperatures within Pioneer Bay:

$$E = r_i - p_i / r_i p_i$$

where r_i is the proportion of time an individual spent in temperature i and p_i is the proportion of temperature i available in the bay. The value of E can range from −1 (indicating full avoidance) to 1 (indicating full affinity), with a value of zero indicating no affinity or avoidance (Wiley and Simpfendorfer, 2007). Electivity analysis was performed for each 6-h time bin within each habitat at the appropriate tidal height, as described above. All recaptured individuals were used within the analysis and combined to fit a single data set.

3. Results

3.1. Critical thermal limits

Critical thermal limits of juvenile whiprays revealed a relatively wide thermal niche for summer temperatures. The range of temperatures tolerated by juvenile mangrove whiprays, estimated from the upper and lower thermal tolerance limits, was 17.5 ± 0.1 °C to 39.9 ± 0.1 °C, resulting in a thermal tolerance scope of 22.4 ± 0.1 °C (Table 1; data are means ± standard deviation).

Table 1

Critical thermal limits, identification number, disc width, and wet mass for juvenile mangrove whiprays, *Urogymnus granulatus,* acclimated to summer temperatures (~28 °C). Means ± standard deviations are presented in bold. Abbreviations: Critical thermal maximum, CT_{Max}; Critical thermal minimum, CT_{Min}.

	Animal ID	Disc width (cm)	Wet mass (kg)	Critical thermal limit (°C)
CT_{Min}	131	32	2.5	17.2
	128	33	3.5	18.2
	127	33	2.5	17.4
	132	31	2.0	17.1
	133	30	2.5	17.3
	134	35	2.8	17.6
		32.3 ± 1.8	**2.6 ± 0.5**	**17.5 ± 0.4**
CT_{Max}	121	31	2.1	40.5
	123	32	2.1	40.5
	64	31	2.0	39.6
	122	32	2.2	38.8
	130	32	3.0	40.1
	135	34	2.3	38.5
		32.0 ± 1.1	**2.3 ± 0.4**	**39.7 ± 0.9**

3.2. Respirometry

There were no strong effects of temperature acclimation on oxygen uptake rates (Fig. 3). $\dot{M}O_{2routine}$ was not significantly different (Welch's *t*-test, $t = 1.72$, DF = 4.87, $p = 0.148$) between 28 °C ($\dot{M}O_{2routine} = 87.4 \pm 17.6$ mg O_2 kg^{-1} h^{-1}) and 32 °C (73.2 ± 5.8 mg O_2 kg^{-1} h^{-1}), as corroborated by a Q_{10} value near 1 ($Q_{10} = 1.6$). Similarly, $\dot{M}O_{2max}$ was not significantly different ($t = 1.26$, DF = 7.99, $p = 0.244$) between 28 °C ($\dot{M}O_{2max} = 524.2 \pm 201.5$ mg O_2 kg^{-1} h^{-1}) and 32 °C (366.5 ± 195.0 mg O_2 kg^{-1} h^{-1}) and had a Q_{10} of 2.4. Excess post-exercise oxygen consumption was significantly lower ($t = -3.31$, DF = 6.61, $p = 0.014$) at 28 °C (EPOC = 20.4 ± 7.5 mg O_2 kg^{-1}) compared to 32 °C (33.4 ± 4.5 mg O_2 kg^{-1}). Conversely, recovery time significantly ($t = 2.76$, DF = 4.21, $p = 0.049$) differed between 28 °C (2.75 ± 0.1 h) and 32 °C (2.6 ± 0.01), where rays recovered faster at 32 °C, despite having higher EPOC.

3.3. Habitat temperature profile

Water temperatures in Pioneer Bay were collected between 4 and 26 February 2018. Diel variations in temperature ranged from as little as 5.5 °C to as much as 21.3 °C for individual temperature loggers. Mean water temperatures varied between habitats, with the reef flat and mangroves experiencing the highest temperatures during mid-afternoon (Fig. 4). Hour of day affected the temperature across all habitats, with highest temperatures recorded during late afternoon and lowest during the night. Within the mangroves, highest hourly temperatures recorded during high tide were 41.6 °C with a low of 21.1 °C and average of 29.1 °C (Fig. 4A). Across the reef flat, the highest recorded temperatures were 43.5 °C during low to moderate tide periods with a low of 22.3 °C and an average of 29.3 °C (Fig. 4B). On the reef crest the highest recorded temperatures were 32.5 °C and lowest being 23.9 °C with an average of 28.5 °C. (Fig. 4C). Kolmogorov-Smirnov tests revealed significant differences in temperature distributions between habitats (mangrove vs. reef flat: $D = 0.271$; mangrove vs. reef crest, $D = 0.309$; reef flat vs. reef crest, $D = 0.056$; all $p < 0.001$).

3.4. Temperature influences on juvenile whiprays

Mean water temperatures experienced by juvenile mangrove whiprays during 2 weeks at liberty in this study ranged between 28 °C and 30 °C (Fig. 5). Of 14 tagged individuals, temperature loggers were recovered from seven during the study. Some individuals were recorded

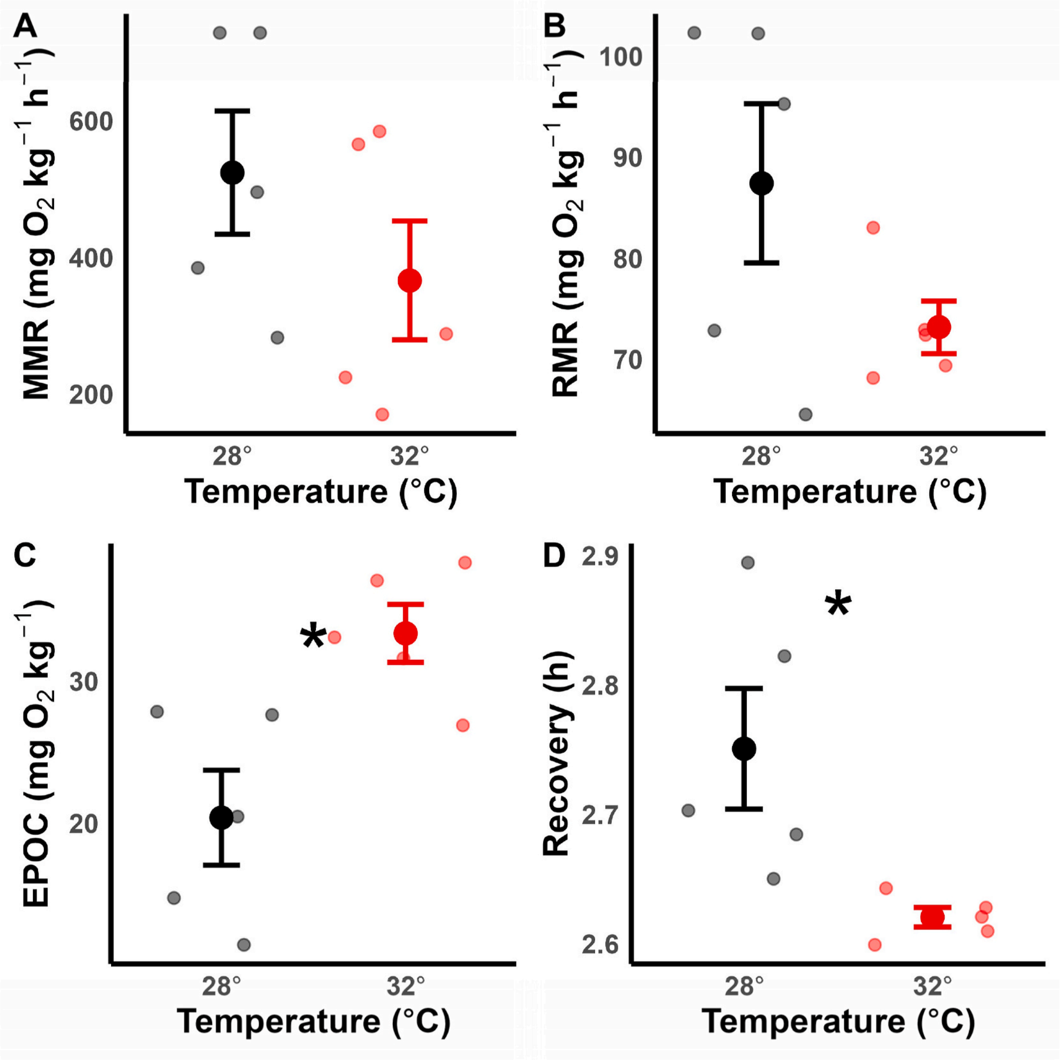

Fig. 3. Oxygen uptake rates of juvenile mangrove whiprays, *Urogymnus granulatus,* at 28 °C and 32 °C. Maximum metabolic rate (MMR; A) estimated as maximum oxygen uptake rate, routine metabolic rate (RMR; B) estimates as routine oxygen uptake rate, excess post-exercise oxygen uptake (EPOC; C), and recovery time (D) were calculated during 5 h of respirometry following a 3-min chase and 1-min bought of air exposure. Data are presented as means ± standard error, with individual observations representing data from individual whiprays. Asterisks denote statistically significant differences ($p < 0.05$) between 28 °C and 32 °C.

occurring in temperatures as warm as 38 °C for short periods of time (Fig. 5); however, this was not a usual occurrence. The lowest recorded temperature by an individual was 23.6 °C. Frequency plots showed that individuals remained at temperatures between 29 °C and 30 °C for, on average, 5.5 h (Fig. 5).

