

RESEARCH ARTICLE

Acclimation potential of Arctic cod (*Boreogadus saida*) from the rapidly warming Arctic Ocean

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ABSTRACT

As a consequence of the growing concern about warming of the Arctic Ocean, this study quantified the thermal acclimation responses of *Boreogadus saida*, a key Arctic food web fish. Physiological rates for cardio-respiratory functions as well as critical maximum temperature ($T_{c,max}$) for loss of equilibrium (LOE) were measured. The transition temperatures for these events (LOE, the rate of oxygen uptake and maximum heart rate) during acute warming were used to gauge phenotypic plasticity after thermal acclimation from 0.5°C up to 6.5°C for 1 month (respiratory and $T_{c,max}$ measurements) and 6 months (cardiac measurements). $T_{c,max}$ increased significantly by 2.3°C from 14.9°C to 17.1°C with thermal acclimation, while the optimum temperature for absolute aerobic scope increased by 4.5°C over the same range of thermal acclimation. Warm acclimation reset the maximum heart rate to a statistically lower rate, but the first Arrhenius breakpoint temperature during acute warming was unchanged. The hierarchy of transition temperatures was quantified at three acclimation temperatures and was fitted inside a Fry temperature tolerance polygon to better define ecologically relevant thermal limits to performance of *B. saida*. We conclude that *B. saida* can acclimate to 6.5°C water temperatures in the laboratory. However, at this acclimation temperature 50% of the fish were unable to recover from maximum swimming at the 8.5°C test temperature and their cardio-respiratory performance started to decline at water temperatures greater than 5.4°C. Such costs in performance may limit the ecological significance of *B. saida* acclimation potential.

KEY WORDS: Climate change, Sea ice ecosystem, Arctic food web, Arrhenius plots, Metabolic rate, Cardio-respiratory performance

INTRODUCTION

Physical and biological conditions in the Arctic Ocean are changing at unprecedented rates (Gaston et al., 2003; Polyakov et al., 2005; Steele et al., 2011; Barber et al., 2015; Berge et al., 2015; Carmack et al., 2015, 2016). Both the quality (Krishfield et al., 2014) and quantity (Vaughan et al., 2013; Perovich et al., 2014) of summer (from July to September) sea ice has decreased appreciably. Sea surface temperature (SST) anomalies up to 5°C were recorded during the summer of 2007 and in some regions of the Arctic Ocean, the 2007 SST summer mean was 7°C greater than the previous 30

year average (Steele et al., 2008; Timmermans and Proshutinsky, 2014). Water temperatures at depths below the surface layer (60–800 m) are also increasing as a result of warming inflows from the subarctic Atlantic and Pacific (Polyakov et al., 2010; Shimada et al., 2006). In summary, the Arctic marine ecosystem is changing physically (e.g. increased temperatures, loss of sea ice, increased stratification, altered light climate), chemically (reduced pH) and biologically (poleward migration of non-native species), all of which will impact the structure of the food web (Gaston et al., 2003; Perry et al., 2005; Grebmeier et al., 2006; Yamamoto-Kawai et al., 2011; Wassmann, 2011; Hutchings et al., 2012; Barber et al., 2015; Carmack et al., 2016; Steiner et al., 2015).

The abundant Arctic cod *Boreogadus saida* survives in ice-covered, sub-zero waters because of the presence of anti-freeze glycoproteins, specialized kidney function (Osuga and Feeny, 1978; Christiansen et al., 1996) and the ability to digest food at –1.4°C water temperatures (Hop et al., 1997). They are a key Arctic marine food web fish species that is potentially threatened with extirpation (Cheung et al., 2008) due to warming and the loss of ice-associated niches (Wyllie-Echeverria et al., 1997). While empirical observations of a northward retreat from their southern-most distributions, e.g. waters off Disko Bay, Greenland, Iceland-East Greenland waters and the Barents Sea (Hansen et al., 2012; Farrell et al., 2013; BarentsPortal, 2013; Astthorsson, 2016), add evidence to these dire predictions for the future of Arctic cod, only a limited number of field-based – and even fewer laboratory-based – thermal physiology studies exist for this key Arctic marine species.

A central question concerns the ability of *B. saida* to acclimate to these changing thermal conditions as there is no consensus for existing observations. Physiological studies show that adult *B. saida* acclimated to both 0.5°C and 3.5°C can be acutely warmed to 10.5°C or 12.4°C, respectively, before peak maximum heart rate ($f_{H,max}$) is reached (i.e. the T_{max}) (Drost et al., 2014). Yet the temperature when heart rate first starts to fail to keep up with acute warming (see Farrell, 2016), the first Arrhenius breakpoint temperature (T_{AB}), was just 3.6°C and 4.7°C, respectively (Drost et al., 2014). These T_{AB} results are similar to the temperature preferendum of *B. saida*, which is between 2.8 and 4.4°C (over a 0–8°C range) depending on the time of day (Schurmann and Christiansen, 1994). Normal embryonic development in newly hatched larvae occurs between –1.0 to 3.5°C, but not $\geq 5^\circ\text{C}$ (Sakurai et al., 1998; Kent et al., 2016) and Graham and Hop (1995) found that developing eggs and newly hatched larvae will die or exhibit severe deformities when exposed to 9°C for 24 h. Also, T_{AB} for heart rate (f_H) of 3.5°C acclimated larval *B. saida* is $3.3 \pm 0.3^\circ\text{C}$ (Drost et al., 2015). Yet, a recent study showed similar daily growth rates of juvenile *B. saida* at 5 and 9°C, which were both faster than at 0°C (Laurel et al., 2016). Lastly, distribution analysis of larval *B. saida* catch data from the Barents Sea Ecosystem Survey (1986–2008) indicate that 85.5% of the 0–1 year age group are found in water temperatures of 1–5°C, with a peak abundance

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List of symbols and abbreviations

AAS	absolute aerobic scope (MMR–RMR) defines the absolute aerobic capacity to perform activities (such as movement, feeding, growth and reproduction)
EKG	electrocardiogram recording of electricity generated by the heart
EPOC	excess post oxygen consumption
FAS	factorial aerobic scope (MMR/RMR)
f_H	heart rate
$f_{H,max}$	maximum heart rate
M_b	body mass
\dot{M}_{O_2}	rate of oxygen uptake (measured in mg O ₂)
Q_{10}	the effect of temperature. Quantifies the increase in a rate caused by a 10°C increase in temperature. When a rate doubles, $Q_{10}=2$; when a rate triples, $Q_{10}=3$
QRS complex	EKG recording that represents ventricular contraction
RMR	routine metabolic rate
SMR	standard metabolic rate: the minimum sustainable level of \dot{M}_{O_2} in fishes – this is an obligatory expense, on top of which all other costs are added
T_{AB}	first Arrhenius breakpoint temperature, when $f_{H,max}$ first fails to keep up with acute thermal warming
T_{AR}	the temperature when $f_{H,max}$ becomes arrhythmic
$T_{c,max}$	critical temperature when fish first roll over as a result of acute warming (3°C h ⁻¹)
T_{crit}	critical temperature when AAS=0 as extrapolated from AAS regression curve – beyond this temperature a fish is forced into an anaerobic and time-limited lifestyle
T_{FS}	the temperature when FAS stays below 2
T_{lpej}	lower pejus temperature when the aerobic scope decreases below 90% of T_{opt} (AAS)
T_{max}	when $f_{H,max}$ first reaches maximum bpm
T_{opt} (AAS)	the optimal temperature under which an animal has the greatest capacity to perform a certain activity
T_{pej}	pejus temperature when peak performance begins to decline
T_{QB}	the temperature when incremental Q_{10} drops permanently below 2
T_{QR}	the temperature when the EKG recording of the QRS peak height (measured from Q to R) starts to permanently decline
T_{upej}	upper pejus temperature when the aerobic scope drops decreases below 90% of T_{opt} (AAS)

between 2 and 4°C depending on average summer temperatures [B. Rajasakaren, Distribution of polar cod (*Boreogadus saida*) in the Barents Sea – A useful indicator of climate change? MSc thesis, University of Bergen, 2013], but catch and acoustic studies report *B. saida* in Arctic waters ranging from 0 to 9°C (Moulton and Tarbox, 1987; Crawford and Jorgenson, 1996; Crawford et al., 2012; Coad and Reist, 2004; Walkusz et al., 2011, 2013).

