Thermal performance responses in free-ranging elasmobranchs depend on habitat use and body size

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Abstract

Temperature is one of the most influential drivers of physiological performance and behaviour in ectotherms, determining how these animals relate to their ecosystems and their ability to succeed in particular habitats. Here, we analysed the largest set of acceleration data compiled to date for elasmobranchs to examine the relationship between volitional activity and temperature in 252 individuals from 8 species. We calculated activation energies for the thermal performance response in each species and estimated optimum temperatures using an Arrhenius breakpoint analysis, subsequently fitting thermal performance curves to the activity data. Juveniles living in confined nursery habitats not only spent substantially more time above their optimum temperature and at the upper limits of their performance breadths compared to larger, less site-restricted animals, but also showed lower activation energies and broader performance curves. Species or life stages occupying confined habitats featured more generalist behavioural responses to temperature change, whereas wider ranging elasmobranchs were characterised by more specialist behavioural responses. The relationships between the estimated performance regimes and environmental temperature limits suggest that animals in confined habitats, including many juvenile elasmobranchs within nursery habitats, are likely to experience a reduction of performance under a warming climate, although their flatter thermal response will likely dampen this impact. The effect of warming on less site-restricted species is difficult to forecast since three of four species studied here did not reach their optimum temperature in the wild, although their specialist performance characteristics may indicate a more rapid decline should optimum temperatures be exceeded.

Introduction

Temperature is widely regarded as the most influential environmental factor affecting biological processes (Huey and Stevenson 1979; Angilletta et al. 2002; Brown et al. 2004; Kingsolver 2009). This is particularly true in ectotherms, where environmental temperature directly dictates body temperature, and therefore, drives changes in a myriad of

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physiological traits and processes that influence an animal's behaviour and interactions with its ecosystem (Huey and Kingsolver 1989; Deutsch et al. 2008; Schulte et al. 2011). Many physiological rates scale with temperature according to a thermal performance curve, where physiological performance gradually increases up to a maximum at an organism's optimum temperature, or T_{opt}, before quickly declining as temperatures approach lethal levels (Fig. 1) (Huey and Stevenson 1979; Angilletta et al. 2002; Angilletta 2006).

Determining the shape and limits of thermal performance curves is valuable for understanding how environmental pressures affect animals, and has gained traction as a method to evaluate a species' susceptibility and potential response to climate change (e.g. Helmuth et al. 2005; Angert et al. 2011; Huey et al. 2012). Although it has historically been difficult to formulate these performance curves for free-ranging populations, a few recent studies have begun to address this problem in fish using accelerometers to collect body movement data at a range of temperatures. To date, this method has produced thermal performance curves for five species
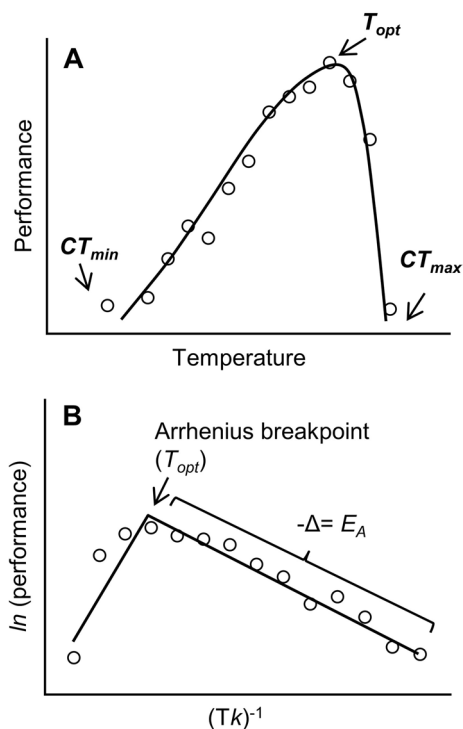
of teleosts (Gannon et al. 2014; Payne et al. 2016), and two elasmobranchs, the estuary stingray *Dasyatis fluviorum* and the tiger shark *Galeocerdo cuvier* (Payne et al. 2016, 2018). Accelerometer-derived body movement is a measure of volitional activity, which is not a direct representation of physiological performance as it does not relay an animal's physiological capacity, as does aerobic scope, maximal sprint speed, or other laboratory-derived metrics. However, movement choices of animals are driven by physiological limitations as well as a host of ecological factors (Wilson et al. 2015), and therefore, measuring volitional activity in nature provides an understanding of how the combination of temperature-driven physiological constraints and ecological factors guide behaviour. Such in situ measurements of activity and behaviour also present the opportunity to link animals' thermal responses with environmental factors that may also be thermally dependent, such as changes in habitat or behaviour of predator and prey species (Dell et al. 2014; Dowd et al. 2015; Irschick and Higham 2016; Childress and Letcher 2017). Equally as important, this method offers the opportunity to quantify thermal performance in species that are difficult to maintain and study in the laboratory, including many large-bodied or endangered elasmobranchs.

Having the ability to measure performance in wild individuals of a range of sizes, populations, and habitats can also help to identify environmental and life-history factors that influence thermal responses. For example, body size has been shown to affect thermal performance regimes in a range of taxa, often observed in ontogenetic shifts in performance (e.g. Krebs et al. 1998; Klok and Chown 2001; Winne and Keck 2005; Komoroske et al. 2014). These studies have generally found higher thermal tolerance in small juveniles compared to larger adults, including higher optimum and critical temperatures. This difference in performance has mainly been attributed to habitat use, as the smaller juveniles tend to live in more spatially constrained habitats due to factors such as predator avoidance. While these constrained habitats offer many benefits, they also tend to reach high temperatures and offer low potential for behavioural thermoregulation through selection of microhabitats (Krebs et al. 1998; Winne and Keck 2005; Bowler and Terblanche 2008). Consequently, animals that are bound to specific locations are often put under greater thermal pressure than those living in less restricted habitats, and therefore, require greater thermal tolerance.