Within mangrove habitat (Figs. 5A and 6A), there was a significant interaction between logger type and hour bin (linear mixed effects model, $F_{3,\ 50{,}606} = 956.9$, $p < 0.001$). Mangrove whiprays were significantly warmer than mangrove habitat from 18:00–24:00 (*emmeans* pairwise comparison, $p < 0.001$) and 00:00 to 06:00 ($p < 0.001$). Conversely, mangrove whiprays were cooler than mangrove habitat during 12:00–18:00 ($p = 0.012$) but did not differ from environmental temperatures during 06:00–12:00 ($p = 0.810$).

Within reef flat habitat (Figs. 5B and 6B), there was a significant interaction between logger type and hour bin (linear mixed effects model, $F_{3,\ 20{,}801} = 568.1$, $p < 0.001$). Mangrove whiprays were cooler than the environment from 00:00–06:00 (*emmeans* pairwise comparison, $p = 0.041$) and 06:00–12:00 ($p = 0.016$). Conversely, mangrove whiprays were warmer than reef flat habitat between 12:00–18:00 ($p < 0.001$) and did not differ in temperature between 18:00–24:00 ($p = 0.666$).

Based on tidal height, mangrove whiprays were not predicted to occupy the reef crest between 06:00–18:00 (Figs. 5C and 6C). There was a significant interaction between logger type and hour bin in reef crest habitat (linear mixed effects model, $F_{1,\ 9041} = 9.0$, $p = 0.002$). Mangrove whiprays were warmer than available reef crest habitat between 00:00–06:00 (*emmeans* pairwise comparison, $p < 0.001$) and cooler than available habitat between 18:00–24:00 ($p = 0.035$).

3.5. Electivity analysis

The temperature of Pioneer Bay throughout the duration of the sampling time ranged from 21.1 to 43.5 °C. Temperature electivity patterns showed distinct affinities at different times of day within each habitat (Fig. 7). Relative to mangrove habitat, mangrove whiprays showed positive electivity at 27–31 °C between 00:00–06:00, 28–30 °C between 06:00–12:00, 29–32 °C between 12:00–18:00, and 30–35 °C between 18:00–24:00 (Fig. 7A). Within reef flat habitat, mangrove whiprays showed positive electivity at 25–28 °C between 00:00–06:00 (Fig. 7B). Interestingly, mangrove whiprays exhibited positive electivity at 24–28 °C and 31–36 °C but showed negative electivity at 29–30 °C between 06:00–12:00. Similarly, mangrove whiprays showed positive electivity at 27–28 °C and 32–37 °C but showed negative electivity at 29–31 °C between 12:00–18:00. Further, between 18:00–24:00

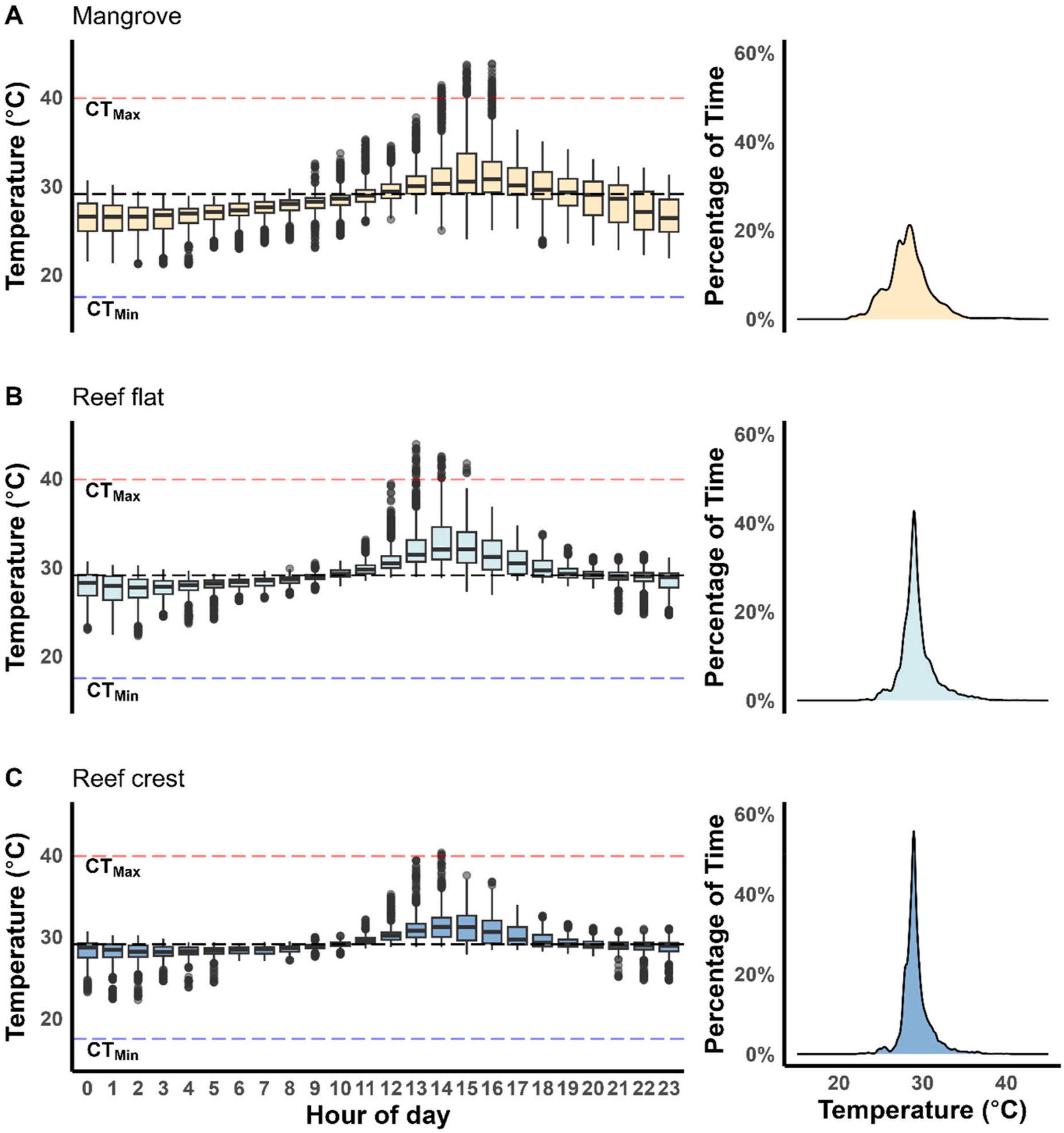

Fig. 4. Hourly temperatures across each habitat, demonstrating the variability between environments (a) mangrove habitat, (b) reef crest habitat, (c) reef flat habitat. In lefthand panels, box plots are delimited by 25%, 50%, and 75% percentiles. Lines represent 1.5 times the interquartile range (IQR) and points represent individual observations exceeding 1.5·IQR. Dashed lines represent the average critical thermal maximum (CT_{Max}; red), body temperature (black), and critical thermal minimum (CT_{Min}; blue) of juvenile mangrove whiprays, *Urogymnus granulatus*, found within Pioneer Bay. Density plots of temperatures within habitat types are presented in righthand panels. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

mangrove whiprays showed positive electivity at 26–28 °C and 30–35 °C but showed negative electivity at 29 °C. Finally, in the reef crest, mangrove whiprays exhibited positive electivity at 28 °C between 18:00–24:00 and at 28–30 °C between 00:00–06:00 (Fig. 7C).

