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Comparison of thermal tolerance and standard metabolic rate of two Great Lakes invasive fish species

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ABSTRACT

Round goby (*Neogobius melanostomus*) and western tubenose goby (*Proterorhinus semilunaris*) invaded the Laurentian Great Lakes at approximately the same time and area yet have shown substantial differences in their post-invasion success with more rapid establishment and development of much larger abundances of round goby populations throughout the invaded habitat. In this study, we compared differences in physiological performance (thermal tolerance and standard metabolic rate) between round and tubenose goby collected from the Huron-Erie corridor. Tubenose goby were observed to have lower thermal tolerance but exhibited similar standard metabolic rate across environmental temperatures compared to round goby. At temperatures exceeding 31 °C, tubenose goby demonstrated significantly higher mortalities and shorter times to death relative to round goby. The observed differences in thermal tolerance were consistent with differences in the native geographic ranges observed for each species at their southern ranges. The observed differences in physiological performance combined with species differences in other life history traits such body size, reproduction, feeding ecology and habitat affiliation may also explain differences in the invasiveness experienced by these two Great Lakes invasive fish including a greater ability of round gobies to occupy extreme habitats with large water temperature fluctuations.

Introduction

Round goby (*Neogobius melanostomus*) and western tubenose goby (*Proterorhinus semilunaris*; hereafter referred to as tubenose goby) were first reported in the St. Clair River of the Laurentian Great Lakes in 1990 (Jude et al., 1992). Both species entered the Great Lakes at approximately the same time via ship ballast water although the subsequent range expansion and degree of invasiveness attributed to each species post-invasion substantially differed. Round goby established populations throughout the entire Great Lakes basin within the first decade of their reported appearance, while confirmation of tubenose goby presence remained restricted to Lake St. Clair and the western basin of Lake Erie for most of its invasion history (Vanderploeg et al., 2002; Kocovsky et al., 2011). Only within the last decade have the tubenose goby been reported in eastern Lake Erie and more recently in Lake Superior and Lake Ontario (Kocovsky et al., 2011; Fuller et al., 2013). The two species have also exhibited similar differences in their rate of invasive range expansion in other regions such as the Rhine basin, France (Manné et al., 2013).

The two fish species in question exhibit a number of differences in their life history traits which may impact their ability to survive transport vectors (e.g. ship ballast), exploit various habitats and food resources, and/or overcome competition and predator interactions (Shea and Chesson, 2002). Although both species share many commonalities in near shore habitats and substrate affiliations (Jude and DeBoe, 1996; Erös et al., 2005; Dopazo et al., 2008; Didenko, 2013), round goby achieve larger body sizes, show a broader diet niche including utilizing higher trophic level prey items, and have higher diet plasticity in time and space compared to tubenose goby and other goby species (G.M. Andraso et al., 2011; G. Andraso et al., 2011; Števove and Kováč, 2013; Pettitt-Wade et al., 2015).

Species-specific differences in physiological tolerance and/or metabolic performance attributes may also contribute to differences in each invader's ecological footprint and/or ability to exploit extreme habitats. Differences in physiological tolerance such as acute thermal tolerance correspond to differences in fundamental niche, whereas differences in metabolic performance, e.g. standard metabolic rate, are likely to relate to realized niche differences depending on the nature of resource availability, community composition and interactions of the above factors with abiotic conditions (Beever et al., 2016). Pörtner and Farrell (2008) introduced the oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis, which states that thermal tolerance, physiological

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performance and field distribution of ectothermic animals are causally determined by oxygen transport capacity representing a key limitation to their fundamental niche. In contrast, differences in metabolic performance measured as feeding rate versus water temperature interaction between native (*Mysis salemaai*) and invasive (*Hemimysis anomala*) mysids of Ireland showed competitive advantages of the invasive species under climate warming scenarios (Penk et al., 2016). The latter implies a greater realized adaptive capacity of the invader (Beever et al., 2016) under disturbance regimes (climate warming) that occur due to differences in metabolic temperature optima between the species of contrast corresponding to a higher invasive impact.

Between the two Great Lakes invasive gobies, round goby has achieved much greater attention with respect to metabolic rate and acute thermal tolerance characterization. Lee and Johnson (2005) characterized the standard metabolic rate (SMR) of round goby across a wide range of temperatures and body sizes, while Cross and Rawding (2009) characterized the critical thermal maximum (CTMax) of this species. No comparable data for tubenose goby are available, and such data are vital to understand whether species-specific differences in physiology have contributed to the species geographic expansion histories or differences in ecological impact. Therefore, the objective of the present study was to determine and compare thermal tolerance and SMR of round and tubenose goby in order to determine if physiological tolerance and/or differences in bioenergetics requirements occur between the two invasive fish species.