Thus, *B. saida* clearly have some capacity for thermal acclimation as do (despite the differences in evolution) Antarctic species, which experience true stenothermal conditions year round (Pörtner et al., 2000; Lannig et al., 2005; Seebacher et al., 2005; Franklin et al., 2007). Thermal acclimation likely translates into a capacity for *B. saida* to exploit the thermally stratified Arctic Ocean in the summer (see Fig. 1A). Nevertheless, our understanding of the thermal physiology of *B. saida* remains far from complete. Notably, studies of oxygen uptake are limited to measurements of routine metabolic rate (RMR) between –1.5 and 6.0°C (Holeton, 1974; Steffensen et al., 1994; Hop and Graham, 1995; Kunz et al., 2016). Based on temperature and holding

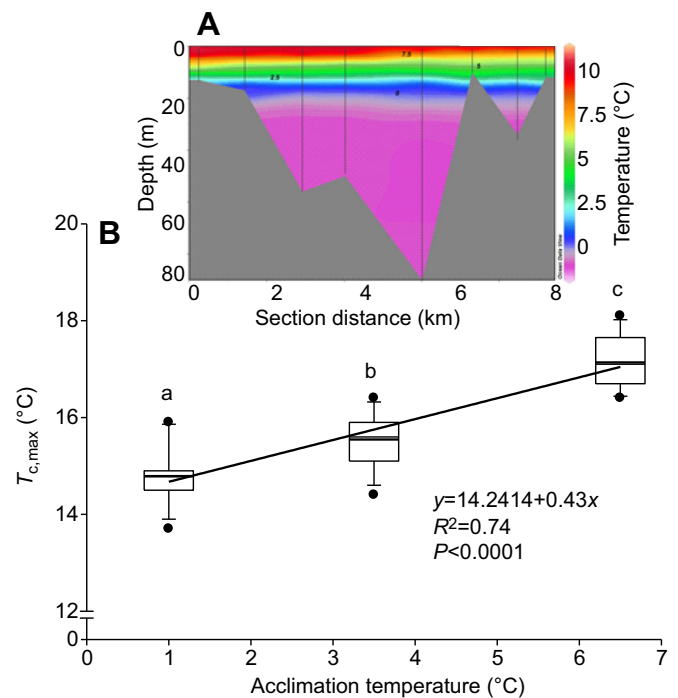


Fig. 1. Slope of $T_{c,max}$ acclimation potential compared with sea surface temperature maximum. (A) In Cambridge Bay, Nunavut, water temperatures ranged from –1.5°C at >30 m depth to ~10°C at the surface on August 11th, 2011, as shown above from a 9 km transect measuring temperature and depth at 8 stations. (B) Box plots of the critical thermal maximum ($T_{c,max}$; mean \pm s.e.m.) of individual *Boreogadus saida* ($n=13$) acclimated for 1 month at 1.0, 3.5 and 6.5°C. The boundary of the box closest to zero indicates the 25th percentile, a line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Error bars above and below the box indicate the 90th and 10th percentiles and black circle symbols are the outlying points. Different letters at each acclimation temperature denote statistical difference for mean values using one-way ANOVA ($P<0.05$) and slope=0.43, derived from the linear regression line equation. *Boreogadus saida* were collected near Cambridge Bay (69°N, 105°W), Nunavut, Canada.

duration for *B. saida*, these studies have produced remarkably similar values of oxygen uptake. Nothing is known about the absolute aerobic scope for *B. saida* or its acclimation potential. Therefore, the present study combined three measurements to characterize thermal tolerance and acclimation potential, including: (1) $T_{c,max}$ (a replacement for upper incipient lethal temperature; Fry, 1947); (2) absolute aerobic scope (AAS; Fry, 1947); and (3) $f_{H,max}$ (Fry, 1947; Casselman et al., 2012). Both the aerobic scope (e.g. Brett, 1962; Ultsch et al., 1980; McKenzie et al., 2012; Eliason et al., 2013a; Killen et al., 2014; Del Raye and Weng, 2015) and f_H (Stillman, 2002; Blank et al., 2004; Braby and Somero, 2006; Franklin et al., 2007; Sidhu et al., 2014; Chen et al., 2013; Verhille et al., 2013; Anttila et al., 2014; Ferreira et al., 2014) measurements have been reinstated to investigate the thermal niches of fishes in this era of rapid climate change. We tested the hypothesis that the cardio-respiratory system of *B. saida* would thermally acclimate at 0.5, 3.5 and 6.5°C. We also hypothesized that breathing rates in 1°C acclimated fish would always return to resting after being chased faster than 6.5°C acclimated fish, which in fact turned out to be the opposite. We did, however, anticipate that the suite of physiological rate transition temperatures would show a predictable order, as seen previously in goldfish (Ferreira et al., 2014; Farrell, 2016). We additionally hypothesized that regardless of acclimation

temperature, the temperature at which cardiac arrhythmias develop (T_{AR}) would be lower than $T_{c,max}$ and that the temperature for peak AAS (T_{opt}) would be similar to T_{AB} .

MATERIALS AND METHODS

Animal care

Fish were collected, held and tested in accordance with permits issued by the Kitikmeot Hunters and Trappers Association – Nunavut, the Canadian Council on Animal Care (A10-0236), the University of British Columbia Committee on Animal Care (A11-0267), the Freshwater Institute Science Laboratories Animal Care Committee – Arctic Aquatic Research (FWI-ACC-2012-050) and the Vancouver Aquarium Animal Care Committee (2011–04). Adult *Boreogadus saida* (Lepechin 1774) were caught in August 2011 and in July 2012 near Cambridge Bay on Victoria Island, Nunavut, Canada (69°12'N; 105°05'W), as detailed previously (Drost et al., 2014). In brief, *B. saida* were held at 0°C for up to 4 weeks at Cambridge Bay to ensure good health before being transported by air at 0°C to the Vancouver Aquarium, British Columbia, Canada. At the Vancouver aquarium laboratory, *B. saida* were held in a closed-system 450 litre tank with a daily 50% replacement of sump water as well as cleaning. Fish were fed to satiation with frozen krill, usually every 1–2 days and were exposed to a fluorescent light and dark cycle that represented Vancouver (49°N) daylight conditions. Food was withheld for a minimum of 36 h before any experimentation. The order of experiments minimized the risk of fish mortality, testing $f_{H,max}$ first and $T_{c,max}$ last.

Thermal acclimation

Fish were maintained at acclimation temperatures of 1.0, 3.5 and 6.5°C ($\pm 0.5^\circ\text{C}$) for a minimum of 1 month before $T_{c,max}$ and AAS measurements were performed. A 6 month acclimation period was used prior to $f_{H,max}$ measurements. Limited fish numbers required the use of some, but not all fish, for more than one test and at more than one acclimation temperature. Previous studies have shown a significant reduction in resting metabolic rate after >5 months in captivity (Hop and Graham, 1995), but the present fish were in captivity much longer before testing, some for more than 1 year. Also, the response of $f_{H,max}$ to acute warming was similar when measured in Cambridge Bay just 10 days after capture and acclimation to 0.5°C and 3.5°C when compared with measurements at Vancouver aquarium more than 6 months after capture (Drost et al., 2014).