4. Discussion

The purpose of this study was to define the thermal niche of juvenile mangrove whiprays to better understand patterns of habitat use in a thermally and tidally dynamic environment. Results from this study demonstrate that mangrove whiprays possess high critical thermal thresholds for summer conditions, but narrow thermal safety margins, which reflects the high temperatures they experience during peak summer periods in the shallow reef habitats in which they occur (Davy et al., 2015; Kanno et al., 2019; Martins et al., 2020). Further, estimates of metabolic rates were not strongly affected by short-term temperature acclimation, which may be an adaptive response among juvenile sharks and rays to seek refuge in tropical nursery areas (Bouyoucos et al., 2022; Dabruzzi et al., 2013; Lear et al., 2019). Finally, mangrove whiprays exhibited signs of thermotaxic behaviour, as demonstrated by unique temperature preference within different habitats in Pioneer Bay. Together, these data demonstrate that juvenile mangrove whiprays are hyperthermic specialists and follow the tide not only for potential refuge from predators, but also for refuge from unfavourable water temperatures, as has been suggested in other sharks (e.g., Hight and Lowe, 2007; Papastamatiou et al., 2015). However, mangrove whiprays appear capable of tolerating extreme temperatures within Pioneer Bay (e.g., T_b approaching 38 °C), which suggests that mangrove whiprays may also

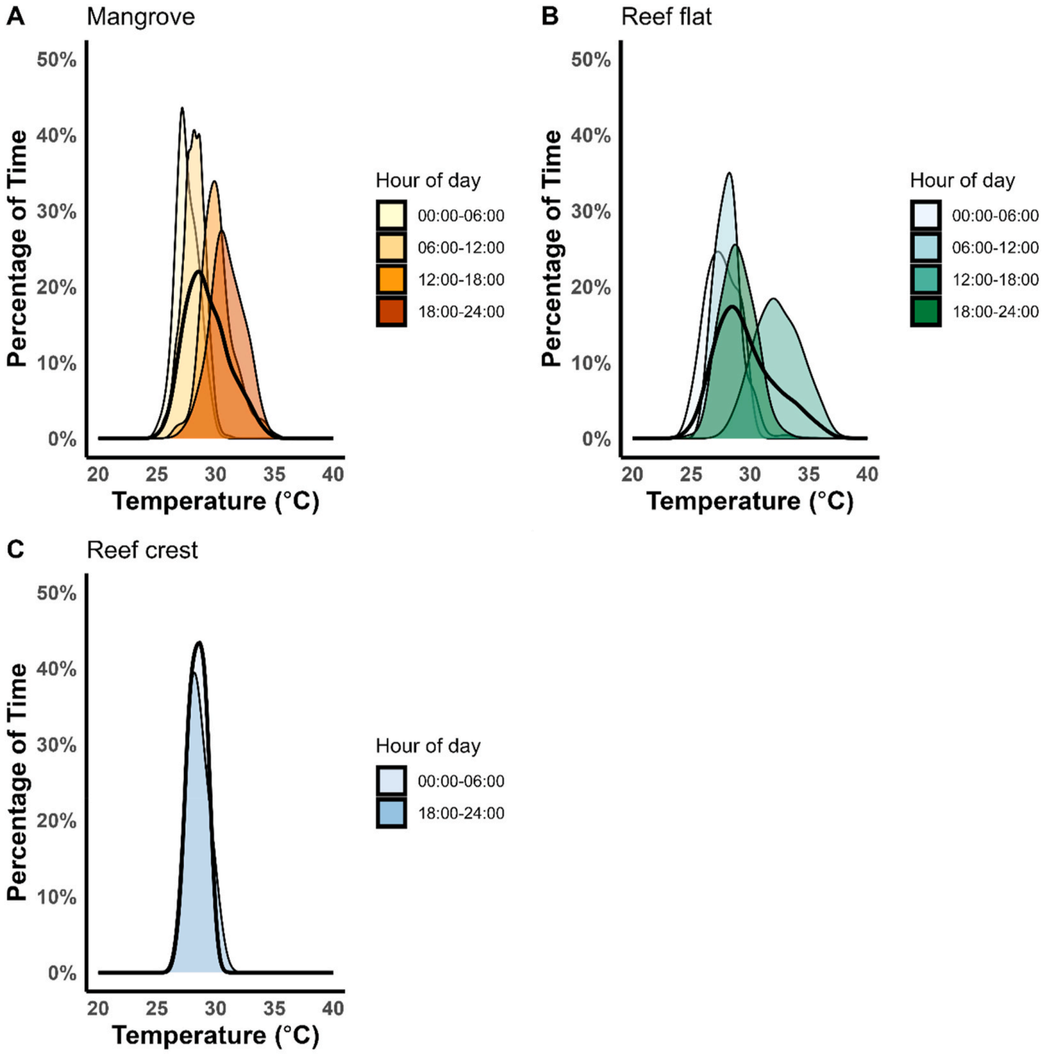

Fig. 5. Percentage of time tagged juvenile mangrove whiprays, *Urogymnus granulatus*, spent at different temperatures in three habitats within Pioneer Bay. Coloured shading denotes 6-h time bins during tagged deployments. The thick black line represents the summed distribution across all time bins. Distributions represent data recorded from seven individual mangrove whiprays.

tolerate unfavourable temperatures that may exclude potential predators (Martins et al., 2018).

Mangrove whiprays exhibited upper thermal limits comparable to other ray species acclimated to similar conditions. Relative to juvenile bluespotted ribbontail rays, *Taeniura lymma*, acclimated to 27.2 °C (Dabruzzi et al., 2013), juvenile mangrove whiprays acclimated to 28 °C had a higher CT_{Min} (12.1 °C vs. 17.5 °C, respectively) and comparable CT_{Max} (40.4 °C vs. 39.9 °C, respectively). Adult Atlantic stingrays, *Hypanus sabinus*, acclimated to 20.5 °C or 35.1 °C had CT_{Min} of 4.8 °C and 10.8 °C, respectively, and CT_{Max} of 39.2 °C and 43.2 °C, respectively (Fangue and Bennett, 2003). Marginally higher CT_{Max} estimates in previous studies relative to the current study on mangrove whiprays may be the result of faster heating rates ($\sim$0.3 °C min^{-1}) used for *T. lymma* and *H. sabinus* (Dabruzzi et al., 2013; Fangue and Bennett, 2003), which have been shown to produce higher CT_{Max} estimates (Illing et al., 2020). Differences in CT_{Min} between these species could stem from several potential reasons. For example, the lower acclimation temperatures used for *T. lymma* and *H. sabinus* should produce lower CT_{Min} estimates. Another possible explanation may be the differences in cooling rates. Thus, the potentially relatively poor cold tolerance of mangrove whiprays requires further examination.

Metabolic rate estimates showed a moderate sensitivity to temperature. Routine and maximum oxygen uptake rates exhibited Q_{10} values of 1.6 and 2.4 that are likely indicative of passive thermodynamic effects on metabolic rate rather than active metabolic compensation (Havird et al., 2020). Similarly, neonatal blacktip reef sharks (*Carcharhinus melanopterus*) from a population exhibiting characteristics of hyperthermic specialists demonstrated moderate-to-low thermal sensitivity (i.e., $Q_{10} < 2$) of standard, routine, and maximum oxygen uptake rates, both over acute (i.e., hours) and longer-term (i.e., weeks) periods (Bouyoucos et al., 2020, 2022). Conversely, juvenile *T. lymma* exhibited relatively high thermal sensitivity of routine oxygen uptake rates ($Q_{10} = 3.48$) following acute temperature change (Dabruzzi et al., 2013); whereas, *H. sabinus* exhibited moderate thermal sensitivity ($Q_{10} = 2.10$) of routine metabolic rate to rapid, acute temperature change (Di Santo and Bennett, 2011a). It is unclear, however, whether acclimation would have yielded less thermally sensitive oxygen uptake rates in *T. lymma* and whether acute temperature change would have yielded more thermally sensitive oxygen uptake rates in mangrove whiprays. Based on observed trends in $\dot{M}O_{2max}$ in mangrove whiprays, it is possible that mangrove whiprays maintain their aerobic scope – the difference between maximum and standard metabolic rate estimates (Clark et al., 2013; Rummer et al., 2016) – as water temperatures increase. Indeed, tropical fishes that live near their upper thermal limits have been shown to maintain their aerobic scope with increasing temperatures (e.g., Norin et al., 2014; Rummer et al., 2014).

