This is the Accepted Version of a paper published in the Journal Estuarine, Coastal and Shelf Science:


[https://doi.org/10.1016/j.ecss.2017.06.032](https://doi.org/10.1016/j.ecss.2017.06.032)

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Accepted Manuscript

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PII: S0272-7714(16)30585-6
DOI: 10.1016/j.ecss.2017.06.032
Reference: YECSS 5522

To appear in: Estuarine, Coastal and Shelf Science

Received Date: 7 November 2016
Revised Date: 8 May 2017
Accepted Date: 25 June 2017

Please cite this article as: Waltham, N.J., Sheaves, M., Acute thermal tolerance of tropical estuarine fish occupying a man-made tidal lake, and increased exposure risk with climate change, Estuarine, Coastal and Shelf Science (2017), doi: 10.1016/j.ecss.2017.06.032.

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Acute thermal tolerance of tropical estuarine fish occupying a man-made tidal lake, and increased exposure risk with climate change

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Keywords: Acute Effect Temperature (AET), fish, thermal refugia, tropical estuary, climate change

Running title: Acute thermal tolerance and climate risks for tropical estuary fish
Highlights

• Constructed tidal lakes provide new and additional habitat for fish
• Summer lake surface water temperature frequency exceeded acute thresholds for fish
• Summer lake bottom water provide important thermal refugia for fish
• Future climate change will double surface acute thermal exposure
• Current bottom water refugia will almost certainly be reduced under future climate
Abstract

Understanding acute hyperthermic exposure risk to animals, including fish in tropical estuaries, is increasingly necessary under future climate change. To examine this hypothesis, fish (upper water column species - glassfish, *Ambassis vachellii*; river mullet, *Chelon subviridis*; diamond scale mullet, *Ellochelon vaigiensis*; and ponyfish, *Leiognathus equulus*; and lower water bottom dwelling species – whiting *Sillago analis*) were caught in an artificial tidal lake in tropical north Queensland (Australia), and transported to a laboratory tank to acclimate (3wks). After acclimation, fish (between 10 to 17 individuals each time) were transferred to a temperature ramping experimental tank, where a thermoline increased (2.5°C/hr; which is the average summer water temperature increasing rate measured in the urban lakes) tank water temperature to establish threshold points where each fish species lost equilibrium (defined here as Acute Effect Temperature; AET). The coolest AET among all species was 33.1°C (*S. analis*), while the highest was 39.9°C (*A. vachellii*). High frequency loggers were deployed (November and March representing Austral summer) in the same urban lake where fish were sourced, to measure continuous (20min) surface (0.15m) and bottom (0.1m) temperature to derive thermal frequency curves to examine how often lake temperatures exceed AET thresholds. For most fish species examined, water temperature that could be lethal were exceeded at the surface, but rarely, if ever, at the bottom waters suggesting deep, cooler, water provides thermal refugia for fish. An energy-balance model was used to estimate daily mean lake water temperature with good accuracy (+ 1°C; $R^2 = 0.91$, modelled vs lake measured temperature). The model was used to predict climate change effects on lake water temperature, and the exceedance of thermal threshold change. A 2.3°C climate warming (based on 2100 local climate prediction) raised lake water temperature by 1.3°C. However, small as this increase might seem, it led to a doubling of time that water temperatures were in excess of AET thresholds at the surface, but also the bottom waters that presently provide thermal refugia for fish.
1. Introduction

Despite being incredibly productive habitats for fish (Blaber et al., 2010; Manson et al., 2005; Nagelkerken et al., 2015), across much of the world tropical estuaries continue to be modified for human gain (Rozas, 1992; Wen et al., 2010). An example of this modification occurs where property developers excavate large tracts of natural wetlands (e.g., mangroves, saltmarsh), or dig out terrestrial habitat to create artificial, urban water development, designed to increase extent of usable waterfront land (Lindall et al., 1973; Waltham and Connolly, 2013). Residential urban waterways have been built on most continents, and collectively contribute to over 4,000 km linear of engineered habitat for fish (Waltham and Connolly, 2011). In utilising these built waterways fish (Claassens, 2016; Waltham and Connolly, 2006) are susceptible to contamination and poor water quality (Maxted et al., 1997), and hydraulic connectivity with downstream estuaries may be altered (Zigic et al., 2002). Furthermore, their position in low lying areas of coastal floodplains raise concerns about vulnerability to sea level rise, shoreline erosion (Harvey and Stocker, 2015), and that climate change might reduce the utility of these man-made habitats for fish (Waltham and Connolly, 2011).