Critical thermal maximum ($T_{c,max}$)

$T_{c,max}$ was defined in this study as the temperature when a fish first began to roll over during acute warming at a rate of 3°C h^{-1} ($0.05^\circ\text{C min}^{-1}$). Each $T_{c,max}$ measurement used 10 fish that were progeny from the 2011 wild fish that had bred at the Vancouver aquarium (4 years old) and 3 fish that were wild-caught (estimated at 6 years old) collected in either 2011 or 2012 near Cambridge Bay. The range in mass was from 32.9 to 101.8 g, with the combined average mass of 65.8 ± 5.4 g (see Table S1 for individual fish mass). For each test, fish were not fed for 48 h before transfer into an individual insulated cooler with aerated and temperature-controlled InstantOcean seawater (<http://www.instantocean.com>; volume=27 litre; salinity=30 ppt) where they were held overnight to recover from handling stress at their acclimation temperature. Water temperature was regulated with a refrigerant coil attached to a programmable chiller (Fisher Isotemp 3016d) and two thermometers (Fisher Scientific Type K digital thermometer probe; FireSting Y, with $\pm 0.1^\circ\text{C}$ precision) that were calibrated to 0°C in ice-water during the

trials using a Fisher Scientific Type K digital thermometer. Black netting was placed over the top of the cooler to maintain low light conditions and ensure fish containment. Water was acutely warmed until the fish first lost equilibrium rather than waiting for a full 10 s of disequilibrium (Chen et al., 2015). This endpoint and a quick transfer into a recovery tank at 4°C prior to return to their holding tank resulted in no fish mortality. No fish was retested without at least a 7 day recovery period.

Absolute aerobic scope (AAS)

Routine oxygen uptake (RMR) was measured from the decline in dissolved oxygen saturation of water within two custom-made, intermittent-flow, airtight and lightproof respirometers $8.0 \times 15.5 \times 22.5$ cm. Gut evacuation from repletion in *B. saida* took 36–70 h at -1.5 to -0.5°C , with an average of 51 h (Hop et al., 1997). Thus, after a 48 h fasting period, a fish was transferred to each of the two respirometers, which were connected to a 32 litre, closed-circuit sump that contained two refrigerant coils attached to two programmable chillers (Fisher Isotemp 3016d; www.fisherssci.com) filled with 60% propylene glycol antifreeze. The seawater sump was continuously aerated and also held a magnetic drive pump. Water temperature was controlled by the recirculating chillers and measured to a precision of $\pm 0.1^\circ\text{C}$ (Fisher Scientific Type K digital thermometer probe). A pilot experiment that measured oxygen uptake over 47.5 h while wild-caught *B. saida* became accustomed to the respirometer found that RMR stabilized between 12 h and 22 h (see Fig. 2A, inset). Consequently, all RMR measurements began following an overnight acclimation of minimally 12 h. Water temperature was adjusted at a rate of 3°C h^{-1} to the desired acute test temperature for that experiment: 0.5, 2.0, 3.5, 5.0 and 7.5°C for the 3.5°C acclimation group, and 0.5, 2.5, 4.5, 6.5 and 8.5°C for the 1.0°C and 6.5°C acclimation groups. At the test temperature, fish were held for 1 h before measuring RMR using closed respirometry that recorded the depletion of oxygen from the water with a fibre optic oxygen meter for up to 30 min (Firesting O₂, PyroScience, Aachen, Germany). This procedure was repeated 2–3 times and the lowest value was reported as RMR. Then, the fish was removed from the respirometer and placed in a ~12 litre circular tank containing aerated water at the test temperature for exhaustive exercise. Chasing involved a 5 min period of hand chasing, gentle tail pinches and lifting until unresponsive to touch, followed by brief air exposure (Norin and Clark, 2016). The fish was returned to the respirometer and oxygen uptake measurement resumed within 30 s and continued over 5–30 min, depending on the test temperature. The maximum oxygen uptake (MMR) was calculated from the steepest 2–5% decrease in percentage water saturation, which occurred consistently at the start of recording. Water oxygen saturation never decreased below 75% saturation for any measurement. After the MMR measurement, fish were weighed, pit tagged (if newly tested) and returned to their acclimation tank. AAS was calculated as $\text{MMR} - \text{RMR}$ and factorial aerobic scope (FAS) as MMR/RMR . Excess post-exercise oxygen consumption (EPOC) was measured at 0.5 and 1 h after MMR to compare the % return to initial RMR values for the 1.0°C and 6.5°C acclimated fish. Tests with the 1.0°C acclimation group used 20 fish bred at the Vancouver Aquarium with a mean mass of 59.8 ± 2.7 g. Tests with the 3.5°C acclimation group used 19 wild fish caught in 2011 with a mean mass of 111.5 ± 6.1 g. Tests with the 6.5°C acclimation group used 11 fish bred at the Vancouver Aquarium and 6 wild fish caught in 2012 with a mean mass of 74.1 ± 7.6 g.

Maximum heart rate ($f_{H,max}$)

The response of $f_{H,max}$ to acute warming used a technique and apparatus detailed previously (Casselmann et al., 2012) and modified

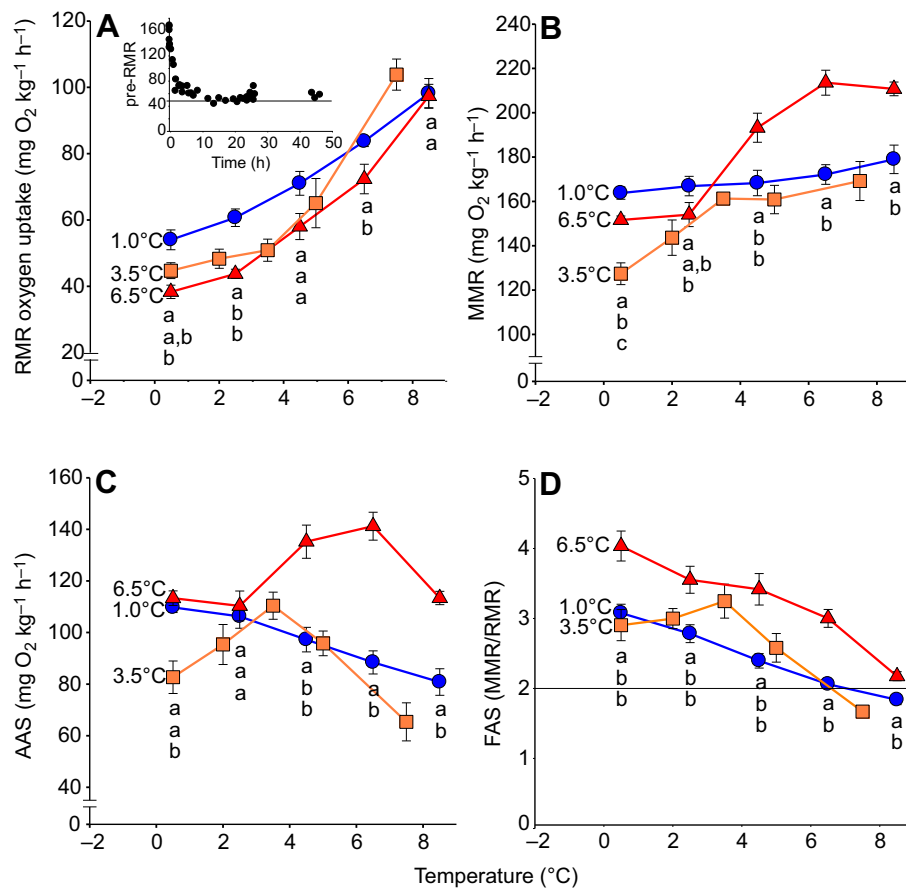


Fig. 2. Oxygen uptake of *Boreogadus saida* acclimated to 1.0, 3.5 and 6.5°C. Oxygen uptake (mean±s.e.m.) of fish acclimated to three temperatures: 1.0°C, blue circle, $n=8$; 3.5°C, orange square, $n=6$; 6.5°C, red triangle, $n=8$ (except at test temperature 8.5°C, when $n=6$). Means that do not share a letter are significantly different ($P<0.05$). (A) Individual routine metabolic rate (RMR). Inset shows oxygen uptake by wild-caught fish 0–47.5 h after introduction to the respirometer. (B) Maximum metabolic rate (MMR). (C) Aerobic scope (AAS), the absolute difference between MMR and RMR. (D) Factorial aerobic scope (FAS), the fraction of MMR and RMR. Means that do not share a letter are significantly different. Data for 3.5°C acclimated fish at test temperatures 3.5 and 7.5°C are not included in the statistical analysis.