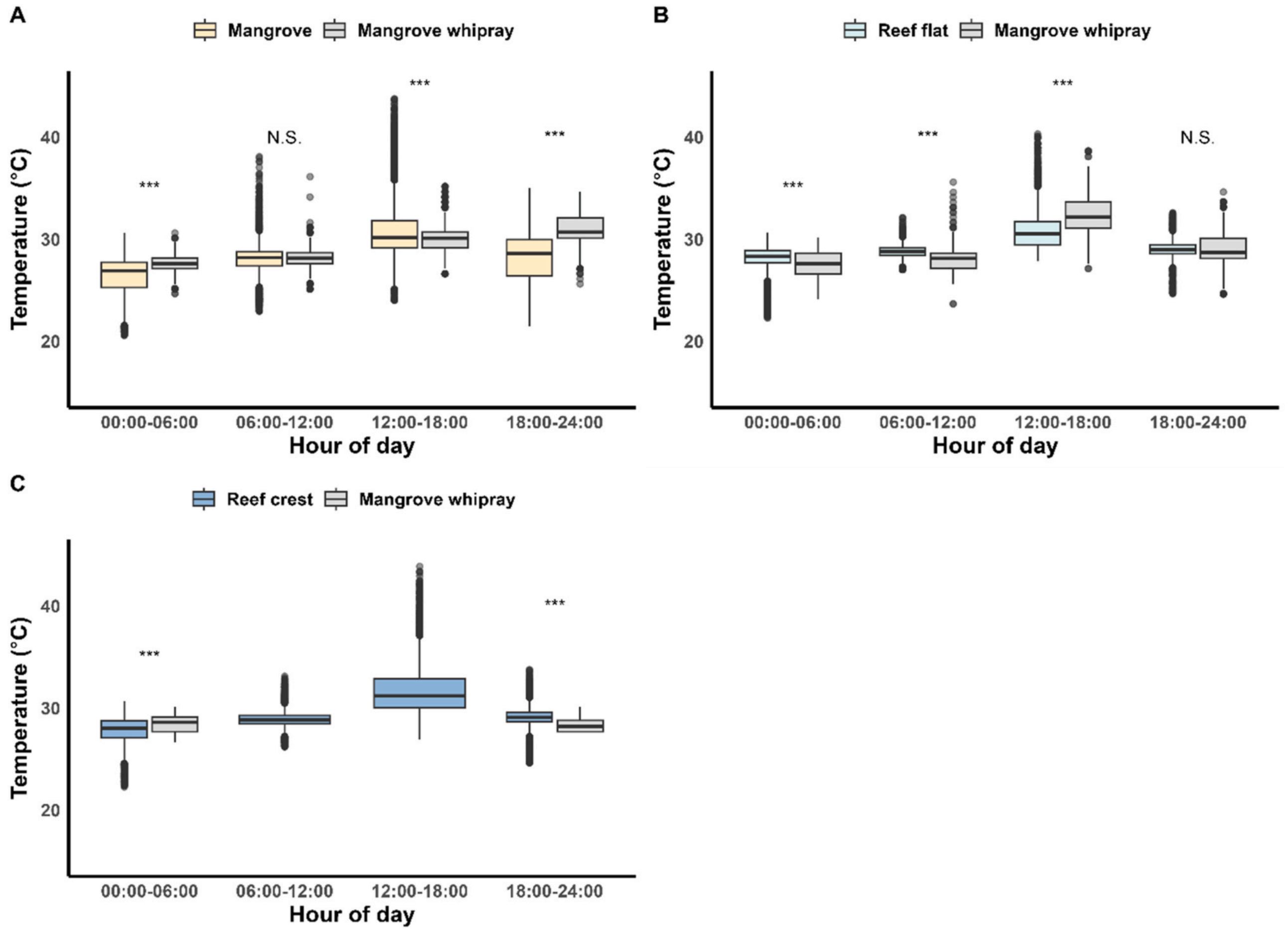

Fig. 6. Differences between temperature logged within three Pioneer Bay habitats and juvenile mangrove whiprays (*Urogymnus granulatus*) across 6-h time bins. Box plots are delimited by 25%, 50%, and 75% percentiles. Lines represent 1.5 times the interquartile range (IQR) and points represent individual observations exceeding 1.5·IQR. Asterisks denote significant differences between Pioneer Bay environmental temperatures and whipray body temperatures within hour bins. Note that mangrove whiprays were not predicted to occur in reef crest habitat from 06:00–18:00 because tidal height allowed them to occupy mangrove and reef flat habitats.

Temperature acclimation had an apparent effect on post-exercise aerobic metabolism. Interestingly, even though acclimation did not influence routine and maximum oxygen uptake rates, juvenile mangrove whiprays consumed more oxygen at 32 °C after exercise compared to 28 °C. However, they returned to their routine oxygen uptake rates more quickly. Exercise is ecologically relevant to wild fishes, particularly in the context of predator-prey interactions (Brownscombe et al., 2017). Indeed, a species' ability to allocate oxygen to post-exercise recovery is important for their ability to engage in predator-prey interactions. There is a paucity of data concerning aerobic metabolism in rays (Vilmar and Di Santo, 2022) and fewer studies that test the effects of temperature. For example, in the little skate (*Leucoraja erinacea*), a temperate ray species, EPOC took longer to recover to minimum (not routine) oxygen uptake rates at higher temperatures (Di Santo, 2016), which directly contrast the results in the present study. In comparison, a tropical shark, *C. melanopterus*, exhibited no observed temperature-dependence of EPOC after acclimation or at a range of diel temperatures in their natural habitat (Bouyoucos et al., 2018, 2020). Generally, EPOC is characterised by a large, short-lived increase in metabolic rate, followed by a longer, slower decrease in metabolic rates back to resting levels (Zhang et al., 2018). Therefore, it is likely that, given the relatively short duration of respirometry experiments (<5 h), the observed temperature effect was not reflective of complete recovery (i.e., to minimum $\dot{M}O_2$) from exercise; although, $\dot{M}O_{2\mathrm{routine}}$ may be a more ecologically relevant baseline for determining recovery in wild fishes. Nonetheless, juvenile mangrove whiprays appear to improve their post-exercise recovery at higher temperatures, which may be related to anti-predator performance (Killen et al., 2015).

Investigating thermal preference in juvenile mangrove whiprays revealed that this species has an affinity for specific temperature ranges within specific habitats. By predicting habitat use based on tidal height, free-ranging juvenile mangrove whiprays demonstrated preference for 27–31 °C in mangroves, but sought even warmer temperatures (up to 35 °C) in the evening. Conversely, mangrove whiprays predicted to be in reef flat habitat either preferred temperatures below 28 °C or above 31 °C and appeared to avoid temperatures near their average body temperature of 29 °C. In this habitat, cooler temperatures were sought from 00:00–12:00, whereas warmer waters were sought at midday. Finally, mangrove whiprays demonstrated very narrow electivity on the reef crest, selecting for their average body temperature. This temperature dependent habitat use is interesting when compared to a different population of mangrove whiprays from a remote tropical atoll with a very small tidal range (St. Joseph Atoll, Seychelles) where habitat use is not affected by water temperatures (Elston et al., 2022). Factors underpinning this temperature electivity are unknown. Studies on sharks within the Everglades National Park (FL, USA) demonstrated positive electivity for temperatures within several degrees of the mean environmental temperature and avoidance of high (i.e., >31 °C) and low (i.e., <25 °C) temperatures (Wiley and Simpfendorfer, 2007). Thus, it is interesting that juvenile mangrove whiprays in the present study exhibited negative electivity at their average body temperature but only within reef flat habitat. The selection of warmer temperatures within