The present study compiled the largest acceleration dataset for free-ranging elasmobranchs, including accelerometer deployments from 252 individuals of 8 species, several of which are considered threatened. Body acceleration and temperature data were used to build thermal performance curves and calculate activation energies for activity in each species. The resulting thermal performance regimes were examined in the context of environmental temperature limits

Fig. 1 **a** Example performance data plotted with a typical thermal performance curve, showing performance maximised at the optimum temperature (T_{opt}), and declining to zero at the minimum and maximum critical temperatures (CT$_{min}$ and CT$_{max}$). **b** The same example performance data in an Arrhenius plot, with the natural logarithm of performance plotted against a corrected temperature, $(Tk)^{-1}$, where T is temperature in kelvin, and k is Boltzmann's constant. The Arrhenius breakpoint of these corrected data was used to determine T_{opt}, and the negative slope of the Arrhenius relationship up to T_{opt} was used to calculate the activation energy, E_A

and life-history traits, including habitat use and life stage, to gain insight into which species or life stages may be most affected by shifting temperature regimes. Small elasmobranchs, including juveniles of many species, often use confined, shallow, habitats which can undergo substantial thermal variation (Heupel et al. 2007; Grubbs 2010), while larger animals often shift their range into more thermally stable open ocean habitats. Therefore, we hypothesized that small animals, including many juveniles, may show higher thermal tolerance than larger animals in less restricted habitats.

Materials and methods

All applicable institutional and national guidelines for the care and use of animals were followed. Work with animals was approved by the Institutional Animal Care and Use committees at Mote Marine Laboratory (protocol # 13-11-NW2) and the University of Miami (protocol #12-030), and by the Murdoch University Animal Ethics Committee (permit #RW2662/14).

Tag types and field methods

Acceleration data loggers (ADLs) (model G6A+, Cefas Technology, Inc, Lowestoft, UK), and acceleration transmitters (model V13 AT, Vemco, Halifax, NS, Canada) were used to collect acceleration and temperature data from eight elasmobranch species over a range of life stages (Table 1). Here, 'juvenile' refers to young animals in their first few

years of life when they occupy nursery habitats, and 'adult' to large immature and sexually mature individuals that use more open habitats. ADLs log data to the memory of the device, and therefore, can record acceleration at high sampling frequencies, but must be recovered to access the data. Conversely, acceleration transmitters transmit data to nearby acoustic receivers and do not need to be recovered, but due to data transmission limitations, can only provide average acceleration values. ADLs recorded triaxial acceleration at 25–30 Hz and temperature at 0.033–1 Hz, depending on the species, and were deployed on adult blacktip sharks *Carcharhinus limbatus* (Müller and Henle), bull sharks *Carcharhinus leucas* (Müller and Henle), tiger sharks *Galeocerdo cuvier* (Péron and Lesueur), and sandbar sharks *Carcharhinus plumbeus* (Nardo), and juvenile blacktip sharks, lemon sharks *Negaprion brevirostris* (Poey), nurse sharks *Ginglymostoma cirratum* (Bonnaterre), and smalltooth sawfish *Pristis pectinata* Latham. Acceleration transmitters were used to record activity of juvenile bull sharks and largetooth sawfish *Pristis pristis* (Linnaeus), also known as freshwater sawfish. These acceleration-temperature transmitters sampled triaxial acceleration at 10 Hz for 20 s of every 2 min period, and temperature once every 2 min. For all species and life-history stages, tag-animal mass ratios remained below 2%, within the guidelines recommended for tagging studies (Winter 1983).

Adult blacktip, sandbar, tiger, and bull sharks were caught using longlines in the Gulf of Mexico near Madeira Beach and Key West, FL, USA between 2013 and 2016, and tagged with ADLs built into custom-made float packages (see Whitmore et al. 2016). These float packages also incorporated a

Table 1 Measurements and accelerometer deployment data for each species and life-history stage

Species	Life stage	*N*	TL range (cm)	Tag type	Deployment duration (days)	Location
Carcharhinidae						
Bull shark (*C. leucas*)	Ad	13	181–269	L	2.3 ± 1.6	Gulf of Mexico, FL, USA
	Juv	14	74–148	T	93 ± 72	Fitzroy River, WA, AUS
Blacktip shark (*C. limbatus*)	Ad	51	126–186	L	1.4 ± 0.7	Gulf of Mexico, FL, USA
	Juv	13	53–73	L	4.2 ± 1.2	Terra Ceia Bay, FL, USA
Sandbar shark (*C. plumbeus*)	Ad	69	162–227	L	1.0 ± 1.0	Gulf of Mexico, FL, USA
Tiger shark (*G. cuvier*)	Ad	40	131–257	L	1.1 ± 0.4	Gulf of Mexico, FL, USA
Lemon shark (*N. brevirostris*)	Juv	20	76–89	L	5.0 ± 0.1	Bimini, BHS
Ginglymostomatidae						
Nurse shark (*G. cirratum*)	Juv	15	67–90	L	4.9 ± 0.1	Bimini, BHS
Pristidae						
Smalltooth sawfish (*P. pectinata*)	Juv	7	81–183	L	5.2 ± 0.1	Peace River, FL, USA
Largetooth sawfish (*P. pristis*)	Juv	10	130–264	T	146 ± 78	Fitzroy River, WA, AUS

Deployment duration is reported as mean ± SD. Note that *N* describes the number of individuals present in analyses for each species, but not all individuals provided data spanning the entire temperature range

TL stretch total length, life stages are: *Juv* juvenile, *Ad* large immature to adult, accelerometer tag type is: *L* data logger, *T* transmitter

VHF tag to assist in recovery (model MM130B, Advanced Telemetry Systems, Isanti, MN, USA), and were attached to the first dorsal fin at two points using a strap that incorporated a galvanic timed release (GTR) (International Fishing Devices, Northland, New Zealand). These releases corroded after 1–8 days at liberty, allowing the float packages to rise to the surface, where they were located and recovered using the VHF tag, with methods described by Lear and Whitney (2016).

Juvenile lemon sharks were caught by dipnet (see Brewster et al. 2018) and juvenile nurse sharks were caught by hand in Bimini, BHS, in 2013 and 2014. Juvenile blacktip sharks were caught using rod and reel in Terra Ceia Bay, FL, USA in 2014 and 2015. All three species were tagged with ADLs joined to continuous acoustic transmitters (model V9, Vemco, or model PT-4, Sonotronics Inc, Tucson, AZ, USA), which were attached to the first dorsal fin of the animals at two points using monofilament. Animals were released and left at large for approximately 6 days before being tracked via their acoustic tags, recaptured, and their tags removed and downloaded.

Juvenile smalltooth sawfish were caught by gillnet in the Peace River, FL, USA in 2014 and 2015. Five fish were tagged with ADLs joined to acoustic tags, similar to the juvenile lemon, nurse, and blacktip sharks. Two additional fish were tagged with an ADL built into a float release package, similar to the adult sharks caught on longlines.