for *B. saida* (Drost et al., 2014). Briefly, two fish were anaesthetized in 75 mg l⁻¹ tricaine methanesulphonate (MS-222, Sigma) until they were unresponsive to a tail pinch before being transferred to individual 30 cm by 10 cm Plexiglas water-bath chambers (water volume=2 litre) where the anaesthetized state was maintained with gill irrigation using seawater containing 50 mg l⁻¹ MS-222. Owing to the possible effect of anaesthesia on unstimulated hearts, we tested the efficacy of the initial atropine injection during test trials and were satisfied that maximum heart rate was maintained throughout the trial period.

The chambers were connected to a 15 litre closed-circuit, continuously aerated seawater sump, which contained a magnetic drive pump and two refrigerant coils attached to programmable chillers (Fisher Isotemp 3016d; www.fisherssci.com) filled with 60% propylene glycol antifreeze. Water temperature was controlled by the recirculating chiller and measured to a precision of ±0.1°C (Fisher Scientific Type K digital thermometer probe). The fish were positioned dorsal side down on a fine mesh screen to enable placement of two custom-made chromel-A electrodes on the skin near the heart to record an ECG (Drost et al., 2014). The acute warming increased water temperature in 0.5°C increments every 15 min (2°C h⁻¹), which allowed both water temperature and $f_{H,max}$ to stabilize. For the 0.5°C and 3.5°C acclimation groups, the experiment was terminated when water temperature reached 9.5°C or earlier if the QRS wave amplitude began to decline so that there was a greater chance of reviving the fish. For the 6.5°C acclimation group, warming continued until cardiac arrhythmia first developed. Thus, T_{max} and T_{AR} were not measured for the 0.5°C and 3.5°C acclimation groups.

Data analysis and statistical testing

The equality of data variance was tested using Levene's method on normally distributed data. $T_{c,max}$ was calculated as the sample mean ±s.e.m. for 13 fish at each acclimation temperature. The results were compared across acclimation temperatures using one-way ANOVA with Tukey *post hoc* test. Wild versus reared were treated as random factors in the analysis. A linear regression was applied to water saturation measurements to determine oxygen uptake (\dot{M}_{O_2} , mg O₂ kg⁻¹ h⁻¹) as:

$$\dot{M}_{O_2} = ([O_2]_{t_1} - [O_2]_{t_2}) \times \frac{V}{(t_2 - t_1)}, \quad (1)$$

where $[O_2]_{t_1}$ is oxygen concentration (mg O₂ l⁻¹) at time t_1 (h); $[O_2]_{t_2}$ is oxygen concentration at time t_2 ; V is the respirometer volume minus the volume (expressed in litres) of the fish, using saltwater correction to relate volume (litres) to body mass (M_b , kg). All oxygen uptake data are presented as mean±s.e.m. To account for differences in body mass, which ranged from 32.5 to 163.8 g (mean=78.1±3.0 g) all individual oxygen uptake measurements were adjusted to a 100 g fish using the equation:

$$\dot{M}_{O_2(100g)} = \dot{M}_{O_2} \times \left(\frac{M_b}{100}\right)^{1-A}, \quad (2)$$

where $\dot{M}_{O_2(100g)}$ is the oxygen uptake for a 100 g fish, \dot{M}_{O_2} is the oxygen uptake for the fish and A is the mass exponent (0.80) describing the relationship between metabolic rate and body rate for *B. saida* (Steffensen et al., 1994). A one-way ANOVA confirmed that RMR and MMR data for wild and reared fish from the 6.5°C

acclimation group were not significantly different and so wild and reared fish were combined (see Table S2).

The AAS data for different acute temperatures were subjected to regression analysis. A log normal, three-parameter regression was a good fit ($R^2=0.99$) for the skewed 1.0°C acclimation data. Whereas Weibull 4 parameter regressions (used for parametric survival analysis; see Ricklefs and Scheuerlein, 2001) were applied to the 3.5°C and 6.5°C acclimation data, which resulted in an R^2 of 0.96 and 0.65, respectively, and a realistic T_{crit} extrapolation, where AAS approaches zero. The log normal regression fitted a curve to the 1.0°C acclimation data to estimate the temperature for peak AAS (T_{opt}) and the lower and the upper pejus temperatures (T_{pej} ; Pörtner et al., 2008), equal to 90% of peak AAS, was calculated. The Weibull regressions also estimated peak and pejus temperatures for 3.5°C and 6.5°C acclimation data, which allowed calculation of a T_{opt} window ($T_{lpej}-T_{upej}$; Eliason et al., 2013a). Statistical differences among acclimation groups and among acute test temperatures were tested using a one-way ANOVA and a Tukey *post hoc* test.

The 1.0°C and 6.5°C acclimation EPOC was measured at 0.5 and 1 h after MMR. Significant differences ($P<0.05$) were identified at the two acclimation temperatures (1.0°C and 6.5°C) and at the five acute test temperatures (0.5°C, 2.5°C, 4.5°C, 6.5°C, 8.5°C), which directed additional Tukey pairwise comparison *post hoc* testing using the transformed proportional data.

$f_{H,max}$ was calculated at each test temperature for individual fish using the R–R interval averaged over 30 consecutive heartbeats from an EKG recording with a rhythmic heartbeat. The mass average for the three acclimation temperatures (0.5, 3.5 and 6.5°C) was 31.8 ± 2.4 g, 80.4 ± 5.7 g and 117.5 ± 7.6 g, respectively. Rate transition temperatures for $f_{H,max}$ were calculated for individual fish (as described in Casselman et al., 2012; Anttila et al., 2013; Drost et al., 2014). The first Arrhenius breakpoint temperature (T_{AB}) (Yeager and Ultsch, 1989) was determined by plotting the natural log of the heart rate ($\ln f_{H,max}$) of individual fish against the inverse of temperature (1000 K^{-1}) and running best-fit linear regressions (SigmaPlot 11.0, Systat Software; www.sigmaplot.com) to determine the lowest temperature when the slope of the Arrhenius line decreased. The incremental Q_{10} transition temperature for $f_{H,max}$ (T_{QB}) was determined by calculating the Q_{10} for each 1°C change in temperature using: $Q_{10}=(f_{H,max2}/f_{H,max1})^{10/(T_2-T_1)}$. T_{QB} was assigned when the incremental Q_{10} decreased and remained below 2.0 because a $Q_{10}>2$ is considered a normal rate of change of routine fish metabolism with temperature (Fry and Hochachka, 1970; Miller and Mann, 1973; Holeyton, 1974). The transition temperature at which the heartbeat first reached the peak $f_{H,max}$ was recorded as T_{max} and the temperature at which the heart first started an arrhythmic heartbeat was recorded as T_{AR} . In addition, the amplitude (mV) of the QR wave was calculated, when possible, from each individual EKG trace at each test temperature and was used to determine the temperature when the QR wave reached a

peak value (T_{QR}). QR wave amplitudes were then expressed relative to the largest value for each individual.