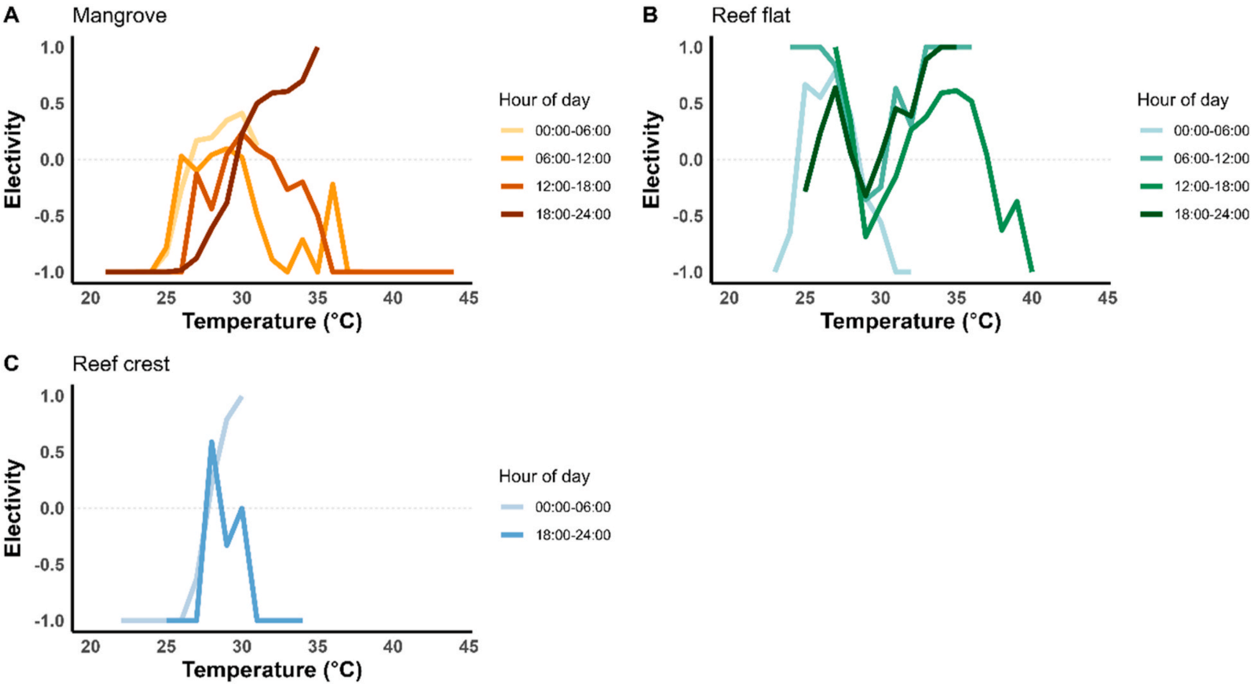

Fig. 7. Juvenile mangrove whipray *Urogymnus graulatus,* electivity indices for water temperature within three Pioneer Bay habitats across 6-h time bins. Lines represents electivity indices for all juvenile mangrove whiprays (n = 7) combined. Negative values indicate avoidance, 0 is neutral, and positive values indicate affinity.

mangroves during the evening may help maximise body temperature and aid in processes such as digestion and growth, which has been previously documented among rays (Di Santo and Bennett, 2011b; Wallman and Bennett, 2006). Indeed, mangrove whiprays were shown to be less active in Pioneer Bay at night (Martins et al., 2021), which may reflect a 'hunt warm, rest warmer' strategy (Papastamatiou et al., 2015). Conversely avoidance of extreme conditions within the peak periods of the day allows individuals to reduce physiological challenges by selecting temperature ranges within their temperature tolerance limits.

Because juvenile mangrove whiprays were not actively tracked in the present study, it was not possible to determine the proximity of rays to temperature loggers across the mangrove, reef flat, and reef crest zones to understand their use of these areas as potential thermal refugia. Indeed, it is possible that mangrove whiprays moved between foraging grounds and refugia that were not represented by the temperature logger array used in this study. Telemetry data from previous studies demonstrates that mangrove whipray movement within Pioneer Bay is strongly driven by tide and mangrove accessibility (Davy et al., 2015; Kanno et al., 2019; Martins et al., 2020); although mangrove whiprays appear to preferentially use mangrove habitat over others in Pioneer Bay (Kanno et al., 2024). Thus, whilst prior knowledge of habitat use from telemetry data can inform interpretation of temperature data recorded from animal-borne data-loggers (Bouyoucos et al., 2020), thermal preference as described by temperature data-loggers alone must be cautiously interpreted.

5. Conclusions

Mangrove habitats may act as thermal refugia for young sharks and rays within nursery areas via two mechanisms: improved physiological performance and exclusion of predators (Davy et al., 2015; Martins et al., 2018). The present study provides indirect support for both notions. Firstly, evidence of thermotaxic behaviour suggests that mangrove whiprays are regulating their body temperature; however, the physiological systems that benefit from this behaviour are unknown. Second, mangrove whiprays' narrow thermal safety margins and low temperature sensitivity of metabolic rate suggest that these animals can tolerate the extreme high temperatures encountered within mangroves. As climate change and ocean warming progress, mangrove habitats may no longer act as thermal refugia for young sharks and rays. The mangrove whipray is listed as 'vulnerable' by the International Union for the Conservation of Nature but is not listed as threatened by climate change (Manjaji Matsumoto et al., 2020). However, as a mangrove associated species, mangrove whiprays on the Great Barrier Reef were assessed as moderately vulnerable to climate change impacts on mangrove ecosystems (Chin et al., 2010). Because climate change is a rapidly emerging threat to (tropical) sharks and rays (Dulvy et al., 2021; Sherman et al., 2023), and an established threat to mangrove ecosystems (Gilman et al., 2008), there is a need for targeted research on the climate change vulnerability of sharks and rays whose life histories are dependent on mangrove ecosystems.

Funding sources

Funding for this research was provided by James Cook University, the Australian Research Council (ARC) Centre of Excellence for Coral Reef Studies, an ARC Discovery Early Career Researcher Award (PDE150101266), and a L'Oréal-United Nations Education, Scientific and Cultural Organisation Women in Science Foundation fellowship.

CRediT authorship contribution statement

Emily Higgins: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Ian A. Bouyoucos:** Writing – review & editing, Writing – original draft, Formal analysis. **Adam T. Downie:** Writing – review & editing, Methodology, Investigation. **Björn Illing:** Writing – review & editing, Methodology, Investigation. **Ana P.B. Martins:** Writing – review & editing, Methodology, Investigation. **Colin A. Simpfendorfer:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization. **Jodie L. Rummer:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors do not declare any competing interests.

Data availability

Data from: Thermal tolerance, performance, and preference in juvenile mangrove whiprays (Original data) (Mendeley Data)

Acknowledgements

The authors are grateful for logistical support provided by Orpheus Island Research Station staff. The authors also acknowledge the Wulgurukaba, Bindal, and Manbarra People as the Traditional Owners and custodians of the lands where this research was conducted and pay our respects to ancestors, Elders, and leaders past, present, and emerging.

References

Andrzejaczek, S., Gleiss, A.C., Jordan, L.K.B., Pattiaratchi, C.B., Howey, L.A., Brooks, E. J., Meekan, M.G., 2018. Temperature and the vertical movements of oceanic whitetip sharks, Carcharhinus longimanus. Sci. Rep. 8, 8351. https://doi.org/10.1038/s41598-018-26485-3.

Andrzejaczek, S., Gleiss, A.C., Pattiaratchi, C.B., Meekan, M.G., 2019. Patterns and drivers of vertical movements of the large fishes of the epipelagic. Rev. Fish Biol. Fish. https://doi.org/10.1007/s11160-019-09555-1.

Baldridge, H.D., 1970. Sinking factors and average densities of Florida sharks as functions of liver buoyancy. Copeia 1970, 744–754. https://doi.org/10.2307/1442317.

Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F., Weinstein, M.P., 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51, 633–641. https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2.

Beitinger, T., Bennett, W., McCauley, R., 2000. Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature. Environ. Biol. Fish. 58, 237–275. https://doi.org/10.1023/A:1007676325825.

Bouyoucos, I., Simpfendorfer, C., Planes, S., Schwieterman, G., Weideli, O., Rummer, J., 2022. Thermally insensitive physiological performance allows neonatal sharks to use coastal habitats as nursery areas. Mar. Ecol. Prog. Ser. 682, 137–152. https://doi.org/10.3354/meps13941.

Bouyoucos, I.A., Morrison, P.R., Weideli, O.C., Jacquesson, E., Planes, S., Simpfendorfer, C.A., Brauner, C.J., Rummer, J.L., 2020. Thermal tolerance and hypoxia tolerance are associated in blacktip reef shark (Carcharhinus melanopterus) neonates. J. Exp. Biol. 223, jeb221937 https://doi.org/10.1242/jeb.221937.

Bouyoucos, I.A., Weideli, O.C., Planes, S., Simpfendorfer, C.A., Rummer, J.L., 2018. Dead tired: evaluating the physiological status and survival of neonatal reef sharks under stress. Conserv. Physiol. 6, coy053 https://doi.org/10.1093/conphys/coy053.