Methods

Sample collection and fish husbandry

Fish used for studies were collected by beach seine and minnow trap from the Detroit River during summer and fall of 2012 and 2014. Both species were collected at the same locations and times. Round goby typically are larger bodied and more abundant than tubenose goby. As such, tubenose goby were retained at the rate of their capture, whereas round goby were size sorted at the time of collection, with only those of comparable size to tubenose goby being retained. Fish were held for 2 months (for use in acute thermal stress trials) or 4 months (for use in standard metabolic rate measurement trials) acclimation periods post field collection in single species communal tanks. Water quality (pH, dissolved oxygen, temperature and conductivity) was monitored weekly. Water temperature was measured using in situ Hobo Tidbit temperature loggers (Hoskin Scientific, Burlington, ON, Canada). Individuals utilized for acute thermal stress trials were maintained in a recirculating system maintained at 22 ± 0.5 °C, which is the preferred temperature of round goby (Lee and Johnson, 2005). Individuals used in standard metabolic rate measurements were held in a flow-through system subject to normal seasonal temperature changes associated with the Detroit River. During the holding period all fish were initially fed live tubificid worms and weaned onto a commercial fish pellet formulation. All experimental studies were performed following ethical review by the University of Windsor Animal Care Committee.

Acute thermal stress

Experimental trials were conducted in two 50 L glass aquaria designated for 'control' and 'treatment' animals. Each tank was partitioned into two equal sections by plastic mesh. The control tank received 5 fish per species, while the treatment 10 fish per species. All individuals were fasted for 24 h prior to trials. Each trial was initiated at 22 °C. The control tank was maintained at 22 °C throughout the experimental period. Water temperatures in the treatment tank were increased at a constant rate of $2°\mathrm{Ch}^{-1}$ until the target temperature (31, 32, 33, 34, 35 °C) was reached for the trial. After the target temperature was reached, water temperature was held constant for 12 h (measured every 10 min) until the trial completion.

Pilot observations and previous work on round goby (Cross and Rawding, 2009) indicated that the onset of muscle spasms is indicative of impending death. This endpoint was used as a surrogate measure of death during each 12 h trial period. Immediately following onset of muscle spasm, individuals were removed and euthanized by overdose of anesthetic agent and the time of death recorded. At trial end the cumulative per cent mortality of each species was determined. Acute thermal stress trials were performed sequentially using different sets of fish from the communal tank for each trial. Triplicate trials were performed at each target temperature.

A general linear model (GLM) was applied to test for species × temperature interactions using the combined data to determine if differences in LC_{50} between species occurred according to the following model:

$$\text{Mortality (Probit)} = \ln T + \text{Species} + \text{Species} \times \ln T + \text{Constant} \quad (1)$$

where Mortality (Probit) is the probit transformed percent of individuals for a given species succumbing to death after 12 h, ln T is the natural logarithm of temperature (°C) for the trial and Species was set to a categorical value (round goby = 1 or western tubenose goby = 0). Values of 0% and 100% mortality are undefined under probit transformation and therefore were removed before analysis. Prior to performing the GLM, data normality was tested using Lilliefors Test. After testing the model, the interaction term (Species × ln T) was found to be significant ($F_{1,16} = 6.673$, $p < 0.05$) indicating differences in LC50 between the species. As such, linear regressions were subsequently performed separately for each species and used to extrapolate the 12 h LC_{50} and 95% confidence interval (CI) around the LC_{50} value.

Standard metabolic rate

Prior to initiating the SMR study, ambient water temperature of holding tanks was 5 °C and all fish were assumed to have acclimated to cold conditions. Both communal tanks were then switched from flow-through to a recirculation system, with water temperature brought up to 10 °C over 72 h. Following respiration trials at 10 °C, experimental water temperatures within aquaria were then slowly increased to the next temperature treatment over a 72 h period (18 °C, 23 °C, 26 °C, 30 °C) and maintained until the next set of measurements were completed.

To measure individual oxygen consumption a single chamber intermittent flow respirometer (Loligo® Systems, Denmark) was used following Leadley et al. (2016). The respirometry chamber had dimensions of 33 mm diameter × 100 mm length. A submersible galvanic oxygen probe (MINI-DO, Loligo Systems, Denmark) was used to measure oxygen concentration in the respirometry chamber during measurement periods. AutoResp software provided automated system control and data collection. Each measurement trial used one fish per chamber and lasted for 18 to 27 h. During each trial the system was sequentially looped through two stages: (i) the measuring period, where the chamber was sealed with O_2 concentration logged through time, and (ii) the flush period, where oxygenated water was pumped through the chamber until the next measurement period. Measurement/flush periods were set to 300 s and 130 s, respectively except for the 30 °C temperature trials where periods were set to 120 s and 110 s to reduce oxygen sags.

Respirometry trials were conducted under dark conditions using three separate trials on individual fish of each species within each temperature treatment. All individuals were fasted for 24 h prior to trial initiation. Each individual had its total length (mm), standard length (mm), weight (g) and volume (mL; by water displacement) measured (under sedation within a solution of MS222), and was then placed within the trial chamber. Individuals from each species were used only once per trial. The exception was the 26 °C and 30 °C tubenose goby trials, where, due to limited availability of fish, the same three