RESULTS

Loss of equilibrium

$T_{c,max}$ increased significantly by 2.2°C (from 14.9 to 17.1°C), with acclimation from 1 to 6.5°C, which represented a 0.43°C change in $T_{c,max}$ per °C in acclimation temperature (Fig. 1B).

Respiratory performance

RMR increased exponentially with acute warming at all acclimation temperatures (Fig. 2A). However, RMR measured at a test temperature of 0.5°C for 6.5°C acclimation was significantly lower than for 1.0°C acclimation, a response that is consistent with thermal compensation. For 1.0°C acclimated fish, MMR did not increase significantly with test temperature (Fig. 2B) and AAS and FAS decreased with increasing testing temperature (Fig. 2C and D, respectively). The T_{opt} window extended from 0.2°C to 3.4°C (Table 1) for AAS, with the peak (Fig. 3A) occurring at 0.5°C. At a test temperature of 8.5°C, AAS was 73% of that measured at 0.5°C.

The 3.5°C and 6.5°C acclimated fish both increased AAS with acute warming, reaching their peak AAS near their acclimation temperature (Fig. 2B). For 3.5°C acclimated fish, the highest measured FAS value was at 3.5°C (Fig. 2D), the T_{opt} window for AAS was from 1.6 to 5.4°C (Table 1), peak AAS (T_{opt}) occurred at 3.5°C (Fig. 3B), and AAS at a test temperature of 7.5°C was 60% of the peak AAS measured at 3.5°C. For 6.5°C acclimated fish, the T_{opt} window was from 2.4 to 8.1°C (Table 1), T_{opt} was 5.4°C, with the peak AAS at 6.5°C (Fig. 3C). AAS at a test temperature of 8.5°C was 80% of the peak AAS measured at 6.5°C. Thus, both the T_{opt} and the T_{opt} window increased with acclimation temperature (Table 1) and FAS never decreased below 2 provided the test temperature was $<6.5^\circ\text{C}$, independent of acclimation temperature (Fig. 2D).

Peak AAS was similar for 1.0°C and 3.5°C acclimated fish, but peak AAS and FAS were significantly higher for 6.5°C acclimated fish. Even so, some delayed mortality unexpectedly followed the MMR measurement for the 6.5°C acclimated fish tested at 8.5°C (50% of fish) and the 3.5°C acclimated fish tested at 7.5°C (6% of fish). Extrapolation of the AAS curves produced upper T_{crit} values of 15.1°C and 18.2°C, respectively, for 3.5°C and 6.5°C acclimation groups, which were similar to measured $T_{c,max}$ values (15.5°C and 17.1°C, respectively).

As expected, recovery from exhaustion (as measured by the % of AAS available) was more complete after 1.0 h than after 0.5 h ($P=0.000$) for 1.0°C and 6.5°C acclimated fish (Fig. 4). In fact, within 1.0 h, at least 79% of AAS was restored independent of test or acclimation temperatures. For 1.0°C acclimated fish, *post hoc* testing revealed a significantly slower recovery after 0.5 h at test temperatures of 6.5 and 8.5°C ($P=0.0001$) and after 1.0 h, recovery was significantly slower at the 6.5°C test temperature ($P=0.008$). For the 6.5°C acclimated fish, recovery was independent of the acute test temperature ($P=0.072$ after 0.5 h and $P=0.061$ after 1.0 h).

Table 1. Statistical analysis of key transition temperatures between 0.5, 3.5 and 6.5°C acclimation groups

Group	T_{AB}	T_{lpej}^*	T_{opt}^*	T_{upej}^*	T_{QR}	T_{FS}^*	T_{QB}	T_{max}^\ddagger	T_{AR}^\ddagger	$T_{c,max}$
0.5°C	3.6 ^a	0.2	1.0	3.4	5.5 ^a	8.5	5.2 ^{a,b}	10.8 ^a	12.3 ^a	14.9 ^a
3.5°C	4.7 ^a	1.6	3.5	5.4	4.6 ^a	7.5	5.0 ^a	12.3 ^a	13.4 ^a	15.5 ^b
6.5°C	4.3 ^a	2.4	5.4	8.1	6.3 ^a	~9.0	7.8 ^b	10.9 ^a	11.1 ^a	17.1 ^c
	$P=0.209$				$P=0.244$		$P=0.024$	$P=0.224$	$P=0.066$	$P=0.000$

*No statistical analysis was possible on these data derived from modelled data.

†The data for 0.5°C and 3.5°C acclimated fish are from field measurements previously published.

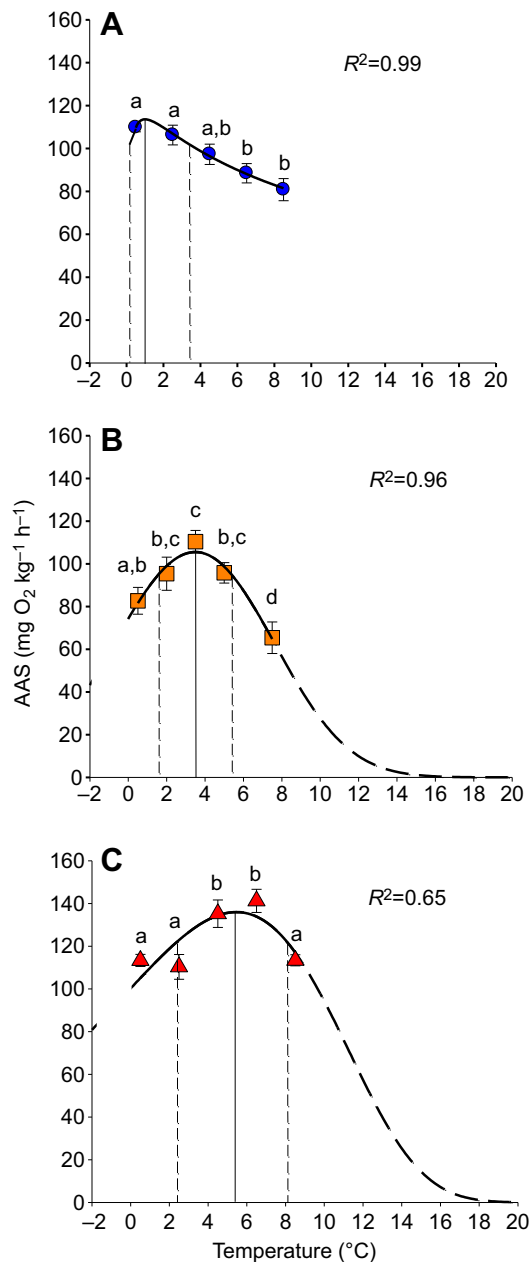


Fig. 3. Optimum temperature and upper and lower pejus estimates for *B. saida*. Optimum temperature (T_{opt} , solid vertical line) and upper and lower pejus estimates (where AAS is 90% at T_{opt} , dashed lines) at (A) 1.0°C, blue circle, $n=8$; (B) 3.5°C, orange square, $n=6$; (C) 6.5°C, red triangle, $n=8$ (except at test temperature 8.5°C, when $n=6$). Regression equations calculated using a log normal, three-parameter regression for the 1.0°C data and Weibull four-parameter regressions for the 3.5 and 6.5°C data. Means that do not share a letter are significantly different ($P<0.05$).