Brownscombe, J.W., Cooke, S.J., Algera, D.A., Hanson, K.C., Eliason, E.J., Burnett, N.J., Danylchuk, A.J., Hinch, S.G., Farrell, A.P., 2017. Ecology of exercise in wild fish: integrating concepts of individual physiological capacity, behavior, and fitness through diverse case studies. Integr. Comp. Biol. 57, 281–292. https://doi.org/10.1093/icb/icx012.

Byrnes, E.E., Lear, K.O., Morgan, D.L., Gleiss, A.C., 2020. Respirometer in a box: development and use of a portable field respirometer for estimating oxygen consumption of large-bodied fishes. J. Fish. Biol. 96, 1045–1050. https://doi.org/10.1111/jfb.14287.

Chin, A., Kyne, P.M., Walker, T.I., McAuley, R.B., 2010. An integrated risk assessment for climate change: analysing the vulnerability of sharks and rays on Australia's Great Barrier Reef. Global Change Biol. 16, 1936–1953. https://doi.org/10.1111/j.1365-2486.2009.02128.x.

Christensen, E.A.F., Andersen, L.E.J., Bergsson, H., Steffensen, J.F., Killen, S.S., 2021a. Shuttle-box systems for studying preferred environmental ranges by aquatic animals. Conserv. Physiol. 9 https://doi.org/10.1093/conphys/coab028.

Christensen, E.A.F., Norin, T., Tabak, I., van Deurs, M., Behrens, J.W., 2021b. Effects of temperature on physiological performance and behavioral thermoregulation in an invasive fish, the round goby. J. Exp. Biol. 224, 237669 https://doi.org/10.1242/jeb.237669.

Clark, T.D., Donaldson, M.R., Pieperhoff, S., Drenner, S.M., Lotto, A., Cooke, S.J., Hinch, S.G., Patterson, D.A., Farrell, A.P., 2012. Physiological benefits of being small in a changing world: responses of Coho salmon (Oncorhynchus kisutch) to an acute thermal challenge and a simulated capture event. PLoS One 7, e39079. https://doi.org/10.1371/journal.pone.0039079.

Clark, T.D., Sandblom, E., Jutfelt, F., 2013. Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. J. Exp. Biol. 216, 2771–2782. https://doi.org/10.1242/jeb.084251.

Collin, R., Rebolledo, A.P., Smith, E., Chan, K.Y.K., 2021. Thermal tolerance of early development predicts the realized thermal niche in marine ectotherms. Funct. Ecol. 35, 1679–1692. https://doi.org/10.1111/1365-2435.13850.

Cowles, R.B., Bogert, C.M., 1944. A preliminary study of the thermal requirements of desert reptiles. Bull. Am. Mus. Nat. Hist. 83, 261–296.

Crear, D., Latour, R., Friedrichs, M., St-Laurent, P., Weng, K., 2020. Sensitivity of a shark nursery habitat to a changing climate. Mar. Ecol. Prog. Ser. 652, 123–136. https://doi.org/10.3354/meps13483.

Crear, D.P., Brill, R.W., Bushnell, P.G., Latour, R.J., Schwieterman, G.D., Steffen, R.M., Weng, K.C., 2019. The impacts of warming and hypoxia on the performance of an obligate ram ventilator. Conserv. Physiol. 7, coz026 https://doi.org/10.1093/conphys/coz026.

Dabruzzi, T.F., Bennett, W.A., Rummer, J.L., Fangue, N.A., 2013. Juvenile ribbontail stingray, Taeniura lymma (Forsskål, 1775) (Chondrichthyes, Dasyatidae), demonstrate a unique suite of physiological adaptations to survive hyperthermic nursery conditions. Hydrobiologia 701, 37–49. https://doi.org/10.1007/s10750-012-1249-z.

Davy, L.E., Simpfendorfer, C.A., Heupel, M.R., 2015. Movement patterns and habitat use of juvenile mangrove whiprays (Himantura granulata). Mar. Freshw. Res. 66, 481. https://doi.org/10.1071/MF14028.

Di Santo, V., 2016. Intraspecific variation in physiological performance of a benthic elasmobranch challenged by ocean acidification and warming. J. Exp. Biol. 219, 1725–1733. https://doi.org/10.1242/jeb.139204.

Di Santo, V., Bennett, W.A., 2011a. Effect of rapid temperature change on resting routine metabolic rates of two benthic elasmobranchs. Fish Physiol. Biochem. 37, 929–934. https://doi.org/10.1007/s10695-011-9490-3.

Di Santo, V., Bennett, W.A., 2011b. Is post-feeding thermotaxis advantageous in elasmobranch fishes? J. Fish. Biol. 78, 195–207. https://doi.org/10.1111/j.1095-8649.2010.02853.x.

Dubois, Y., Blouin-Demers, G., Shipley, B., Thomas, D., 2009. Thermoregulation and habitat selection in wood turtles Glyptemys insculpta: chasing the sun slowly. J. Anim. Ecol. 78, 1023–1032. https://doi.org/10.1111/j.1365-2656.2009.01555.x.

Dulvy, N.K., Pacoureau, N., Rigby, C.L., Pollom, R.A., Jabado, R.W., Ebert, D.A., Finucci, B., Pollock, C.M., Cheok, J., Derrick, D.H., Herman, K.B., Sherman, C.S., VanderWright, W.J., Lawson, J.M., Walls, R.H.L., Carlson, J.K., Charvet, P., Bineesh, K.K., Fernando, D., Ralph, G.M., Matsushiba, J.H., Hilton-Taylor, C., Fordham, S.V., Simpfendorfer, C.A., 2021. Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. Curr. Biol. 31, 4773 e8–4787 e8. https://doi.org/10.1016/j.cub.2021.08.062.

Elston, C., Cowley, P.D., von Brandis, R.G., Lea, J., 2022. Stingray habitat use is dynamically influenced by temperature and tides. Front. Mar. Sci. 8, 754404 https://doi.org/10.3389/fmars.2021.754404.

Ern, R., Chung, D., Frieder, C.A., Madsen, N., Speers-Roesch, B., 2020. Oxygen-dependence of upper thermal limits in crustaceans from different thermal habitats. J. Therm. Biol. 93, 102732 https://doi.org/10.1016/j.jtherbio.2020.102732.

Fangue, N.A., Bennett, W.A., 2003. Thermal tolerance responses of laboratory acclimated and seasonally acclimatized Atlantic stingray, Dasyatis sabina. Copeia 2003, 315–325. https://doi.org/10.1643/0045-8511(2003)003[0315:TTROLA]2.0.CO;2.

Figueira, W.F., Booth, D.J., 2010. Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters. Global Change Biol. 16, 506–516. https://doi.org/10.1111/j.1365-2486.2009.01934.x.

Flowers, K.I., Heithaus, M.R., Papastamatiou, Y.P., 2021. Buried in the sand: uncovering the ecological roles and importance of rays. Fish Fish. 22, 105–127. https://doi.org/10.1111/faf.12508.

Frisk, M.G., Miller, T.J., Fogarty, M.J., 2001. Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. Can. J. Fish. Aquat. Sci. 58, 969–981. https://doi.org/10.1139/f01-051.

Fry, F.E.J., 1971. The effect of environmental factors on the physiology of fish. In: Hoar, W.S., Randall, D.J. (Eds.), Environmental Relations and Behavior. Academic Press, New York, pp. 1–98. https://doi.org/10.1016/S1546-5098(08)60146-6.

Gilman, E.L., Ellison, J., Duke, N.C., Field, C., 2008. Threats to mangroves from climate change and adaptation options: a review. Aquat. Bot. 89, 237–250. https://doi.org/10.1016/j.aquabot.2007.12.009.

Gleiss, A.C., Dale, J.J., Klinger, D.H., Estess, E.E., Gardner, L.D., Machado, B., Norton, A. G., Farwell, C., Block, B.A., 2019. Temperature dependent pre- and postprandial activity in Pacific bluefin tuna (Thunnus orientalis). Comp. Biochem. Physiol. -Part A Mol. Integr. Physiol 231, 131–139. https://doi.org/10.1016/j.cbpa.2019.01.025.

Hammerschlag, N., McDonnell, L.H., Rider, M.J., Street, G.M., Hazen, E.L., Natanson, L. J., McCandless, C.T., Boudreau, M.R., Gallagher, A.J., Pinsky, M.L., Kirtman, B., 2022. Ocean warming alters the distributional range, migratory timing, and spatial protections of an apex predator, the tiger shark (Galeocerdo cuvier). Global Change Biol. 1–16. https://doi.org/10.1111/gcb.16045, 00.