Animals spend a significant proportion of time (and energy) avoiding or escaping stimuli (predation, chemical contamination, noise) that could cause physical harm that reduces fitness or causes death (Connell, 1993). One causal stimulus contributing to animal avoidance is exposure to high temperature (Brett, 1956). Determining effects of temperature on animal behaviour and movement has received increasing attention prompted by climate change concerns and how future, warmer temperature may cause range shifts in distribution of native (James et al., 2017; Stewart et al., 2013; Welbergen et al., 2008), or invasive species (Carveth et al., 2006), or in some cases extinction of vulnerable species (Thomas et al., 2004). For many aquatic species, including fish, temperature directly controls metabolic rate, and can influence growth, resource allocation for reproduction and ultimately, population size (Armstrong et al., 2013; Jobling,
Evidence shows that growth rate and development in fish tend to increase with temperature up to an optimum, provided sufficient food is available (Eaton and Scheller, 1996). However, the long term (chronic) effects of exposure to elevated water temperature can include reduced year class strength (Brown et al., 2016; Nunn et al., 2003), cessation of growth, and increased susceptibility to environmental stresses such as low concentrations of dissolved oxygen (Pearson et al., 2003). Exposure to extreme temperature causes acute hyperthermic (or hypothermic) response, requiring animals to thermoregulate or they will die (Coulter et al., 2016; McCauley and Casselman, 1981). Determining the temperature threshold (defined here as Acute Effect Temperature, AET) provides insight into thermal exposure risk, necessary for species protection and conservation.

This paper reports fine time-interval resolution (20 min) continuous water temperature measurements made in a residential man-made tidal lake in Townsville, northern Queensland, Australia. We used these data to quantify how water temperature changes as the austral summer evolves, and how water temperature varies between the surface and bottom layer in tidal built lakes. We then determine the AET for five common estuarine fish that occupy the lakes using laboratory manipulative experiments, to assess how often lake water temperature approach and exceed these thresholds. Advancements in water thermal energy modelling provides the opportunity to predict temperature exposure risk to aquatic animals using readily available daily weather data (McJannet et al., 2014; McJannet et al., 2012; Wallace et al., 2015). We then use an energy balance model to simulate how climate change might influence the thermal exposure risk for fish occupying engineered tidal lakes.

2. Methods

2.1 Study area
Ross Creek is a small (8 km linear) transitional (Elliott and Whitfield, 2011) estuary in tropical north Queensland (-19.270688° S, 146.788279° E) that flows into Cleveland Bay, and the Great Barrier Reef lagoon, Figure 1a (Sheaves and Johnston, 2010). Located adjacent to Ross Creek is a large constructed residential tidal lake estate, built in the early 1990s as a way to increase residential real estate with waterfrontage (Waltham and Sheaves, 2015), and to treat water quality (sediment and nutrient load reductions) discharged from the surrounding urban and industrial estates before reaching the main estuary and Great Barrier Reef lagoon. The lake system is approximately 7.5 ha, average water depth is between 1.9 to 2.5 m (150ML). The lake has two sections that are connected via a narrow concrete open channel (approximately 150 m long, 10 m width and 1 m depth) which allows water exchange and fish passage between the lakes. A long concrete channel extends from the lake, joining with Ross Creek approximately 3.5 km upstream from the mouth of the creek. A series of four engineered hydraulic arms separate the concrete channel from Ross Creek estuary, and are synchronised to open based on the tidal height of the downstream Ross Creek (though can be manually opened during extreme flood events) (Causeway Floodgate Procedures, Townsville City Council, unpublished manual). The hydraulic control structure permits tidal exchange with Ross Creek, in such a way that it reduces the tidal prism, which is necessary to circumvent situations where increased tidal prism compromises engineering rock walls or bridge foundations, and contributes to erosion along the lake edges (Zigic et al., 2002). Fish visit the lakes and can return to the estuary during times when the hydraulic gates are open. The lakes holds a subset of fish species found in the adjacent estuaries (Sheaves et al., 2012) including a number of diadromous species common throughout the region (Sheaves and Johnston, 2010; Sheaves et al., 2010; Waltham and Davis, 2016). During summer months the lakes become hypoxic, a consequence of high ambient air and water temperature (which reduces the solubility of oxygen in water available for fish), in addition to high densities of oxygen consuming phytoplankton and sediment benthic algae; a trait that
contributes to poor water quality and fish kills in coastal waters of Queensland (Dunn et al., 2012).

