

RESEARCH ARTICLE

Thermal dependence of cardiac function in arctic fish: implications of a warming world

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SUMMARY

With the Arctic experiencing one of the greatest and most rapid increases in sea temperatures in modern time, predicting how Arctic marine organisms will respond to elevated temperatures has become crucial for conservation biology. Here, we examined the thermal sensitivity of cardiorespiratory performance for three closely related species of sculpins that inhabit the Arctic waters, two of which, *Gymnocanthus tricuspis* and *Myoxocephalus scorpioides*, have adapted to a restricted range within the Arctic, whereas the third species, *Myoxocephalus scorpius*, has a wider distribution. We tested the hypothesis that the fish restricted to Arctic cold waters would show reduced cardiorespiratory scope in response to an increase in temperature, as compared with the more eurythermal *M. scorpius*. As expected from their biogeography, *M. scorpioides* and *G. tricuspis* maximised cardiorespiratory performance at temperatures between 1 and 4°C, whereas *M. scorpius* maximised performance over a wider range of temperatures (1–10°C). Furthermore, factorial scope for cardiac output collapsed at elevated temperature for the two high-latitude species, negatively impacting their ability to support aerobically driven metabolic processes. Consequently, these results concurred with our hypothesis, suggesting that the sculpin species restricted to the Arctic are likely to be negatively impacted by increases in ocean temperatures.

Key words: cardiovascular, scope, temperature, conservation physiology.

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INTRODUCTION

Anthropogenic climate change is now regarded as one of the greatest threats to biodiversity and the abundance and distribution of species. Projections for future climate change indicate that 15–37% of species may be committed to extinction in some regions (Thomas et al., 2004). For aquatic ectotherms, climate change is predicted to result in latitudinal range shifts (Roessig et al., 2004; Hiddink and Ter Hofstede, 2008) that, depending on the species, can either extend or contract the range of suitable habitat (Sabatés et al., 2006; MacKenzie et al., 2007; Sharma et al., 2007). Indeed, fish species found in the North Sea such as cod, whiting and anglerfish are already shifting northward (from 50 to 800 km) concurrent with a warming trend spanning the last 25 years. If this trend continues, several commercially important species may withdraw completely from the North Sea by 2050 (Walther et al., 2002; Perry et al., 2005; Rose, 2005). Sometimes forgotten in descriptions of northward migrations in search of cooler water is that marine organisms already using polar areas as habitat have little or no room to move towards colder areas and so their range will contract, making them especially susceptible to the effects of ocean warming.

Fish species endemic to the high latitudes of the Arctic have presumably adapted to thermally stable but frigid waters. Daily temperature variations are less than 1°C and annual temperatures range maximally between –1.86 and +8°C (Steele et al., 2008). This stable and contained thermal environment has quite possibly

provided the opportunity for Arctic fishes to evolve into thermal specialists such that their physiological systems are fine-tuned to the narrow temperature range that they are exposed to. Evolutionary theory predicts there should be a trade-off between specialist and generalist phenotypes (Levins' Principle of Allocation Hypothesis) (Levins, 1968). Based on this principle, ectotherms restricted to highly stable thermal environments should possess specialist phenotypes that maximise peak performance over the narrow temperature range they are exposed to. In contrast, ectothermic species from more variable thermal environments (or distributed over a wide latitudinal gradient) would possess generalist phenotypes that maximise performance breadth (Levins, 1968; Huey and Hertz, 1984), thereby maintaining performance over a wide range of temperatures.