Havird, J.C., Neuwald, J.L., Shah, A.A., Mauro, A., Marshall, C.A., Ghalambor, C.K., 2020. Distinguishing between active plasticity due to thermal acclimation and passive plasticity due to Q_{10} effects: why methodology matters. Funct. Ecol. 34, 1015–1028. https://doi.org/10.1111/1365-2435.13534.

Heupel, M.R., Carlson, J.K., Simpfendorfer, C.A., 2007. Shark nursery areas: concepts, definition, characterization and assumptions. Mar. Ecol. Prog. Ser. 337, 287–297. https://doi.org/10.3354/meps337287.

Heupel, M.R., Kanno, S., Martins, A.P.B., Simpfendorfer, C.A., 2019. Advances in understanding the roles and benefits of nursery areas for elasmobranch populations. Mar. Freshw. Res. 70, 897. https://doi.org/10.1071/MF18081.

Hight, B.V., Lowe, C.G., 2007. Elevated body temperatures of adult female leopard sharks, Triakis semifasciata, while aggregating in shallow nearshore embayments: evidence for behavioral thermoregulation? J. Exp. Mar. Biol. Ecol. 352, 114–128. https://doi.org/10.1016/j.jembe.2007.07.021.

Huey, R.B., 1991. Physiological consequences of habitat selection. Am. Nat. 137, S91–S115. https://doi.org/10.1086/285141.

Illing, B., Downie, A.T., Beghin, M., Rummer, J.L., 2020. Critical thermal maxima of early life stages of three tropical fishes: effects of rearing temperature and experimental heating rate. J. Therm. Biol. 90, 102582 https://doi.org/10.1016/j.jtherbio.2020.102582.

Ivlev, V.S., 1961. Experimental Ecology of the Feeding of Fishes.

Jirik, K.E., Lowe, C.G., 2012. An elasmobranch maternity ward: female round stingrays Urobatis halleri use warm, restored estuarine habitat during gestation. J. Fish. Biol. 80, 1227–1245. https://doi.org/10.1111/j.1095-8649.2011.03208.x.

Kanno, S., Heupel, M., Sheaves, M., Simpfendorfer, C., 2023. Mangrove use by sharks and rays: a review. Mar. Ecol. Prog. Ser. 724, 167–183. https://doi.org/10.3354/meps14452.

Kanno, S., Heupel, M.R., Hoel, K., Schlaff, A., Siddiqi, A., Simpfendorfer, C.A., 2024. Performance and detection range of acoustic receivers in mangrove habitats. J. Fish. Biol. https://doi.org/10.1111/jfb.15817.

Kanno, S., Schlaff, A.M., Heupel, M.R., Simpfendorfer, C.A., 2019. Stationary video monitoring reveals habitat use of stingrays in mangroves. Mar. Ecol. Prog. Ser. 621, 155–168. https://doi.org/10.3354/meps12977.

Killen, S.S., Christensen, E.A.F., Cortese, D., Závorka, L., Norin, T., Cotgrove, L., Crespel, A., Munson, A., Nati, J.J.H., Papatheodoulou, M., McKenzie, D.J., 2021. Guidelines for reporting methods to estimate metabolic rates by aquatic intermittent-flow respirometry. J. Exp. Biol. 224, jeb242522 https://doi.org/10.1242/jeb.242522.

Killen, S.S., Reid, D., Marras, S., Domenici, P., 2015. The interplay between aerobic metabolism and antipredator performance: vigilance is related to recovery rate after exercise. Front. Physiol. 6, 1–8. https://doi.org/10.3389/fphys.2015.00111.

Last, P.R., White, W.T., de Carvalho, M.R., Seret, B., Stehmann, M.F.W., Naylor, G.J.P. (Eds.), 2016. Rays of the World. CSIRO Publishing, Clayton South, Victoria.

Lawson, C.L., Halsey, L.G., Hays, G.C., Dudgeon, C.L., Payne, N.L., Bennett, M.B., White, C.R., Richardson, A.J., 2019. Powering ocean giants: the energetics of shark and ray megafauna. Trends Ecol. Evol. 34, 1009–1021. https://doi.org/10.1016/j.tree.2019.07.001.

Lear, K.O., Gleiss, A.C., Whitney, N.M., 2018. Metabolic rates and the energetic cost of external tag attachment in juvenile blacktip sharks *Carcharhinus limbatus*. J. Fish. Biol. 93, 391–395. https://doi.org/10.1111/jfb.13663.

Lear, K.O., Whitney, N.M., Morgan, D.L., Brewster, L.R., Whitty, J.M., Poulakis, G.R., Scharer, R.M., Guttridge, T.L., Gleiss, A.C., 2019. Thermal performance responses in free-ranging elasmobranchs depend on habitat use and body size. Oecologia 191, 829–842. https://doi.org/10.1007/s00442-019-04547-1.

Lenth, R.V., 2024. Emmeans: Estimated Marginal Means, Aka Least-Squares Means.

Little, A.G., Loughland, I., Seebacher, F., 2020. What do warming waters mean for fish physiology and fisheries? J. Fish. Biol. 97, 328–340. https://doi.org/10.1111/jfb.14402.

Lutterschmidt, W.I., Hutchison, V.H., 1997. The critical thermal maximum: history and critique. Can. J. Zool. 75, 1561–1574. https://doi.org/10.1139/z97-783.

Manjaji Matsumoto, B.M., White, W.T., Ishihara, H.F., Morgan, D.L., 2020. Urogymnus granulatus (amended version of 2016 assessment). IUCN Red List Threat. Species e. T161431A. https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T161431A177282313.enCopyright.

Marshall, D.J., Pettersen, A.K., Bode, M., White, C.R, 2020. Developmental cost theory predicts thermal environment and vulnerability to global warming. Nat. Ecol. Evol. 4, 406–411. https://doi.org/10.1038/s41559-020-1114-9.

Martins, A., Heupel, M., Chin, A., Simpfendorfer, C., 2018. Batoid nurseries: definition, use and importance. Mar. Ecol. Prog. Ser. 595, 253–267. https://doi.org/10.3354/meps12545.

Martins, A.P.B., Heupel, M.R., Bierwagen, S.L., Chin, A., Simpfendorfer, C.A., 2021. Tidal-diel patterns of movement, activity and habitat use by juvenile mangrove whiprays using towed-float GPS telemetry. Mar. Freshw. Res. 72, 534–541. https://doi.org/10.1071/MF20078.

Martins, A.P.B., Heupel, M.R., Oakley-Cogan, A., Chin, A., Simpfendorfer, C.A., 2020. Towed-float GPS telemetry: a tool to assess movement patterns and habitat use of juvenile stingrays. Mar. Freshw. Res. 71, 89. https://doi.org/10.1071/MF19048.

McKenzie, D.J., Zhang, Y., Eliason, E.J., Schulte, P.M., Claireaux, G., Blasco, F.R., Nati, J. J., Farrell, A.P., 2021. Intraspecific variation in tolerance of warming in fishes. J. Fish. Biol. 98, 1536–1555. https://doi.org/10.1111/jfb.14620.

Miklos, P., Katzman, S.M., Cech, J.J., 2003. Effect of temperature on oxygen consumption of the leopard shark, Triakis semifasciata. Environ. Biol. Fish. 66, 15–18. https://doi.org/10.1023/A:1023287123495.

Morgan, R., Finnøen, M.H., Jutfelt, F., 2018. CTmax is repeatable and doesn't reduce growth in zebrafish. Sci. Rep. 8, 7099. https://doi.org/10.1038/s41598-018-25593-4.

Nay, T.J., Johansen, J.L., Habary, A., Steffensen, J.F., Rummer, J.L., 2015. Behavioural thermoregulation in a temperature-sensitive coral reef fish, the five-lined cardinalfish (Cheilodipterus quinquelineatus). Coral Reefs 34, 1261–1265. https://doi.org/10.1007/s00338-015-1353-4.

Nay, T.J., Longbottom, R.J., Gervais, C.R., Johansen, J.L., Steffensen, J.F., Rummer, J.L., Hoey, A.S., 2021. Regulate or tolerate: thermal strategy of a coral reef flat resident, the epaulette shark, <scp> *Hemiscyllium ocellatum* </scp&gt. J. Fish. Biol. 98, 723–732. https://doi.org/10.1111/jfb.14616.

Niella, Y., Butcher, P., Holmes, B., Barnett, A., Harcourt, R., 2021. Forecasting intraspecific changes in distribution of a wide-ranging marine predator under climate change. Oecologia 1, 3. https://doi.org/10.1007/s00442-021-05075-7.