2.2 Estuary fish acute temperature effects experiments

In this study, a subset of local estuarine fish species were examined, including glass perch (Ambassis vachellii), river mullet (Chelon subviridis), diamond scale mullet (Eliocheilon vaigiensis), and pony fish (Leiognathus equulus) – representing upper water column assemblage; and the whiting (Sillago analis) – representing benthic dwelling assemblage. Fish were collected in the lake using a seine net (10mm mesh, 1.8m drop), and transported to the laboratory for acclimation (from the collection site to the laboratory was 30 min, using three 90 L containers each with battery aerators). The laboratory had a single 800 L saltwater tank (salinity 33), set up on a re-circulatory system with water exchange set approximately 10 L/min (MARFU, James Cook University).

In the laboratory, fish were acclimated to a constant temperature (28°C; ±2°C) for three weeks prior to the Acute Effect Temperature (AET) exposure experiment. This acclimation temperature represents approximately the summer average daily water column temperature in the lakes (based on historical water quality monitoring undertaken by Townsville City Council since 1994 - unpublished data). Fish were fed aquaculture pellets (Ridley AgriProducts Pty Ltd) every 2-3 days; all fish were feeding during the acclimation period suggesting that they were not stressed prior to the temperature exposure experiment.

In the AET experiment an experimental glass aquarium tank (0.7 x 0.4 x 0.6 m; ~150 L) was designed specifically for the experiment. Two circulatory pumps were placed in the tank to ensure the tank was well mixed. Water in the experiment tank was continuously replaced at a rate of 2 L/min with water on the acclimation tank system. Photoperiod in the aquarium
laboratory was maintained at 12:12h dark:light cycle. The experimental tank was cleaned after each experiment, resulting in an approximate 80% water exchange.

Between 10 and 16 individual fish were transplanted from the acclimation tank to the experimental tank 2-3 days prior to the AET experiment tank so that fish would acclimate to the new tank setting. During the experimental tank acclimation period, conditions (i.e., water temperature (28°C) and photoperiod) remained the same as the acclimation tank.

At the start of each AET experiment, the water circulation pipe was closed so the tank was a single experimental unit. A programmable thermo-controller (Thermoline, Eurotherm 3216 Control) was used to increase the water temperature at a linear rate of approximately 2-3°C per hour with the experiment commencing at the acclimation temperature (this rate is similar to diurnal water temperature changes experienced in the lake, see below). The time elapsed and water temperature on the thermocline readout display were recorded when fish (one at a time) lost equilibrium or displayed erratic behaviour (Burrows and Butler, 2012). Fish were then immediately placed into a separate recovery container filled with room temperature (28°C) water for up to 30 mins before being relocated to a separate holding tank (to avoid repeated use of fish) that was also on the main water circulatory system (fish total length was measured before release; there were no linear relationship between fish size and AET, for each fish species examined here). The experimental tank was drained, left to cool for 24 hrs, refilled with seawater from the main acclimation tank, ready for the next experiment. Fish AET statistics were determined and are presented in Table 1.

2.3 Lake water temperature logging

To profile water temperature characteristics in the urban tidal lakes, Hobo temperature loggers (Onset Corporation Bourne, Massachusetts) were deployed at two depths at approximately the
deepest point in both lakes: 1) surface; 0.2 m below water surface; and 2) bottom; 0.1 m above the lake bottom. The surface logger was attached to the underside of a 0.15 m diameter buoy to shield it from the sun at all times as direct exposure could produce erroneous results. Loggers were set to record data every 20 min from 31 October 2015 to 30 March 2016 (this logging period represents the summer months for the region, and thereby the maximum likely temperature that fish would be exposed too). This logging frequency was necessary to derive water temperature frequency distributions for the purposes of assessing exposure risks (Wallace et al., 2017; Wallace et al., 2015). The same logger configuration was deployed in Lake 2 (Keyatta Lake) (Fig 1.), unfortunately these temperature loggers, after 21 December 2015, failed and no further data were retrieved. This limited our ability to generate exposure risk plots and to model the temperature. Data for Lake 2 are presented in the Supplementary Notes (see Fig. S1), however, is not included further in this study.