The Arctic is inhabited by both stenothermal and eurythermal species, which presents an ideal grouping of ectotherms to examine the thermal dependence of physiological systems and to determine whether there are physiological trade-offs associated with stenothermy. Such knowledge is particularly crucial for Arctic fish species because Arctic water temperatures are showing the most rapid change in temperature globally (Turner et al., 2007; Walczowski and Piechura, 2006; IPCC, 2007) and some species of fish (e.g. polar cod, *Boreogadus saida*; Arctic cod, *Arctogadus glacialis*) have already shifted their distribution northwards, presumably to avoid warm waters (Gaston et al., 2003; Schiermeier, 2007). It is believed that the increases in air and

water temperatures in the Arctic over the past few years are a consequence of increases in greenhouse gases in the upper atmosphere (Turner et al., 2007; Walczowski and Piechura, 2006; IPCC, 2007). How these relatively small but significant increases in temperature affect the performance and fitness of fish restricted to Arctic waters is unknown.

Understanding and predicting how organisms will respond to climate change is becoming increasingly important and a variety of approaches to assess organismal condition and fitness are necessary (Pörtner and Farrell, 2008; Pörtner and Knust, 2007; Wang and Overgaard, 2007; Seebacher and Franklin, 2012; Cooke et al., 2013). Here, we investigated the effect of acute increases in temperature on cardiorespiratory performance in three related species of sculpins (Family Cottidae) that inhabit the shallow waters around Qeqertarsuaq (Disko Island), Greenland. Two species, the Arctic sculpin (*Myoxocephalus scorpioides*) and the Arctic staghorn sculpin (*Gymnocanthus tricuspis*), are high-latitude species, with a more northerly and restricted habitat range compared with the third species, the shorthorn sculpin (*Myoxocephalus scorpius*), which is found in global marine environments encompassing water temperatures from 0 to 18°C. We predicted that *M. scorpioides* and *G. tricuspis* are stenothermal species and possess specialist phenotypes, maximising cardiorespiratory performance over a narrow temperature range, whereas *M. scorpius* is eurythermal and possesses a generalist phenotype, maintaining performance over a wider range of temperature.

MATERIALS AND METHODS

Experimental Animals

The shorthorn sculpin, *M. scorpius* (Linnaeus 1758, $N=9$, 140±13 g), Arctic sculpin, *M. scorpioides* (Fabricius 1780, $N=4$, 150±13 g) and Arctic staghorn sculpin, *G. tricuspis* (Reinhardt 1830, $N=10$, 125±13 g) were captured by baited hook and line from shallow waters around Qeqertarsuaq, near the Arctic Circle in west Greenland (69°15'N, 53°34'W). Fish were quickly transferred to small holding tanks and transported to the Arctic Station (University of Copenhagen), where they were maintained in a re-circulating, aerated aquarium at 6–7°C under a natural photoperiod. The water temperature in the aquarium was similar to the local sea surface temperatures where the fish were captured. The fish were not fed for up to 1 week in captivity. Experimentation was covered by an ethical permit from the University of Gothenburg.

Surgery

To assess the response of sculpins to temperature change, we examined the thermal sensitivity of respiratory and cardiac performance. Opercular movements associated with gill ventilation were visually observed and counted over 30 s periods. Heart rate and relative cardiac output were measured with a flow probe implanted after the fish were first anaesthetised in 1:5000 MS222 (tricaine methanesulphonate; Sigma, St Louis, MO, USA) solution and then placed on a surgical sling with the gills irrigated with a maintenance dose of anaesthetic (1:10,000 MS222). A small (1 cm) incision was made on the ventral surface directly above the ventral aorta and the vessel was carefully exposed anterior to the pericardium. A Doppler, cuff-type, flow probe (1–2 mm diameter cuffs constructed in Perspex) was placed around the ventral aorta. Silk sutures (3-0) were used to close the incision and to attach the wires from the flow probe to the dorsal surface of the fish. Fish were manually ventilated with fresh seawater until they became responsive and resumed voluntary ventilation. Fish were allowed to recover overnight from surgery in a large tank (2×0.7×0.7 m,

1×w×h) maintained at 7°C, which also served as the experimental arena for exercise and recovery.