Juvenile bull sharks and largetooth sawfish were caught via gillnet or handline in the Fitzroy River, WA, AUS in 2016 and 2017. Acceleration transmitters were surgically implanted in the body cavity of the fish using methods outlined by Whitty et al. (2017). Acoustic receivers (Vemco model VR2W) were moored approximately every 500 m throughout the study area (see Whitty et al. 2017). Animals were tagged in the dry season, when river flow was limited and fish were confined to isolated refuge pools in the main channel of the river. As a result, animals stayed within the receiver array with receiver coverage near 100%, transmitting acceleration and temperature data almost continuously for between 5 and 299 days.

Acceleration data processing and analysis

Data from the first 12 h after capture were excluded from analyses for all species to minimise any behavioural effects of capture stress. For largetooth sawfish and juvenile bull sharks, the acceleration transmitters processed raw acceleration data onboard, separating static and dynamic acceleration with a 4 s running mean, and calculating a root mean square (RMS) of acceleration, or the square root of the sum of squared dynamic acceleration from all three axes (often termed vectorial dynamic body acceleration, or VeDBA; Qasem et al. 2012). The RMS and a temperature reading

were transmitted about every 2 min to acoustic receivers, which were downloaded at the end of the study.

For all other species, acceleration data collected by ADLs were analysed using Igor Pro (Wavemetrics, Inc., Portland, OR, USA). Static and dynamic acceleration were separated using a 3 s box smoother (Shepard et al. 2008), which was the minimum smoothing time sufficient to remove the tailbeat signal from the static acceleration traces. Overall dynamic body acceleration (ODBA) was calculated as the sum of the absolute value of the dynamic acceleration from all three axes. ODBA was substantially different for the two accelerometer attachment techniques for smalltooth sawfish, likely due to different amounts of drag and water flow over the tag. Therefore, tailbeat frequency (TBF) was used as an alternative activity metric to ODBA for this species, calculated by a continuous wavelet transformation of the sway acceleration axis (Sakamoto et al. 2009; Whitney et al. 2010). Tagging methods were consistent within all other datasets. Although tag-mass ratios between species and relative drag of tags may have differed between species or tagging types, all of the thermal performance analyses (see below) were based on relative measures of activity within a group, and therefore, maintaining consistent tagging methods within a group eliminated any potential bias from using different tagging techniques.

To assess volitional activity levels, mean ODBA or TBF and mean temperature were calculated for each hour of the deployment for every individual. Although acceleration data were collected at different sampling frequencies for different species, the hourly mean ODBA for each species was calculated from a minimum of 90,000 acceleration measurements for ADL-tagged animals, and approximately 6000 measurements (30 mean acceleration measurements based on 20 s of 10 Hz data) for acoustically tagged species. Therefore, the different sampling frequencies were unlikely to affect the calculated hourly mean ODBA or TBF (Halsey et al. 2009a). For all ADL-tagged animals, the tags were externally attached, and therefore, measured external water temperature rather than body temperature. However, because these animals were generally small bodied and typically experienced limited daily temperature variation, external temperature was assumed to represent body temperature. For species capable of buccal pumping (nurse sharks, lemon sharks, and smalltooth sawfish) resting and active periods were separated using k-means clustering analyses in the Ethographer extension for Igor Pro (Sakamoto et al. 2009; Whitney et al. 2010). Hourly activity means for these species were calculated using only data where the fish were actively swimming. Acoustic activity data from largetooth sawfish were separated into resting and active points using a mixture model with the 'mixtools' package in R (Benaglia et al. 2009), which identified two clusters of points separated at 0.015 g. Activity points below 0.015 g were classified as

resting, and points above 0.015 g were classified as active. Therefore, activity points from largetooth sawfish below 0.015 g were also excluded from analyses to eliminate resting behaviour. Because nurse sharks were typically only active for short periods, 10 min activity and temperature means were calculated instead of hourly means. If an animal was active for less than 20% of a 10 min or 1 h interval, that interval was omitted.

Activity-temperature measurement pairs were binned by 1 °C for each individual, resulting in a mean volitional activity measure for every 1 °C bin each individual experienced. Binned activity points were excluded if an individual spent less than 5 h in a temperature bin during the deployment. For each species overall, temperature bins were excluded if they only included data from one individual. In this way, thermal performance regimes for each species were estimated using data from multiple individuals spending more than 5 h within each 1 °C temperature bin.

Environmental temperatures

An environmental temperature regime was established for each species using long-term temperature data for each habitat. If daily temperature data were available for a habitat for an entire year concurrent with accelerometer deployments, a frequency distribution of environmental temperatures was compiled. Such data included temperature data from loggers placed throughout the Fitzroy River nursery habitat for juvenile bull sharks and largetooth sawfish (HOBO Pendant data loggers, model UA-002-xx, Onset, Bourne, MA, USA), long-term temperature monitoring data from the Southwest Florida Water Management District for juvenile smalltooth sawfish, and daily sea surface temperatures reported by the National Oceanic and Atmospheric Administration (NOAA) for the adult coastal shark species tagged in FL, USA, during the regions and temporal periods where each species is usually present (https://www.nodc.noaa.gov/dsdt/cwtg/egof.html). Typical seasonal presence of these animals was based on catch rates in year-round fishing efforts in the current work and verified against species distributions and temperature ranges reported by Grace and Henwood (1997). All these temperature data were collected concurrently with accelerometer deployments. Temperature data from the blacktip shark nursery in Terra Ceia Bay, FL, were not available for the study period (2014–2015). Instead, temperature data collected in 2017–2018 by temperature loggers placed in Terra Ceia Bay were used (J. Gardiner, unpublished data).

Long-term daily temperature data were not available for juvenile lemon and nurse sharks tagged in Bimini, BHS, and therefore, frequency distributions of environmental temperatures were not compiled for these species. Instead, simple minimum and maximum environmental temperatures were reported. These temperature limits were recorded by short-term Thermochron iButton temperature loggers (Model DS1921H, Maxim Integrated, San Jose, CA, USA) placed throughout the Bimini nurseries in the warmest (August–September) and coldest (November–March) months of the year. The timing of these temperature logger deployments coincided with accelerometer deployments for juvenile lemon and nurse sharks.