When comparing the difference in recovery between 1°C and 6.5°C acclimated fish over all test temperatures, the 6.5°C acclimated fish recovered significantly faster at 0.5 h ($P=0.027$). However, there was no statistical difference in recovery between temperature acclimations after 1.0 h ($P=0.342$).

$f_{H,max}$

As expected, $f_{H,max}$ increased with acute warming for each individual and acclimation group (Fig. 5). Indeed, warming accelerated $f_{H,max}$ by a consistent amount between 0.5 and 1.5°C

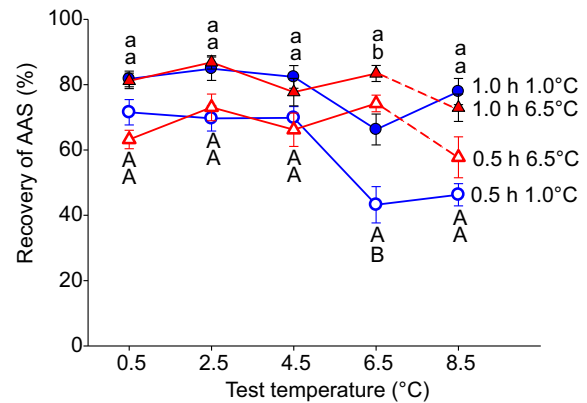


Fig. 4. The recovery of absolute aerobic scope following exhaustive exercise as a function of test temperature for *Boreogadus saida* acclimated to either 1°C or 6.5°C. The % recovery was calculated from RMR, MMR and the oxygen uptake measured at both 0.5 h and 1 h into the recovery period. Comparison of the percentage recovery to previously tested RMR (mean values \pm s.e.m.) of oxygen uptake between acclimation temperatures 1°C (blue circle); 6.5°C (red triangle) after 0.5 h (open symbol) and 1 h (filled symbol) at each test temperature. The solid lines connect data with the same sample size ($n=8$) and dashed lines highlight the change in sample size ($n=6$) for 6.5°C acclimated fish at 8.5°C test temperature. Different capital letters denote statistical significance for the 0.5 h data and different small letters denote statistical significance for the 1.0 h data ($P<0.05$).

($Q_{10}\sim 3$) independent of acclimation temperature. Neither T_{AB} , T_{QB} nor peak $f_{H,max}$ varied significantly with acclimation temperature, with the exception of the 6.5°C acclimation group, which had a significantly higher T_{QB} ($P=0.024$) (Table 1). T_{AR} and T_{max} for 6.5°C acclimated fish were compared with published field data for T_{max} and T_{AR} using 0.5°C and 3.5°C acclimated fish (Table 1) in the absence of T_{AR} and T_{max} measurements here. T_{AR} and T_{max} did not differ significantly among acclimation temperatures. However, individual variation in T_{AR} was considerable, ranging from 7.6 to 15.2°C.

DISCUSSION

Fish energetics rely on oxygen being extracted (respiration) from the water and delivered (cardiac system) to tissues (Campbell et al., 2009). Both of these vital processes are temperature dependent (Crozier, 1924). Here, we identified thermal limits and rate transition temperatures for cardio-respiratory performance that can potentially dictate migration and limit survival (Fry, 1947; Pörtner, 2001; Farrell, 2002; Somero, 2005; Farrell, 2007; Pörtner and Farrell, 2008; Farrell et al., 2009; Iftikar and Hickey, 2013; Deutsch et al., 2015). Even though the thermal performance of biochemical reactions, cells, tissues, organs and organ systems may be quite disparate (Schulte, 2015), the thermal niche of a whole animal must be bounded by its critical thermal limits ($T_{c,max}$ and $T_{c,min}$ – the latter taken here as freezing point of seawater at -1.8°C , in the absence of experimental data). Yet, Antarctic stenotherms, even with a narrow window of thermal tolerance, do acclimate to warmer temperatures to some degree (Pörtner et al., 2000, 2007; Lannig et al., 2005; Seebacher et al., 2005), despite the fact that their biogeographic and thermal isolation is more extreme than that of Arctic fishes and has been this way for around 30,000 years. For example, Seebacher et al. (2005) acclimated the Antarctic notothenioid *Pagothenia borchgrevinki* to 4°C, a temperature likely to be 3.5°C greater than they experience in the wild. We proposed and provided support for the hypothesis that the cardio-respiratory system of *B. saida* have some capacity for thermal