Experimental set-up and protocol

The wire leads from the flow probe were carefully taken from the fish, suspended above the tank and connected to a Doppler flowmeter (Model 545C-4, University of Iowa, Iowa City, IA, USA). The analog signals from the flowmeter were directed to a Powerlab (ADInstruments, Bella Vista, NSW, Australia) and sampled at 40 Hz. A Toshiba laptop computer running Chart software (ADInstruments) provided a real-time display of the cardiac output signal (=flow in the ventral aorta) and heart rate, as calculated from the pulsatile flow signals.

The experimental protocol for each species started by recording resting cardiorespiratory performance and then, immediately afterwards, a 10 min bout of intense, forced exercise. Fish were exercised by lightly tapping the tail with a wooden stick to elicit repeated startle responses. All fish tested showed signs of exhaustion after the 10 min exercise period, at which time fish were hyperventilating and refractory to the tail being struck. Ventilation rate, relative cardiac output and heart rate were measured initially at the ambient temperature of 7°C and then at the other three test temperatures (1, 4 and 10°C) in a randomised order. Between each temperature trial, a fish was allowed to recover from exhaustion for a minimum of 5 h before the water temperature was changed over a 2 h period. A fish was re-exercised after 1 h at the new temperature. Thus, these measurements were repeated at four test temperatures (1, 4, 7 and 10°C) for each fish, for a total of 36 tests. Once the fish had been exposed to all four test temperatures, they were re-tested at 7°C to determine whether there were any deleterious effects of exposure to the different temperature treatments. There was never a significant difference between the initial and final variables measured at 7°C. Fish were killed humanely at the end of the experimental run.

Analysis

Resting values for cardiorespiratory function at each temperature were obtained from quiescent fish, resting on the bottom of the aquarium prior to exercise. An estimate of maximal cardiorespiratory performance was obtained immediately after exhaustive exercise. Each cardiovascular measurement was derived from the mean value for a 30–40 s period that corresponded closely with the visual counting of ventilation frequency. Factorial scope for ventilation rate, heart rate and relative cardiac output was calculated by dividing maximal values (immediately after exercise) by resting values, while absolute scope was calculated by subtracting the resting values from the maximum values. Thus, an absolute scope of zero corresponds to a factorial scope of unity. To quantify the effects of temperature on cardiorespiratory function, Q_{10} values were calculated across the full range of test temperatures (1–10°C) using the van't Hoff equation: $Q_{10}=(R_2/R_1)^{(T_2-T_1)}$, where R_1 and R_2 are the physiological rate parameters at temperatures T_1 and T_2 , respectively. Results are presented as means ± s.e.m.

The effects of temperature on resting and maximal ventilation rate, heart rate and cardiac output were analysed using a one-way repeated measures ANOVA. A two-way repeated measures ANOVA was used to examine for interactions between test temperature and exercise. A two-way repeated measures ANOVA was also used to assess differences in the response of the factorial scope of ventilation rate, heart rate and cardiac output to temperature among the three fish species. Holm–Sidak tests were used to make pairwise comparisons. Comparisons of Q_{10} values were made using Student's *t*-test.