Thermal performance analysis

Statistical analyses were conducted in R, version 3.4.2 (R Core Team 2017). To calculate activation energies, E_A (eV), and optimum temperatures for each species, a Boltzmann–Arrhenius relationship was created by plotting the natural logarithm of the binned mean ODBA (or TBF for smalltooth sawfish), against $(Tk)^{-1}$, where T is absolute temperature (K) and k is Boltzmann's constant, 8.62×10^{-5} eV/K (Fig. 1). Previous studies have shown that ODBA and TBF both scale with body size, with smaller individuals typically displaying greater ODBA and TBF than larger individuals in a range of species, including elasmobranchs (Halsey et al. 2009b; Whitney et al. 2012). Therefore, body size (measured as stretch total length, TL) was included as a predictor in the Boltzmann–Arrhenius model, allowing body size to change the intercept of this relationship (see Electronic Supplement 1 for a detailed description of Arrhenius model formulation). For species where activity began to decline at high temperatures, the optimum temperature (T_{opt}, the temperature at which performance is maximised) was determined by calculating the Arrhenius breakpoint temperature (Casselman et al. 2012; Chen et al. 2013). This was done by performing a breakpoint analysis on the Arrhenius relationship using the segmented package in R (Muggeo 2008). E_A was calculated as the negative slope of the Arrhenius relationship (Gillooly et al. 2001; Irlich et al. 2009), excluding data from temperatures above the optimum temperature so that E_A described the relationship between activity and temperature only in its positive range.

Following the calculation of T_{opt}, the individually binned volitional body movement data were fit with a thermal performance curve via minimum least squares nonlinear regression using the 'minipak.lm' package (Elzhov et al. 2016), with the following two-part equation for performance (P) (Deutsch et al. 2008; Gannon et al. 2014; Payne et al. 2016):

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

where S is a scalar, T_{opt} is the temperature (T) determined by the Arrhenius breakpoint, CT_{max} is the upper critical temperature where P is zero, σ is the standard deviation for the normally distributed part of the curve, and s_f is the scaling

factor for body size (measured as TL). S, CT_{max}, σ, and s_f were input into the equation as variables, with values determined by the best-fit equation output by the nonlinear regression. Although T_{opt} could also have been input as a variable instead of a constant, with the value determined by the regression as has been done in previous work (e.g. Gannon et al. 2014; Payne et al. 2016), we instead used the Arrhenius breakpoint to estimate T_{opt}. This method produced models with substantially better fit (measured as lower AICc) than models where T_{opt} was included as a variable. Previous studies using similar methods have also not included body size as a predictor in thermal performance curve calculation, however, the large size range in some of our datasets and the relationship between ODBA or TBF and body size (Halsey et al. 2009b; Whitney et al. 2012) necessitated this correction (see Electronic Supplement 1 for a detailed description of performance curve model formulation).

For species with activity responses that showed a T_{opt} and where thermal performance curves were estimated, the performance breadth was also calculated. The performance breadth was defined as the temperatures where performance reached at least 90% of the maximum value of performance observed at the T_{opt} (Ferreira et al. 2014; Farrell 2016).

Results

Acceleration data were successfully collected from all species, with logger deployments ranging from 18 to 204 h, and acceleration transmitter deployments ranging from 5 to 299 days (Table 1). Body movement was positively correlated with temperature in all species (e.g. Fig. 2) up to T_{opt}. Activity increased with temperature in accordance with the Boltzmann–Arrhenius model for reaction rates, with $r^2 > 0.75$ for the Arrhenius relationships in each species

(Fig. 3). E_A ranged between 0.13 eV (juvenile blacktip and lemon sharks) and 0.76 eV (adult bull sharks) (Table 2). Juveniles in confined habitats generally had lower values of E_A compared to adults in open habitats, with the mean E_A for juveniles (0.23 ± 0.12 eV) significantly lower than the mean E_A for adults (0.58 ± 0.24 eV; t test $P = 0.029$, $T = -2.73$, $df = 7$). This indicates that species occupying more open habitats had steeper slopes to their relationships between temperature and activity. The exception to this trend was adult sandbar sharks, which had a low E_A of 0.23 similar to values from nursery-bound juveniles (Fig. 3).

An Arrhenius breakpoint, representing T_{opt}, was determined for seven of the ten datasets, and two-part performance curves were fit to each (Fig. 4). Not all individuals provided activity data for the full temperature range, and therefore, sample sizes for calculating Arrhenius breakpoints and thermal performance curves varied throughout the temperature range (see Fig. 4). Adult tiger shark, sandbar shark, and bull shark activity did not show an Arrhenius breakpoint or decline in activity at high temperatures. Therefore, performance curves and optimum temperatures could not be estimated for these species; however, the lack of a decline in performance at high temperatures indicated that T_{opt} for these species was higher than the data collection temperature range, providing a lower limit for T_{opt} (Table 2). Estimates of T_{opt} in the species showing a decline in activity ranged from 29.8 to 33.3 °C, between 2.1 and 6.9 °C lower than the corresponding maximum environmental temperatures (Table 2, Fig. 4). Comparing these T_{opt} estimates with the frequency distributions of environmental temperatures in each habitat produced an approximation of the percent of time during a year that animals spend above their T_{opt}. This ranged from < 2.5 to 24.2% for adult animals in open ocean habitats, and from 10.7 to 39.2%