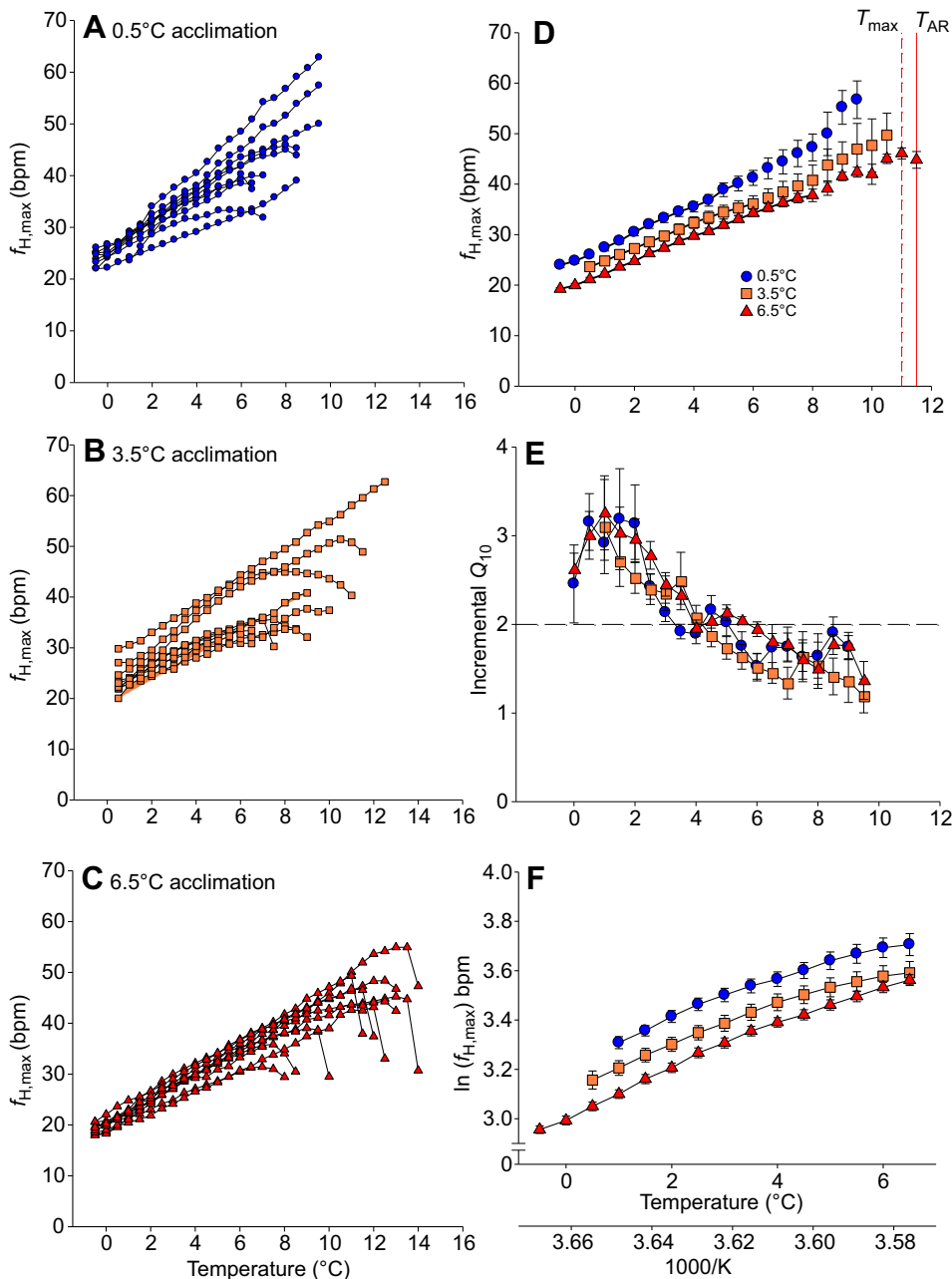


Fig. 5. Individual responses of maximum heart rate to acute warming of anesthetized *B. saida* acclimated to 0.5, 3.5 or 6.5°C. The individual responses of $f_{H,max}$ to acute warming of anesthetized *B. saida* ($n=10$) that had been acclimated for 6 months to (A) 0.5°C, blue circle; (B) 3.5°C, orange square; (C) 6.5°C, red triangle. (D) The mean (\pm s.e.m.) response in $f_{H,max}$ to acute warming. The vertical dashed and solid lines depict the T_{max} and T_{AR} data that were measured for the 6.5°C acclimated group. Data points are connected by lines indicating that the sample size remains unchanged. (E) Incremental Q_{10} for $f_{H,max}$ for each 1°C change, as derived from the individual responses shown in A. The temperature at which the Q_{10} irrevocably remained below 2 (black horizontal reference line) was assigned as the second breakpoint temperature (T_{QB}) \pm s.e.m. (F) The first significant rate decrease in heart rate as water temperature increases (T_{AB}) was determined for individual fish at each acclimation temperature using best-fit regression analysis of data arranged in Arrhenius plots. The mean ($n=10$) natural log of heart rates ($\ln f_{H,max}$) at three acclimation temperatures \pm s.e.m. are depicted. The 0.5°C acclimation data have been published previously (Drost et al., 2014) and are included for a full comparison of acclimation temperatures.

acclimation, which may translate into a capacity for *B. saida* to exploit the thermally stratified Arctic Ocean in the summer (see Fig. 1A).

These new results add significantly to the earlier findings for this species (Drost et al., 2014, 2015). Indeed, the maximum cardio-respiratory capacity of *B. saida* did well over a range of temperatures that it is likely to experience both under ice and even in Arctic surface water during peak summer temperatures (see Fig. 1A). This discovery poses a challenge to whether or not this species should be considered a true polar stenotherm, unlike, for example, burbot, a freshwater cold stenothermal fish that loses cardiac pumping capacity beyond 1°C despite a steadily increasing heart rate (Tiitu and Vornanen, 2002). We also observed a variety of compensatory responses to thermal acclimation that would benefit *B. saida* in a warmer environment. These compensations include an increase in $T_{c,max}$, increases in

peak AAS and FAS, a $>2^{\circ}\text{C}$ increase in the T_{opt} window for AAS, a faster recovery of AAS after exhaustion and a significant downregulation of $f_{H,max}$.

Boreogadus saida, when acclimated to 6.5°C, could maintain their vertical orientation up to 17.3°C and had a $T_{c,max}$ that was 2.2°C higher than 1.0°C acclimated fish. Fry (1971) defined thermal acclimation as at least a 1.0°C increase in $T_{c,max}$ when acclimation temperature is increased by 3°C (ratio=0.33). Thus, *B. saida* met the standard criterion for thermal acclimation. Similarly, stenothermal Antarctic fish species were able to significantly increase $T_{c,max}$ by $>2^{\circ}\text{C}$, with a range of 15 to 18°C, when tested at ambient -1.5°C and then acclimated to 4°C water temperatures (Somero and DeVries, 1967; Podrabsky, and Somero, 2006; Bilyk and DeVries, 2011). From an evolutionary perspective, there is a remarkable similarity in the ratio of $T_{c,max}$ to acclimation temperature for different fish species, which is 0.43 for *B. saida*, 0.41 (range 0.27–

0.50) for 20 species of North American freshwater fishes (Beitinger et al., 2000) and 0.44 (range 0.24–0.65) for 8 Antarctic species (Bilyk and DeVries, 2011).

From an environmental perspective, it is interesting that the measured $T_{c,max}$ for both *B. saida* and Antarctic species, lies well beyond present day surface water temperatures in both polar environments (Fig. 1A). $T_{c,max}$ is a thermal tolerance limit and one probably not normally experienced in their thermal niche (Kerr, 1976). For instance, 16°C acclimated *B. saida* died in a laboratory feeding study (Laurel et al., 2016). The same study found that the maximum growth rate for *B. saida* occurred at acclimation temperatures between 5 and 9°C, a result that is consistent with the observation here that 6.5°C acclimated fish had the highest AAS and FAS.

A link between increased AAS (and FAS) and increased growth (and condition factor) was also found in a warm acclimation study of spine cheek anemone fish (Donelson, 2015). Cardio-respiratory links to performance were also demonstrated in 14°C acclimated rainbow trout (*Oncorhynchus mykiss*), which had a T_{upej} between 19 and 20°C (Chen et al., 2015), decreased food consumption rate at 19°C and starved at 22°C (Myrick and Cech, 2000). The apparent link between cardio-respiratory transition temperatures and performance has been further illustrated in the eurythermic goldfish (*Carassius auratus*). A T_{opt} of 20°C was calculated for goldfish acclimated to 12°C water temperature (Ferreira et al., 2014). The maximum swimming rate of goldfish, acclimated to 15°C water temperatures, declined at 20°C (Fry and Hart, 1948; Johnston and Temple, 2002). Furthermore, T_{max} of goldfish acclimated to 12°C water was 27°C (Ferreira et al., 2014), which is the same temperature that goldfish acclimated to 10°C lost their ability to escape predators (Johnston and Temple, 2002).

Measurements of EPOC provided additional evidence of acclimation to 6.5°C in *B. saida* because recovery was fastest at 6.5°C, particularly when compared with 1°C acclimated fish at the same test temperature, which was contrary to our hypothesis that the colder acclimated group would perform better. Improved performance with acclimation is species specific. Each species has different capacities to perform life-sustaining activities, with individual variation. However, for all species it is predicted that temperature acclimation changes the shape of their aerobic scope curve and the values for T_{opt} and the T_{opt} window for AAS (Pörtner and Farrell, 2008; Schulte, 2015), as seen recently for the eurythermal goldfish (12–28°C; Ferreira et al., 2014). We found that the *B. saida* aerobic scope curve, unlike the eurythermal goldfish, broadened with warmer acclimation and both their T_{opt} and the T_{opt} window for AAS increased by ~2°C. Yet, despite the clear evidence of an increase in performance capacity of *B. saida* at warmer temperatures, thermal acclimation may exact a cost to whole animal performance (Woods and Harrison, 2001; Seebacher et al., 2005; Deutsch et al., 2015; Pershing et al., 2015). For instance, acute exposure to a temperature higher than 6.5°C presented severe problems with post-exhaustion mortality at test temperatures higher than the acclimation temperature (as occurred in 50% of 6.5°C acclimated fish tested at 8.5°C), something we never observed at test temperatures of 6.5°C or lower. Thus, the high growth rate seen for *B. saida* at 9°C in a protected laboratory with ample food (Laurel et al., 2016) may not be possible in the natural environment.

Depression of biological rates (i.e. compensation) is another sign of warm acclimation in ectotherm species including arthropods, molluscs, fish, amphibians and reptiles (Lillywhite et al., 1999; Aho and Vornanen, 2001). This was evident in *B. saida* with the significant reduction in $f_{H,max}$ (~7 bpm) at 6.5°C acclimation when

compared with 0.5°C acclimation. A reduction of f_H is predicted with an increase in tolerance to warmer water (Farrell, 1997, 2016) and, at least in rainbow trout, appears to be caused by modification of the pacemaker action potential (Haverinen and Vornanen, 2007). A Q_{10} effect has been used to describe acclimation potential (Du et al., 2010; Seebacher et al., 2015). For *B. saida*, $f_{H,max}$ shows, on average, a moderate acclimation response [$Q_{10(6)}=1.7$] when acclimated from 0.5 to 6.5°C.