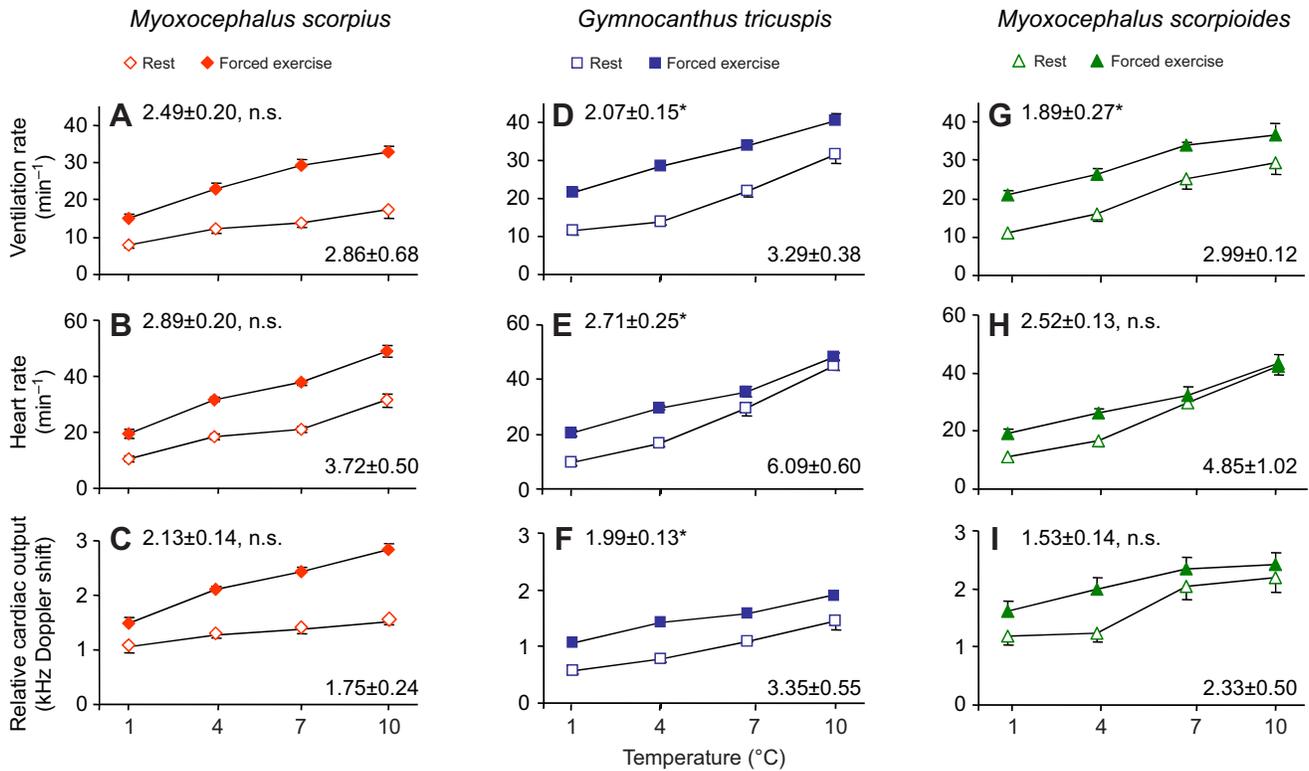


Fig. 1. Temperature has a significant effect on ventilation rate (A,D,G), heart rate (B,E,H) and relative cardiac output (C,F,I) at rest and after exercise in the shorthorn sculpin, *Myoxocephalus scorpius* (A–C), the Arctic staghorn sculpin, *Gymnocanthus tricuspis* (D–F) and the Arctic sculpin, *Myoxocephalus scorpioides* (G–I). The temperature coefficient (Q_{10}) values are presented on the graphs for the effects of temperature from 1 to 10°C on resting (bottom) and maximal rates (top) for each parameter. *Significant difference between resting and maximal Q_{10} values.