Fig. 2 An example of the long-term relationship between body acceleration and temperature, showing mean daily body acceleration and temperature data over a period of approximately 5 months (July to December) from a juvenile bull shark *Carcharhinus leucas* from the Fitzroy River, Western Australia. Data show the gradual increase in body acceleration following the seasonal increase in temperature typical of all species studied here
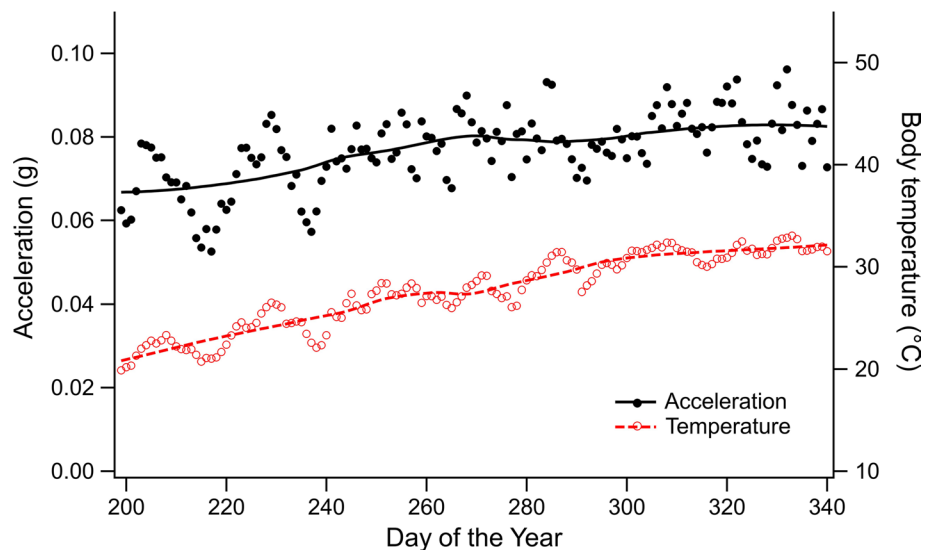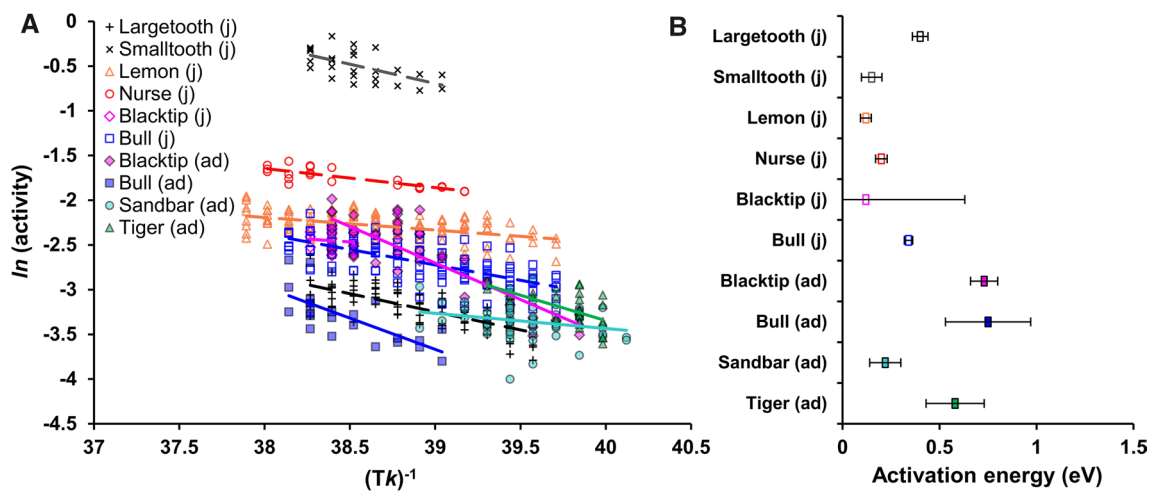
Fig. 3 **a** Arrhenius relationships plotted for each dataset (see Fig. 1). Juvenile datasets (j) are plotted with a dashed line and empty shapes, and adult datasets (ad) with a solid line and solid shapes. Note that activity in smalltooth sawfish was measured as tailbeat frequency (tb s^{-1}), while activity in all other species was measured as overall dynamic body acceleration (g). Sample size for each dataset can be found in Table 1. **b** Activation energies for each dataset with standard error. The error bars for the juvenile blacktip activation energy reflect the large error associated with this point, due to the activation energy for this group calculated from only a 3 °C temperature range, and indicate that this value should be interpreted with care

Table 2 Activation energies (E_A), optimum temperatures (T_{opt}), 90% performance breadth, and the upper limit of the 90% performance breadth for each species and life-history stage in relation to environmental temperature regimes

Species	Life stage	Temp. range (°C)	E_A	Topt (°C)	Max. env. temp. (°C)	% Time above T_{opt}	Performance breadth (°C)	Upper 90% performance limit (°C)
Carcharhinidae								
Bull shark (*C. leucas*)	Ad	23–31	0.69 ± 0.10	> 31	32	< 2.5	–	–
	Juv	19–35	0.32 ± 0.01	31.4 ± 1.7	38	35.6	8.5	34.4
Blacktip shark (*C. limbatus*)	Ad	18–31	0.86 ± 0.09	29.9 ± 0.7	32	24.2	4.8	30.7
	Juv	28–32	0.13 ± 0.51^a	29.8 ± 1.7	33	22.4	9.9	32.7
Sandbar shark (*C. plumbeus*)	Ad	16–25	0.24 ± 0.04	> 25	28	< 18.2	–	–
Tiger shark (*G. cuvier*)	Ad	16–30	0.75 ± 0.07	> 30	32	< 16.8	–	–
Lemon shark (*N. brevirostris*)	Juv	19–36	0.16 ± 0.02	33.3 ± 0.9	37	–	14.2	36.8
Ginglymostomatidae								
Nurse shark (*G. cirratum*)	Juv	25–34	0.23 ± 0.04	32.4 ± 1.0	36	–	7.3	34.0
Pristidae								
Smalltooth sawfish (*P. pectinata*)	Juv	25–32	0.31 ± 0.03	30.7 ± 2.2	33	10.7	7.1	31.9
Largetooth sawfish (*P. pristis*)	Juv	20–32	0.40 ± 0.07	31.1 ± 0.8	38	39.2	11.3	37.6

The maximum environmental temperatures (Max. env. temp.) and the percentage time that a species' habitat was above T_{opt} (% time above T_{opt}) are listed for each species with available environmental temperature data. Temperature range (Temp. range) designates the temperatures over which data were collected. All temperatures are reported in °C. E_A and T_{opt} are reported ± standard error

Juv juvenile, *Ad* large immature to adult

$^a E_A$ was calculated using only a 3 °C temperature range and should be interpreted with care

for juvenile animals in confined nursery habitats. Performance breadth was smallest in adult blacktip sharks (4.8 °C), and larger for juvenile datasets, ranging from 7.1 to 14.2 °C, with an average of 9.7 ± 2.7 °C (Table 2).