Norin, T., Malte, H., Clark, T.D., 2014. Aerobic scope does not predict the performance of a tropical eurythermal fish at elevated temperatures. J. Exp. Biol. 217, 244–251. https://doi.org/10.1242/jeb.089755.

O'Shea, O.R., Thums, M., Van Keulen, M., Meekan, M., 2012. Bioturbation by stingrays at ningaloo reef, Western Australia. Mar. Freshwater Res. 63, 189–197. https://doi.org/10.1071/MF11180.

Papastamatiou, Y.P., Watanabe, Y.Y., Bradley, D., Dee, L.E., Weng, K., Lowe, C.G., Caselle, J.E., 2015. Drivers of daily routines in an ectothermic marine predator: hunt warm, rest warmer? PLoS One 10, e0127807. https://doi.org/10.1371/journal.pone.0127807.

Payne, N.L., Meyer, C.G., Smith, J.A., Houghton, J.D.R., Barnett, A., Holmes, B.J., Nakamura, I., Papastamatiou, Y.P., Royer, M.A., Coffey, D.M., Anderson, J.M., Hutchinson, M.R., Sato, K., Halsey, L.G., 2018. Combining abundance and performance data reveals how temperature regulates coastal occurrences and activity of a roaming apex predator. Global Change Biol. 24, 1884–1893. https://doi.org/10.1111/gcb.14088.

Pinheiro, J., Bates, D., Core Team, R., 2024. Nlme: Linear and Nonlinear Mixed Effects Models.

R Core Team, 2024. R: A Language and Environment for Statistical Computing.

Rees, B.B., Reemeyer, J.E., Binning, S.A., Brieske, S.D., Clark, T.D., De Bonville, J., Eisenberg, R.M., Raby, G.D., Roche, D., Rummer, J.L., Zhang, Y., 2024. Estimating maximum oxygen uptake of fishes during swimming and following exhaustive chase – different results, biological bases and applications. J. Exp. Biol. 227, 246439 https://doi.org/10.1242/jeb.246439.

Rodgers, G.G., Tenzing, P., Clark, T.D., 2016. Experimental methods in aquatic respirometry: the importance of mixing devices and accounting for background respiration. J. Fish. Biol. 88, 65–80. https://doi.org/10.1111/jfb.12848.

Rummer, J.L., Binning, S.A., Roche, D.G., Johansen, J.L., 2016. Methods matter: considering locomotory mode and respirometry technique when estimating metabolic rates of fishes. Conserv. Physiol. 4, cow008 https://doi.org/10.1093/conphys/cow008.

Rummer, J.L., Couturier, C.S., Stecyk, J.A.W., Gardiner, N.M., Kinch, J.P., Nilsson, G.E., Munday, P.L., 2014. Life on the edge: thermal optima for aerobic scope of equatorial reef fishes are close to current day temperatures. Global Change Biol. 20, 1055–1066. https://doi.org/10.1111/gcb.12455.

Sandblom, E., Gräns, A., Axelsson, M., Seth, H., 2014. Temperature acclimation rate of aerobic scope and feeding metabolism in fishes: implications in a thermally extreme future. Proc. R. Soc. A B 281, 2141490.

Santos, C.P., Sampaio, E., Pereira, B.P., Pegado, M.R., Borges, F.O., Wheeler, C.R., Bouyoucos, I.A., Rummer, J.L., Frazão Santos, C., Rosa, R., 2021. Elasmobranch responses to experimental warming, acidification, and oxygen loss—a meta-analysis. Front. Mar. Sci. 8, 735377 https://doi.org/10.3389/fmars.2021.735377.

Schlaff, A.M., Heupel, M.R., Simpfendorfer, C.A., 2014. Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Rev. Fish Biol. Fish. 24, 1089–1103. https://doi.org/10.1007/s11160-014-9364-8.

Sherman, C., Heupel, M., Moore, S., Chin, A., Simpfendorfer, C., 2020. When sharks are away, rays will play: effects of top predator removal in coral reef ecosystems. Mar. Ecol. Prog. Ser. 641, 145–157. https://doi.org/10.3354/meps13307.

Sherman, C.S., Simpfendorfer, C.A., Pacoureau, N., Matsushiba, J.H., Yan, H.F., Walls, R. H.L., Rigby, C.L., VanderWright, W.J., Jabado, R.W., Pollom, R.A., Carlson, J.K., Charvet, P., Bin Ali, A., Fahmi, Cheok, J., Derrick, D.H., Herman, K.B., Finucci, B., Eddy, T.D., Palomares, M.L.D., Avalos-Castillo, C.G., Kinattumkara, B., Blanco-Parra, M.-P., Dharmadi, Espinoza, M., Fernando, D., Haque, A.B., Mejía-Falla, P.A., Navia, A.F., Pérez-Jiménez, J.C., Utzurrum, J., Yuneni, R.R., Dulvy, N.K., 2023. Half a century of rising extinction risk of coral reef sharks and rays. Nat. Commun. 14, 15. https://doi.org/10.1038/s41467-022-35091-x.

Speed, C., Meekan, M., Field, I., McMahon, C., Bradshaw, C., 2012. Heat-seeking sharks: support for behavioural thermoregulation in reef sharks. Mar. Ecol. Prog. Ser. 463, 231–245. https://doi.org/10.3354/meps09864.

Speers-Roesch, B., Norin, T., Driedzic, W.R., 2018. The benefit of being still: energy savings during winter dormancy in fish come from inactivity and the cold, not from metabolic rate depression. Proc. R. Soc. B Biol. Sci. 285, 20181593 https://doi.org/10.1098/rspb.2018.1593.

Stevens, J.D., Bonfil, R., Dulvy, N.K., Walker, P.A., 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES J. Mar. Sci. 57, 476–494. https://doi.org/10.1006/jmsc.2000.0724.

Stuart-Smith, R.D., Edgar, G.J., Bates, A.E., 2017. Thermal limits to the geographic distributions of shallow-water marine species. Nat. Ecol. Evol. 1, 1846–1852. https://doi.org/10.1038/s41559-017-0353-x.

Twiname, S., Audzijonyte, A., Blanchard, J.L., Champion, C., de la Chesnais, T., Fitzgibbon, Q.P., Fogarty, H.E., Hobday, A.J., Kelly, R., Murphy, K.J., Oellermann, M., Peinado, P., Tracey, S., Villanueva, C., Wolfe, B., Pecl, G.T., 2020. A cross-scale framework to support a mechanistic understanding and modelling of marine climate-driven species redistribution, from individuals to communities. Ecography 43, 1764–1778. https://doi.org/10.1111/ecog.04996.

Vilmar, M., Di Santo, V., 2022. Swimming performance of sharks and rays under climate change. Rev. Fish Biol. Fish. 32, 765–781. https://doi.org/10.1007/s11160-022-09706-x.

Vinagre, C., Mendonça, V., Cereja, R., Abreu-Afonso, F., Dias, M., Mizrahi, D., Flores, A. A.V., 2018. Ecological traps in shallow coastal waters—potential effect of heat-waves in tropical and temperate organisms. PLoS One 13, e0192700. https://doi.org/10.1371/journal.pone.0192700.

Wallman, H.L., Bennett, W.A., 2006. Effects of parturition and feeding on thermal preference of Atlantic stingray, Dasyatis sabina (Lesueur). Environ. Biol. Fish. 75, 259–267. https://doi.org/10.1007/s10641-006-0025-1.

Watanabe, Y.Y., Payne, N.L., 2023. Thermal sensitivity of metabolic rate mirrors biogeographic differences between teleosts and elasmobranchs. Nat. Commun. 14, 2054. https://doi.org/10.1038/s41467-023-37637-z.

Wheeler, C.R., Gervais, C.R., Johnson, M.S., Vance, S., Rosa, R., Mandelman, J.W., Rummer, J.L., 2020. Anthropogenic stressors influence reproduction and development in elasmobranch fishes. Rev. Fish Biol. Fish. https://doi.org/10.1007/s11160-020-09604-0.

Wiley, T.R., Simpfendorfer, C.A., 2007. The ecology of elasmobranchs occurring in the Everglades National Park, Florida: implications for conservation and management. Bull. Mar. Sci. 80, 171–189.

Zhang, Y., Claireaux, G., Takle, H., Jørgensen, S.M., Farrell, A.P., 2018. A three-phase excess post-exercise oxygen consumption in Atlantic salmon Salmo salar and its response to exercise training. J. Fish. Biol. 92, 1385–1403. https://doi.org/10.1111/jfb.13593.