RESULTS

Myoxocephalus scorpius

Temperature had a significant influence on the resting and maximal values for ventilation rate, heart rate and relative cardiac output in the shorthorn sculpin (Fig. 1A–C). There was no effect of temperature on relative cardiac stroke volume. Resting ventilation rate increased significantly from $7.7 \pm 1.7 \text{ min}^{-1}$ at 1°C to $17.3 \pm 6.9 \text{ min}^{-1}$ at 10°C ($F_3=9.87$, $P<0.001$), resulting in a Q_{10} of 2.86. After exercise, ventilation rate was approximately twice that of the resting rate at all test temperatures ($F_{1,3}=160.3$, $P<0.001$). Consequently, factorial scope for ventilation rate was maintained between 1 and 10°C (Fig. 2A) and the Q_{10} values for resting and maximal ventilation rates were similar. The changes in heart rate and relative cardiac output in response to the effects of temperature were similar to those of ventilation rate. At all temperatures, the heart rate of *M. scorpius* doubled with exercise (Fig. 1B, $F_{1,3}=136.4$, $P<0.001$). A similar increase was recorded for relative cardiac output (Fig. 1C, $F_{1,3}=61.4$, $P<0.001$). Resting and maximal heart rate in *M. scorpius* also significantly increased with increasing temperature (Fig. 1B, $F_3=174.4$, $P<0.001$; $F_3=119.1$, $P<0.001$, respectively) as did relative resting cardiac output (Fig. 1C, $F_3=8.66$, $P<0.001$) and maximal cardiac output ($F_3=39.5$, $P<0.001$). As a result, factorial scope for heart rate was maintained between 1 and 10°C (Fig. 2B) and Q_{10} values were not significantly different for resting and maximal heart rate (Fig. 1B). Similarly, factorial scope for relative cardiac output was maintained between 1 and 10°C (Fig. 2C) and Q_{10} values for resting (1.75 ± 0.24) and maximal (2.13 ± 0.14) cardiac output were not significantly different.

Gymnocanthus tricuspis

With increasing temperature, resting and maximal ventilation rate, heart rate and cardiac output were all significantly elevated in *G. tricuspis* (Fig. 1D–F, all $P<0.001$). There was no effect of temperature on relative cardiac stroke volume. For all parameters, temperature had a greater effect on resting rates compared with maximal rates and this was reflected in higher Q_{10} values for resting versus maximum ventilation rate, heart rate and cardiac output (Fig. 1D–F, all $P<0.05$). For *G. tricuspis*, the maximum factorial scope for heart rate occurred at 1°C and factorial scope for cardiac output decreased significantly from 2.18 ± 0.32 at 1°C to 1.38 ± 0.10 at 10°C ($F_3=8.95$, $P<0.001$), largely because resting and maximal heart rate of *G. tricuspis* at 10°C were not significantly different, indicating the scope to increase heart rate had completely collapsed at this high temperature (Fig. 1D–F, Fig. 2). This was due to resting heart rate being highly temperature dependent over the temperature range tested ($Q_{10}=6.09 \pm 0.60$) unlike maximal heart rate ($Q_{10}=2.71 \pm 0.25$). The factorial scope for ventilation rate also decreased with temperature, but did not completely collapse like heart rate (Fig. 2).

Myoxocephalus scorpioides

The response of *M. scorpioides* to elevated temperatures and forced exercise was similar to that of *G. tricuspis*. Increases in temperature significantly elevated resting and maximal ventilation rate, heart rate and relative cardiac output (Fig. 1G–I, all $P<0.001$). However, cardiorespiratory performance declined significantly at high temperatures, as reflected by significant decreases in factorial scope for ventilation rate, heart rate and cardiac output (Fig. 2A–C). Again, there was a nearly complete collapse of scope for heart rate at 10°C,