Although CT$_{max}$ could also be estimated for species showing a decline in activity using Eq. (1), for our datasets, these estimates relied on considerable extrapolation, as animals typically did not spend substantial time

Fig. 4 Body activity–temperature relationships for each dataset. Thermal performance curves are plotted for datasets showing a decline in activity at high temperatures, with the curve plotted using the mean stretch total length (TL) from each dataset. Dashed vertical lines indicate optimum temperatures estimated at the Arrhenius breakpoint (see Fig. 1). Blue vertical lines show the limits of the 90% performance breadth. For species with available long-term environmental temperature data, mean daily temperature frequency distributions are plotted in grey, showing the percentage of time when the respective habitat of each species was at each temperature. Where long-term daily temperature data were not available, red dashed vertical lines denote minimum and maximum environmental temperatures for the habitat. Juvenile datasets are designated by (juv), and large immature and adult datasets by (ad). Overall dynamic body acceleration (ODBA) was used as the performance metric for all species except smalltooth sawfish, where tailbeat frequency (TBF) was used instead because of divergent ODBA measured by the two tagging techniques used in this species. Sample sizes for all datasets can be found in Table 1 (color figure online)
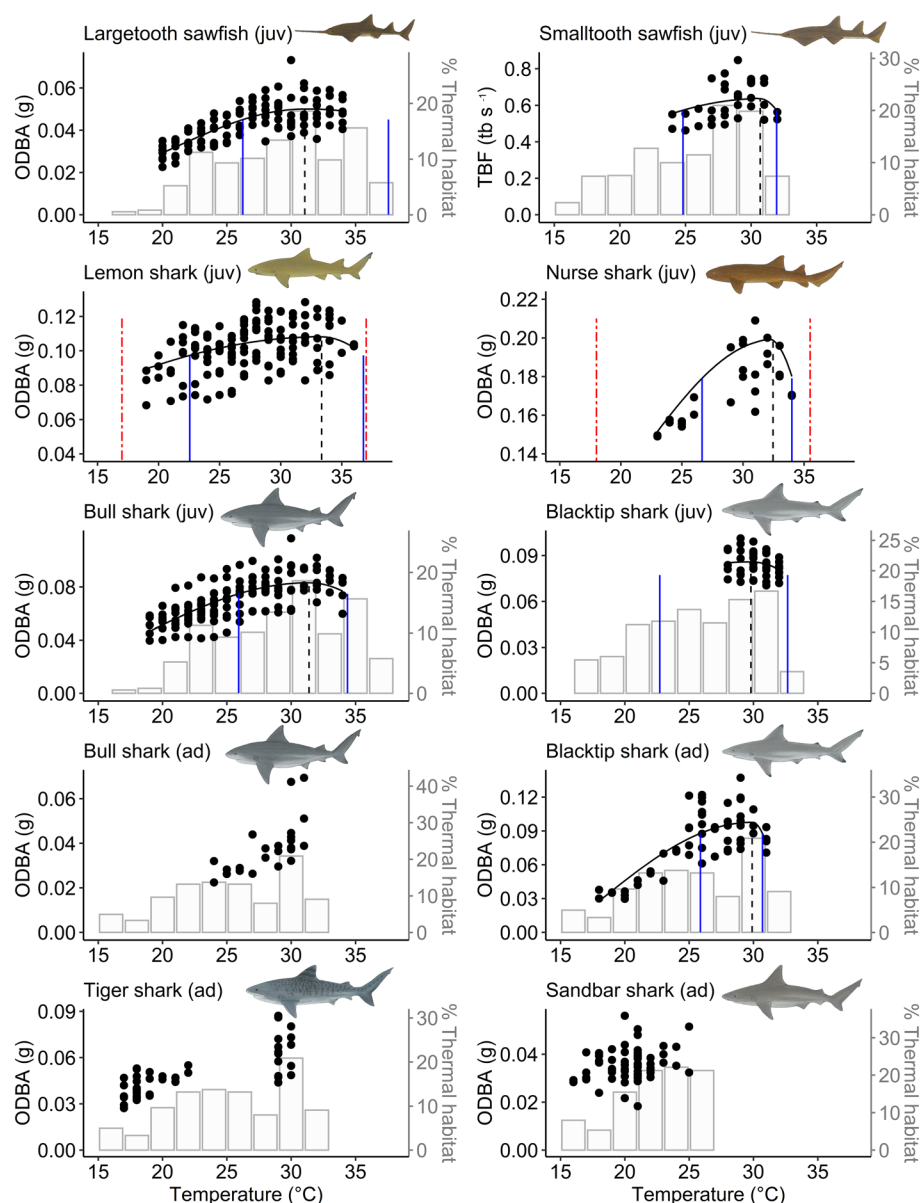
at temperatures above T_{opt}. Consequently, the downward slopes of the thermal performance curves and CT_{max} in each species were estimated based on only a few data points and may incur large errors, and thus are not reported here.

Discussion

Our field measurements of body activity and temperature provided activation energies for all species and life-history stages, as well as thermal performance curves, estimates of T_{opt}, and estimates of the performance breadth for seven of the ten datasets. This information provides a first look into how temperature correlates with behaviour and activity

patterns for many of these species. These analyses also revealed some important patterns in the thermal tolerance regimes of species and life stages occupying different habitat types. Constructing thermal performance curves from volitional activity of wild individuals relies on fish spending time at a range of temperatures. Consequently, this method was more successful for animals confined to habitats that reached high temperatures, including nursery-bound juveniles. However, even in species where a full thermal performance curve could not be estimated, the difference in activation energies and the relationships between environmental temperature and performance regimes quantified here still lend an important ecological perspective to how temperature affects these animals.

Thermal performance curves and optimum temperatures

Acceleration data allowed for the estimation of performance curves, including an estimated T_{opt} and performance breadth, for all juveniles occupying confined nursery habitats. This trend can be attributed to the confined space use of juveniles in nursery habitats compared to the larger wide-ranging animals. Most of the juveniles studied here remain in restricted nursery habitats for up to several years to take advantage of protection from larger predators and increased food availability (Heupel et al. 2007; Grubbs 2010). Because juveniles are often limited to specific habitats, they may be forced to remain in a particular area even if temperatures rise above optimal levels, making it easier to collect data above the T_{opt} in these animals.

On the other hand, the migratory capability of larger elasmobranchs allows these animals to move to more suitable habitats when temperatures rise, making it difficult to collect wild activity data above their T_{opt}. Adult blacktip sharks were the exception to this trend. Despite their potential to migrate to cooler, offshore habitats, this group showed a decline in activity at high temperatures indicating that this species remained in waters even after temperatures exceeded their T_{opt}. Blacktip sharks are known to be associated with shallow coastal habitats (Castro 1996; Drymon et al. 2010), and may remain in these areas even at temperatures above T_{opt} for other life-history reasons such as food availability, protection from larger sharks, or to remain close to reproductive locations.