One area of concern is that anaesthetics, as a result of their known membrane-destabilizing properties, could alter the thermal response of $f_{H,max}$ and perhaps help trigger cardiac arrhythmias. The physiological basis of cardiac arrhythmias is being explored (Badr et al., 2016; Vornanen, 2016), but more important to present concerns, they are observed with acute warming of perfused working heart preparations (A. Badr and M. Vornanen, pers. comm.) where no anaesthetic is present. Cardiac arrhythmias are also observed in unanaesthetized fish during acute warming (Clark et al., 2008; Eliason et al., 2013b), but the presence of intact control mechanisms hampers interpretation of the results. In terms of the accuracy of the rate transition temperatures for $f_{H,max}$, a comparison of two anaesthetics with different mechanisms of action (15 ppm clove oil and 50 ppm MS-222) produced similar results for $f_{H,max}$ in coho salmon, with MS-222 having the lower individual variability for T_{AB} (Casselman et al., 2012). Furthermore, the same study measured T_{opt} for aerobic scope for unanaesthetized coho salmon and it was not significantly different from the T_{AB} estimated from $f_{H,max}$ for any of the anaesthetic treatments tested. Thus, while any effect of anaesthetics on $f_{H,max}$ with this technique seem to minor at best, care is still needed in choosing the best type and dose of anaesthetic when other fish species are tested.

A ‘Fry thermal polygon’ can be used to distinguish various zones of thermal tolerance for reproduction, activity, tolerance and lethality with respect to acclimation temperature (Fry, 1947). In our study, the cardio-respiratory transition temperatures (i.e. performance limits) were incorporated into a modified Fry temperature polygon to graphically represent *B. saida* windows of thermal tolerance (Farrell, 2016). Previously, the rate transition temperatures for $f_{H,max}$ and AAS have been placed in a hierarchy within a Fry thermal polygon for goldfish (Ferreira et al., 2014) and

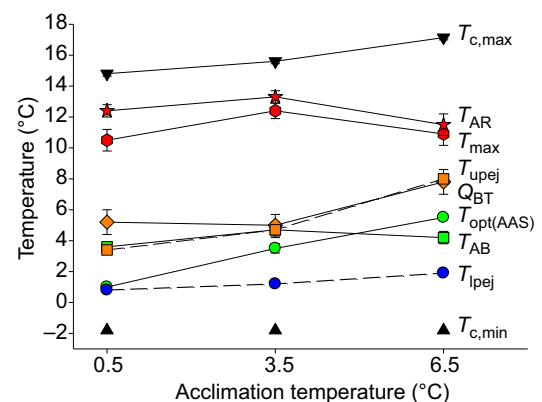


Fig. 6. Fry thermal polygon for *B. saida*. The minimum lethal temperature ($T_{c,min}$) for *B. saida* is assumed, across all acclimation groups, to be -1.8°C (the approximate freezing temperature of surface seawater). The transition temperatures depicted include: lower temperature pejus (T_{lpej}), Arrhenius break point temperature (T_{AB}), AAS derived temperature optimum [$T_{opt(AAS)}$], incremental Q_{10} (<2) break point (Q_{BT}), upper temperature pejus (T_{upej}), peak heart rate (T_{max}); arrhythmic $f_{H,max}$ (T_{AR}) and loss of equilibrium ($T_{c,max}$). Dashed lines indicate values based on 90% T_{opt} . All data are presented as mean \pm s.e.m except for $T_{c,min}$, T_{opt} , T_{lpej} and T_{upej} .

rainbow trout (Chen et al., 2015). We do likewise in Fig. 6. Both previous studies found that T_{AR} was 1–3°C below $T_{c,max}$. Similarly, T_{AR} for *B. saida* was at least a 2°C below $T_{c,max}$. However, the relationship between T_{opt} and T_{AB} varied according to acclimation temperature because, while T_{opt} approximated the acclimation temperature in all three fish species, T_{AB} was independent of acclimation temperature in *B. saida*. Thus, with 0.5°C and 3.5°C acclimation, T_{opt} was slightly lower than T_{AB} and closer to the T_{upej} values, whereas with 6.5°C acclimated fish, the T_{AB} was almost 1°C lower than T_{opt} . Even so, the absolute differences between T_{AB} and T_{opt} were never large and T_{AB} was always within the T_{opt} window (Fig. 6).

Abrupt changes in respiration and heart rate due to increasing temperature, highlight ecologically relevant physiological limitations. The results of this study demonstrate the potential rewards of combining whole animal cardio-respiratory performance with ecosystem observations. Transition temperatures, when added to Fry temperature polygon graphs, estimate a hierarchy of temperature limits to fundamental activities that could also include other physiological functions such as reproduction and growth.

When considering the full life history of *B. saida*, it appears that egg development is the critical life stage with respect to temperature, a limit of 3–3.5°C (Sakurai et al., 1998; Kent et al., 2016). Similarly, 3.3°C (Drost et al., 2015) is the larval T_{AB} value, when hearts first fail to keep up with steadily increasing water temperature. As researchers have known for decades, the *B. saida* life history is inextricably linked with Arctic sea ice. Sakshaug and Skjoldal (1989) coined the term ‘ice-edge effect’ to describe the physical and biological activities that occur around the marginal ice zone, which are vital feeding grounds for *B. saida* larvae and juveniles (Bradstreet et al., 1986; Arrigo, 2014). Food, safety and the results from this study all suggest that ice-induced water temperature suppression, within the zones of reproduction and early larval development, explain the abundance of *B. saida*, estimated to be in the billions, under ice (David et al., 2016). Such abundance is required to maintain existing marine Arctic food webs (Hop and Gjøsaeter, 2013).

In conclusion, adult *B. saida* were able to acclimate to 6.5°C temperatures after 1 month of exposure. We also observed, over this 3 year study, a remarkable resilience and an intransience of certain physiological responses, as demonstrated by comparing heart rates of *B. saida* from different locations, different acclimation temperatures and different life stages. Heart rate, $\dot{M}O_2$ and $T_{c,max}$ all show phenotypic plasticity when *B. saida* are acclimated to warmer temperatures.

The greater than expected thermal performance of larvae and adult *B. saida* suggests that the under sea ice ecosystem serves as a critical component of their biographic distribution and survival. Certainly, as has been proposed in recent studies, the loss of sea ice, the potential for increased competition and predation (Penney et al., 2014; Hop and Gjøsaeter, 2013; Suzuki et al., 2015), changes in prey type, abundance, availability and synchronicity (Sakshaug and Skjoldal, 1989; Li et al., 2009; Grote et al., 2015) can all help to explain *B. saida* habitat retraction. However, the results from this study suggest that migration and survival could also be dictated by water temperatures that exceed optimum conditions for cardio-respiratory performance. For instance, there may be a significant cost to acclimation and changes in respiratory and cardiac performance, such as when *B. saida* hearts first fail to keep up with water temperatures (T_{AB}) <5°C. Higher resolution oceanographic and comparative multi-stressor physiological data

are needed to fully describe the eco-physiology of this intriguing fish species, which may be migrating northwards with ocean warming, but can clearly physiologically tolerate temperatures well above those of its current habitat.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Field work: H.E.D., A.P.F. and E.C.C.; study design: H.E.D., M.L. and A.P.F.; data collection: H.E.D., M.L. and E.C.C.; writing and revision: all authors; publication submission: H.E.D., A.P.F. and M.L.

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.140194.supplemental>

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