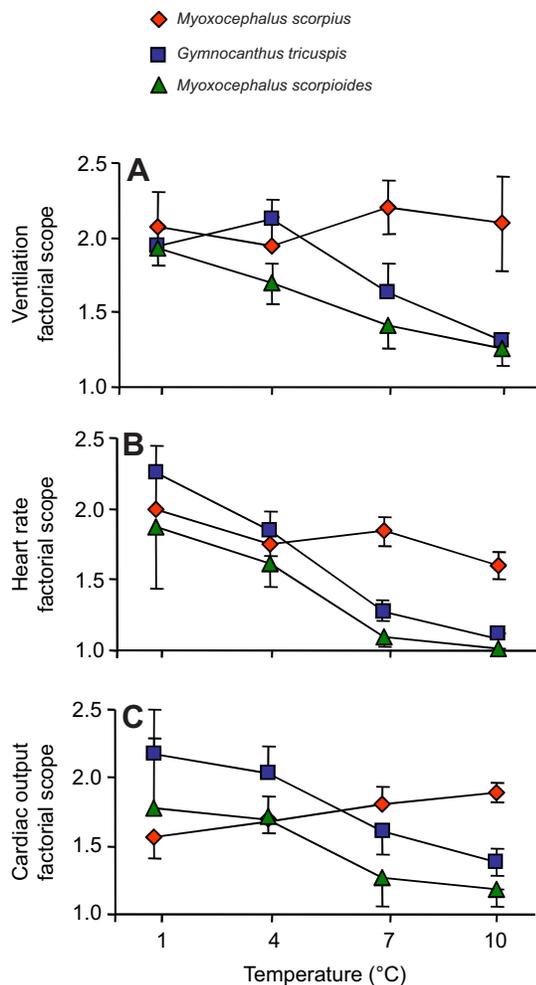


Fig. 2. The effect of temperature on factorial scope for (A) ventilation rate, (B) heart rate and (C) cardiac output in *M. scorpius*, *G. tricuspis* and *M. scorpioides*. Factorial scope=1 indicates no difference between resting and maximal cardiac performance. *Myoxocephalus scorpius* was able to maintain scope for cardiorespiratory performance between 1 and 10°C; however, the more arctic-restricted species, *G. tricuspis* and *M. scorpioides*, showed a significant loss of cardiorespiratory performance at higher temperatures.

as maximal heart rate was equivalent to that recorded at rest, resulting in little scope for cardiac output.

Species comparisons

Using factorial change between the resting and maximal performances for ventilation rate, heart rate and cardiac output, we found that the eurythermal shorthorn sculpin maintained its factorial scope for cardiorespiratory performance across the entire 1–10°C test temperature range (Fig. 2A–C). This was possible because the thermal dependence of resting and maximal rates (for respiration, heart rate and cardiac output) was similar across the temperature range (Fig. 2A–C); Q_{10} values were not significantly different between resting and maximal rates. In contrast, the two endemic Arctic species of sculpin, the Arctic sculpin, *M. scorpioides*, and the Arctic staghorn sculpin, *G. tricuspis*, maintained factorial scope for cardiac performance only between 1 and 4°C (Fig. 2). In fact, at the highest test temperature, the scope of the cardiorespiratory system virtually disappeared because resting rates for ventilation, heart rate and cardiac output either approached or equalled maximal rates (Fig. 1D–I). This

cardiorespiratory collapse was reflected by resting rates generally having higher Q_{10} values than maximal rates (Fig. 1D–I).

DISCUSSION

Our findings are in accord with the Principle of Allocation Hypothesis proposed by Levins (Levins, 1968). The Arctic-restricted species of sculpin (*M. scorpioides* and *G. tricuspis*), which have been exposed to a relatively stable thermal environment over evolutionary time, appear to have a specialist phenotype as indicated by a narrow cardiorespiratory performance thermal niche compared with *M. scorpius*, a generalist that can be found inhabiting a wide range of temperatures and that has apparently maximised its thermal performance breadth. Clearly, fish evolve to function well within a specific range of temperatures, whereas exposure to temperatures outside of this range results in suboptimal performance that can ultimately result in a reduction in fitness and lead to death, a principle first advanced by Fry (Fry, 1947). The collapse of maximum cardiorespiratory performance at higher temperatures for *M. scorpioides* and *G. tricuspis* would impact long-term survival of these two high latitude species because absolute aerobic scope to support processes such as digestion, locomotion and reproduction would either be reduced above 7°C or approaching zero at higher temperatures. The results for these two endemic species contrast sharply with those of the shorthorn sculpin, *M. scorpius*, which has a larger but more southern latitudinal range, and maintained cardiorespiratory performance up to 10°C.