Although T_{opt} could not be specifically estimated for species that did not show a decline in activity within the data collection temperature range, these data did provide a lower limit to T_{opt} in these species. This can be useful in determining how animals' thermal performance regimes relate to the environmental temperatures they experience. For example, while T_{opt} could not be estimated for adult bull, tiger, and sandbar sharks, data were collected up to within 1 °C of the maximum environmental temperature measured in the habitats of these species, indicating that these animals rarely spend time above their T_{opt} in the wild. It is also notable that the T_{opt} estimated here for tiger sharks, > 30 °C, was substantially higher than the T_{opt} for the same species estimated by Payne et al. (2018) of 22 °C. This 22 °C T_{opt} was estimated based on acceleration data collected from five tiger sharks in Hawaii which were larger (2.4–3.9 m) than the animals studied here, and typically inhabit cooler, pelagic environments than the warmer, relatively shallow areas in the Gulf of Mexico where the tiger sharks in the present study were tagged. The differences in T_{opt} could be due to sharks behaviourally interacting with their habitat and thermal environment in different ways, for example, the more pelagic sharks likely experience a wide range of temperatures through changing their vertical habitat use, while the shallower Gulf of Mexico animals would experience temperature variation more through broad scale seasonal temperature changes. Additionally, these tiger shark populations are genetically distinct (Bernard et al. 2016), and could have evolved different thermal tolerance ranges. The sharks in Payne et al. (2018) were also all tagged during the same time of year, and thus acceleration data were not collected from animals seasonally acclimated to a large temperature range, but rather sharks experiencing an acute temperature change. Regardless, the differences in estimated thermal performance regimes between these two studies emphasise that caution needs to be exercised when applying thermal performance data from one population or environment to another, particularly if different ecologies may result in the expression of divergent behaviours.

Vulnerability to temperature change

Comparing the estimates of T_{opt} and the 90% performance breadth with environmental temperature distributions and limits lends valuable information about how thermal performance of individuals may regulate their success or the threats they are likely to experience in their respective habitats. In most cases, the maximum temperatures measured in confined nursery habitats were several degrees higher than the T_{opt} estimated for the corresponding juveniles. As a result, some of these animals may be forced to spend a substantial amount of time at temperatures above their T_{opt}, for example, mean environmental temperatures in the Fitzroy River were above the T_{opt} of freshwater sawfish for nearly 40% of the year. However, while they may spend prolonged periods above T_{opt}, for most juveniles, the maximum environmental temperature was close to the upper limit of their 90% performance breadth (see Fig. 4). Therefore, while these animals may hover on the cusp of declining performance for a substantial part of the year, they would not regularly experience temperatures that cause a substantial decrease in performance. This is largely due to these juvenile animals having a wide performance breadth which covers a large proportion of the temperatures they experience annually. For example, the habitats for juvenile blacktip sharks, smalltooth sawfish, largetooth sawfish, and bull sharks remained at temperatures within their 90% performance breadth for between 57 and 73% of the year, while the habitat for the wider ranging adult blacktips was only within their 90% performance breadth for 30% of the year. In combination with the generally low activation energies calculated for juveniles, this indicates that animals occupying confined habitats tend to have a flatter shape to their thermal performance curves compared to species in more open habitats, or a more muted behavioural response to temperature. These gradual curves with wide performance

breadths are typical characteristics of performance regimes in 'thermal generalists' (Gilchrist 1995; Kingsolver 2009), and may be key in allowing animals, including many juveniles, to survive and succeed in shallow, protected coastal areas with greater temperature variation and high maximum temperatures.

The performance regimes established for the larger animals in more open habitats show a different story. T_{opt} in most species occupying more stable open ocean habitats was estimated to be near or above the maximum measured environmental temperature, meaning that the upper limit to their performance breadth would likely be well above any environmental temperatures they experience. Considering the high capacity for these animals to migrate long distances and exploit different habitats, they are less likely to be required to spend substantial time above T_{opt} or near the limits of their performance breadth, and as a result are not likely to regularly experience the same type of thermal pressure as smaller site-restricted animals. Potentially because of this reduced threat of decreased performance at high temperatures, non-site-restricted species generally had higher activation energies, meaning that the shape of their performance curves was steeper. Steeper curves result in narrower performance breadths, which we saw in adult blacktip sharks, and are more typical of 'thermal specialists' (Gilchrist 1995; Kingsolver 2009). While steep and narrow curves introduce a higher risk of physiological distress above T_{opt}, steeper slopes also allow these species to have a greater range in physiological performance over a small change in temperature.

There are several possible explanations for the shift in thermal performance characteristics between small elasmobranchs in confined habitats and larger elasmobranchs in more open habitats. In general, the activation energies calculated here for larger animals (mean 0.58 eV) are similar to activation energies for voluntary activity in a range of other taxa (mean 0.52 eV; Dell et al. 2011), as well as the average activation energy for metabolic rate of 0.6–0.7 eV (Gillooly et al. 2001, 2002; Irlich et al. 2009). The similarity in activation energies of most physiological traits with those of metabolic rate is thought to indicate that physiological performance is largely linked to metabolic demands and capacities (Gillooly et al. 2001; Brown et al. 2004; Dell et al. 2011). However, the lower activation energies in smaller elasmobranchs, including the juveniles in this study, are not likely due to a systematic difference in temperature dependence of metabolic demands governed by body size, though to our knowledge, shifts in temperature dependence of metabolic rate with body size have not been examined in elasmobranchs. As an alternative possibility, performance traits that are tightly linked to survival, such as escape velocities in prey species, often have lower activation energies (Dell et al. 2011). For example, Dell et al. (2011) found an

average activation energy for escape velocities of 0.39 eV in a range of species. Smaller elasmobranchs that typically occupy more confined habitats, including juveniles, are more susceptible to predation than their larger counterparts, and may maintain high performance across temperatures to limit predation risk, resulting in low activation energies. If maintaining high performance at low temperatures is costly, the larger animals with lower predation risk may allow performance to drop at low temperatures, as a low performance capacity may impact foraging success in these larger animals, but is less likely to affect survival (i.e. the life dinner principle; Dawkins and Krebs 1979; Dell et al. 2011).