2.4 Estimating lake water temperatures

Water temperature was estimated using the energy balance model (McJannet et al., 2014; Wallace et al., 2015). The model was originally developed for estimating daily evaporation from open water bodies of various sizes (ranging from waterbodies ~ 60 m wide, ~ 600 km² in area), but it can also calculate the daily mean water body temperature in order to specify the changes in heat storage (to a well-mixed water column). The main input of energy to the model is solar radiation and the main loss occurs via heat conduction to the atmosphere and evaporation. It is also possible for energy to enter/leave water if there is flow, however, this effect can be ignored here given the tidal exchange is small, when considering the total lake volume (approximately < 0.01% of total lake volume is exchanged each day).

The lake water temperature model requires daily weather data, which were obtained from the Australian Government SILO database (http://www.nrw.qld.gov.au/silo/). The SILO database
consists of interpolated meteorological variables on a 0.05° (5 km) grid for the whole of Australia (Jeffrey et al., 2001). The variables available from SILO used in the temperature model are air temperature, vapour pressure, solar radiation and rainfall, and the way these variables are used to calculate all of the terms in the model are described by (McJannet et al., 2008). The model also requires daily mean wind speed (to calculate the evaporation rate) and as this is not available in the SILO database, a fixed wind speed of 1.3 m s$^{-1}$ was applied in the model; the consequence of this assumption is discussed later in the paper. Evaporation rate is also dependent on the water body size, in terms of both surface area and depth. Water area affects the ‘wind function’ used in calculating evaporation (McJannet et al., 2012). Water depth primarily affects heat storage and the model is run from the beginning of the year so that its depth predictions match waterhole depth measurements made during the model period November 2015 to March 2016 (Supplementary Fig S3). Sensitivity analysis shows that altering the water surface area or depth by a factor of 2 only changes modelled water temperature by 0.8% and 0.2% respectively.

### 3. Results and Discussion

#### 3.1 Lake water temperature

During the logging period, weather conditions were generally fine during November to February period, as is typical for this time of year in the region. In this period the water column consistently exhibited pronounced diel temperature periodicity and occasional diurnal stratification (Fig 2). Typically one or two hours after sunrise each day the near-surface water temperature began to rise at almost a linear rate for a period of 8 hrs reaching daily maxima as high as 40.4 °C (mean 33) during the early evening hours (14:00 to 17:00). The mean increase in water temperature at the near-surface during the day (06:00 to 14:00) was 2.8 °C h$^{-1}$ (max 6.5 °C h$^{-1}$). For the remaining 16 hrs of the day the near-surface water temperatures gradually
declined reaching a minimum 24.0 °C (mean 30.8 °C; max 38.2 °C), shortly before sunrise (04:00 to 08:00).

In order to properly quantify the temperature regime in constructed urban tidal lakes, would require logging water temperature over a number of spatiotemporal scales, in order to incorporate the full range of engineering designs of these urban lakes (e.g., where flow is controlled using tidal gates, tidal pipes, rock bund walls, as each have varying differences in the hydrodynamic exchange of tidal water with the downstream primary estuary (Waltham and Connolly, 2007)), and to also examine among year differences in thermal regimes. Data here were collected during a single summer period, and therefore provide an indicative guide of the annual minimum and maximum conditions expected at this time of the year. The methodology applied here of determining acute thermal thresholds (laboratory experiments), combining with high frequency continuous water temperature data, in addition to water balance models to examine future exposure risks under climate change (Wallace et al., 2015), are the key focus of this paper; these methods are transferable to elsewhere, to examine thermal exposure risks to tropical estuarine fish species.