By definition, aerobic scope is the ability to provide oxygen to working tissues beyond existence, which includes growth, reproduction and locomotion, i.e. organismal performance. The delivery of oxygen to the tissue/cells of fish relies on respiratory and cardiovascular transport systems and it has been suggested that it is the limitation in the cardiorespiratory system that sets the limits for performance at higher temperatures (Pörtner and Farrell, 2008; Pörtner and Knust, 2007; Wang and Overgaard, 2007). This contention is supported by recent studies that show unchanged arterial blood oxygen saturation (P_{aO_2}) when exercised salmon are exposed to an increased temperature that is just beyond their optimal performance temperature and cardiac collapse has been triggered (Clark et al., 2008; Steinhausen et al., 2008). More recently, Keen and Gamperl found that when trout were prevented from ram ventilating, P_{aO_2} decreased as temperature was increased (Keen and Gamperl, 2012).

Pörtner and colleagues have provided a conceptual physiological model for the effect of temperature on whole-animal performance (Pörtner and Farrell, 2008; Pörtner and Knust, 2007) in which the significant reduction in absolute aerobic scope that occurs at both the lower and upper pejus (getting worse) temperatures is the result of a mismatch between the demand for oxygen and the capacity to supply oxygen to the tissues. Temperature extremes, where absolute aerobic scope falls to zero, result in a temporary anaerobic survival mode. Pörtner and Knust found that in the eelpout, *Zoarces viviparus*, a species from the North and Baltic Seas, a loss of aerobic scope at the upper pejus temperatures as a consequence of oxygen limitation resulted in a subsequent decrease in growth rate (Pörtner and Knust, 2007). Here, the pejus temperature for the Arctic-restricted sculpins (*M. scorpioides* and *G. tricuspis*) appears to be between 4 and 7°C, based on the collapse of maximum cardiac performance. The impact of a decrease in cardiac scope at higher temperatures could, in the short term, reduce aerobic locomotor performance and digestive efficiency and, in the long term, decrease growth rates, immune competence and reproductive capacity.

While the results of this study provide a valuable insight into the differing responses of three species of Arctic sculpin to acute

temperature increases, predicting the impact of future long-term climate change is more complex. One possible ecological scenario is that the shorthorn sculpin, *M. scorpius*, will maintain its position or expand its range within the region, being able to maintain performance at the elevated temperatures, while the two Arctic-restricted sculpins (*M. scorpioides* and *G. tricuspis*) will be restricted to more northward or deeper cool waters. Displacement of fish to higher latitudes and hence cooler waters has been documented for several fish species presumably as a consequence of global warming of the oceans (Williams, 2005; Sabatés et al., 2006; MacKenzie et al., 2007; Sharma et al., 2007). However, the benthic lifestyle of sculpins and their limited aerobic locomotor capacity as compared with pelagic species may limit or preclude long distance migration to avoid high temperatures. Alternatively, the Arctic-restricted species, although typically regarded as being stenothermal, may have the capacity to compensate *via* acclimatisation (thermal phenotypic plasticity) to higher temperatures, recompensing for the negative effects observed here associated with an acute elevation of temperature, and thus retain their current niches/latitudes. Indeed, thermal phenotypic plasticity of the cardiorespiratory system has recently been shown for an Antarctic fish, previously regarded as stenothermal (Seebacher et al., 2005; Franklin et al., 2007; Franklin and Seebacher, 2009).

In summary, as the temperatures increase in the Arctic, it is likely that the two species of sculpin, *M. scorpioides* and *G. tricuspis*, with restricted northern habitat ranges will be impacted by increases in ocean temperatures unless they can be shown to have thermal phenotypic plasticity. Determining what species are most sensitive to future climate change mandates identification of species that have a narrow thermal niche. The challenge ahead will require a multidisciplinary approach (Franklin and Seebacher, 2012; Cooke et al., 2013), where physiological studies of mechanisms are combined with behavioural and ecological measures to better determine why and which species may be at risk of global warming.

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AUTHOR CONTRIBUTIONS

M.A. organised the expedition to Greenland. All authors contributed to the conception and design of the study, data collection, and analysis and writing of the manuscript.

COMPETING INTERESTS

No competing interests declared.

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