Considering that many elasmobranchs, including most of those studied here, show ontogenetic shifts in habitat use, it is likely that these animals shift their thermal performance responses throughout ontogeny. The direct comparisons of thermal performance regimes between juvenile and adult stages are limited here to two species (bull sharks and blacktip sharks), and therefore, it is difficult to determine with certainty whether such ontogenetic shifts occur. However, both of these species show higher activation energies and steeper slopes to their performance curves as adults than as juveniles, a trend supported by the data from other juvenile and adult life stages studied here in different species. The shifting of thermal performance responses with ontogeny has been observed in a range of other taxa, where the higher temperatures and fewer opportunities for thermoregulation typical of confined juvenile habitats generally lead to increased thermal tolerance in juveniles compared to adults. Previous studies have recorded this shift through changes in T_{opt} or CT_{max} (e.g. Krebs et al. 1998; Klok and Chown 2001; Winne and Keck 2005; Bowler and Terblanche 2008). In the present study, T_{opt} could only be estimated for both juveniles and adults of blacktip sharks, which showed a near identical T_{opt} (29.8 °C and 29.9 °C, respectively). The T_{opt} for juvenile and adult bull sharks may also be similar, at 31.3 and > 31 °C, respectively. Though these comparisons are limited to two species, these results do not suggest an ontogenetic shift in T_{opt} for activity. However, in both species, activation energies substantially increased between juvenile and adult life stages. Rather than a horizontal shift in physiological performance, it is possible that the shape of the thermal responses shifts through ontogeny. As a result, juveniles can maintain shallow, gradual curves with wide performance breadths to mitigate the inability to avoid unfavourable thermal conditions, while adults may develop steeper, narrow curves to achieve high levels of performance once they gain the ability to migrate long distances and select habitats with preferred thermal characteristics. Such shifting in the shape of thermal performance regimes between ontogenetic stages has been observed previously in insects (Bowler and Terblanche 2008); however, to our knowledge, this process has not been documented in fish.

With the direct comparisons of thermal performance regimes between juvenile and adult stages limited here to two species, it is not possible to distinguish whether the shifts in thermal performance regimes are driven specifically by ontogeny, or are a by-product of shifting habitat use between ontogenetic stages. This could be further examined by studying the thermal performance regimes of both juveniles and adults from species that do not use specific nursery habitats, such as tiger sharks or other pelagic species, or those where adults remain in relatively shallow areas, such as lemon sharks. Regardless of this, there is a clear difference in the thermal performance and thermal pressures experienced by smaller animals occupying confined habitats and larger animals in open water habitats, whether driven by ontogenetic development, habitat use, or a combination of the two factors, which have implications for how animals in each group are likely to respond to changing temperature regimes.

Responses to environmental change

With the capacity to migrate long distances and environmental temperature limits well within the putative 90% performance breadth for most large elasmobranchs in open water habitats, these animals have a substantial buffer in their thermal response that may allow them to cope with climate change-induced increases in temperature without major impacts to their daily behaviour and activity. Conversely, smaller species in confined habitats that already spend substantial time above their T_{opt} and in the upper limits of their performance breadth are at risk of experiencing substantial physiological effects following a relatively small increase in environmental temperature (Angilletta et al. 2002; Huey et al. 2012; Dowd et al. 2015).

In general, animals can mitigate long-term changes in temperature in several ways. First, animals can shift their geographic distribution to remain within their preferred temperature regimes. This has already been observed in many marine taxa, including fish (Perry et al. 2005; Burrows et al. 2011; Sunday et al. 2012), and for the wide-ranging elasmobranchs in open habitats, this may be feasible. For example, the large migration of blacktip sharks off the coast of South Florida is known to be driven by water temperature (Castro 1996; Kajiura and Tellman 2016), with some indications that this species is shifting northward. However, permanent shifts in distributions may not be possible for most animals connected to specific habitats, including some nursery-bound juveniles. This is particularly true for juveniles of philopatric species that are genetically associated with specific nurseries, including several of the elasmobranchs studied here (Feldheim et al. 2014, 2017; Chapman et al. 2015). However, there is some evidence of latitudinal shifts in nursery habitats in response to rising temperatures when multiple potential nursery habitats for a species are available on a latitudinal gradient (Bangley et al. 2018). Animals could also alleviate effects of climate change through evolution of thermal performance regimes in response to rising environmental temperatures (Angilletta et al. 2002; Sinclair et al. 2016); however, particularly considering the long generation times typical of elasmobranchs, genetic adaptation of thermal performance may not be able to keep pace with climate change in many species.

With potentially limited capabilities for latitudinal range shifts or evolution of thermal performance regimes, elasmobranchs that are bound to specific habitats and confronted with high-temperature regimes will instead likely have to mitigate the physiological effects of rising temperatures through changes in behavioural patterns (Kearney et al. 2009; Bonebrake et al. 2014; Sunday et al. 2014; Woods et al. 2015). These behavioural effects of changing temperatures, including elevated energy demands, capacity for activity, and habitat use, can have far-reaching impacts on success and long-term fitness of these animals (Gunderson and Leal 2016). For example, animals may mitigate rising temperatures by shifting patterns of behavioural thermoregulation, diel activity cycles, or use of microhabitats to avoid high temperatures, but these shifts will also affect interactions with predator and prey species (Dell et al. 2014). Limiting activity or time spent at high temperatures or in certain microhabitats may also constrain an animal's energy budget by reducing foraging opportunities or effort alongside increased metabolic demands (Kearney et al. 2009; Sinervo et al. 2010). In the case of juvenile elasmobranchs confined to nursery habitats, reducing the fitness of these animals through behavioural pathways could substantially affect adult population size or viability in these species, as juvenile survival is one of the most important indicators of population growth or persistence in elasmobranchs, particularly in long-lived and slow-maturing species (Cortés 2002, 2004; Mollet and Cailliet 2002).

Forecasting the consequences of climate warming is often done by evaluating the critical temperature limits and potential lethal endpoints of rising temperatures (Deutsch et al. 2008; Hoffmann 2010; Somero 2010). However, the sub-lethal daily or seasonal effects on behaviour and physiological performance are likely the more common result of rising temperature regimes, and have the potential to significantly alter the fitness of animals spending substantial time in environments above their T_{opt}. These sub-lethal behavioural effects of rising temperatures should be carefully considered when forecasting climate change impacts for these species or ecosystems, and can be helpful in guiding conservation efforts for species facing challenges from climate change. For example, thermal performance regimes can be used to forecast likely shifts in migration patterns of wide-ranging animals, or predict the temperatures that

may spur shifts in behavioural patterns in animals associated with specific habitats that do not have the capacity to migrate (Deutsch et al. 2008; Huey et al. 2012; Sinclair et al. 2016). Many elasmobranchs, including several studied here, are considered vulnerable, threatened, or endangered, and are also ecologically important as high trophic level predators. Understanding the interplay between the physiologies of these species and their environments is crucial to determining how these animals will cope with fluctuating thermal regimes in the future.

Author contribution statement KOL and ACG conceived the study design and methodology. KOL carried out the analyses and led the writing of the manuscript with guidance from ACG and NMW. All authors assisted with data collection, contributed to the drafts, and gave approval for publication.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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