Water temperatures near the bottom increased at a more gradual rate each day, with an increasing trend sustained for a longer period (15 hrs), therefore daily maximum was reached after sunset (mean 29.3 °C; max 36.5 °C). The mean hourly (during the day) increase in the near-lake bottom was 0.3 °C h⁻¹ (max 1.8 °C h⁻¹). The fact that bottom water temperature continued to increase (lag) after sunset is a consequence of either continuing thermal heat exchange after sunset (conduction), or the effect of partial mixing with the warmer surface water.
An important fact in the data here is that lake water temperature changed across the logging period (Fig 2a), where the water column was vertically well mixed (surface and bottom waters remained similar), but at other times the column was diurnally stratified, where surface and bottom waters were separated by several degrees Celsius (Fig. 2b). Changes in mixing often coincided with rainfall events, the most notable occurring on 10 January 2016 (91.8 mm over 72 hours, Townsville airport, station number 32040), where the initial influx of cool rainwater decreased surface water temperature by 6 °C in just 3 hours, compared to only 3 °C in this time period in the bottom water temperature. It can be seen that rainfall causes dramatic changes in the thermal regime in the lake, where diurnally stratified profile then became vertically well mixed, which occurred on 28 December 2015 after 91.8 mm of rainfall fell in 3 days (Fig 2b).

The period where the near-surface waters (and to a lesser extent bottom waters) were coolest occurred between 20 February and 18 March 2016, where a series of rainfall events (totaling 561 mm over several weeks) occurred in the region. In this time series, after each rainfall event surface water temperature progressively increased again until the next rainfall event. In fact, between 11 and 18 March 2016 the bottom water temperature was higher than at the surface, which indicates the ability for deeper waters to store thermal energy for relatively long periods.

### 3.2 Fish temperature threshold experiments

The AET of five estuarine fish species ranged between 33.1 °C (minimum) and 39.9 °C (maximum), Table 1. Of these fish species, the range between lowest AET and the highest for an individual species was 6.7 °C, which occurred for the whiting, *Sillago analis*, while the smallest difference (0.9 °C) was found for diamond scale mullet, *Ellochelon viagiensis*. Interestingly, in a study of thermal tolerance of marine fish in Indonesia, Eme and Bennett (2009) revealed a similar thermal tolerance for *E. viagiensis* of 38°C when acclimated at about 25°C, compared to (AET$_{50}$) 39.5°C when acclimated at 28°C in the present study.
The narrow range in AET has been found in other studies using estuarine fish species (Cheng et al., 2013; Heath et al., 1993; Rajaguru and Ramachandran, 2001), but also tropical freshwater fish species (Burrows and Butler, 2012). Table 1 provides an overview of the percentage of time that each fish species exceeded the thresholds using the surface and bottom logging temperature data. For example, the surface dwelling glass perch, *Ambassis vachellii*, exceeded the minimum AET (35.1°C) 26% of the logging time at the surface, and less than 3% of the logging time at the bottom waters. In contrast the benthic dwelling whiting, *Sillago analis*, minimum AET threshold (33.1°C) was exceeded 58% of the logging time at the surface, and 28% of the logging time at the bottom waters. When exposed to water temperature above these thermal thresholds, we assume fish would search for cooler thermal refugia. Both lakes have limited edge vegetation for shading (Fig. 1B); to this end the most likely response for fish would be to descend the water column to the bottom, cooler lake waters (Figure 3b), where neither of the above thresholds are exceeded during the summer months. The need to migrate through the water column has been also suggested for freshwater fish occupying ephemeral waterholes within the tropical seasonal rivers of northern Australia (Wallace et al., 2017). While providing thermal refugia, the cooler bottom waters have critically low, hypoxic, dissolved oxygen concentrations (unpublished data Townsville City Council). By continually adjusting position to regulate against high water temperature and dissolved oxygen, fish would use important energy reserves leaving them more susceptible to critical water quality conditions, compromising reproductive fitness and predation susceptibility (Eaton et al., 1995). The energy balance model used here shows that thermoregulation will increase under future climate change, for some fish this increase is considerable. For example, the ponyfish, *Leiognathus equulus*, AET is exceeded between 14% of the logging time (based on maximum AET), but could be has high as 47% (using the minimum AET) at the surface, and up to 14% of the logging time in the bottom waters (based on minimum AET) under future climate conditions (Table 1).
The acclimation tank temperature used in our experiment (28 °C) is commonly reported in the literature (Burrows and Butler, 2012). Clearly these data show that aquatic organisms inhabiting transitional coastal waters are exposed to constantly fluctuating water temperature, which raises questions regarding the validity of acclimating at a constant temperature (Rajaguru and Ramachandran, 2001); it would seem advisable to simulate the natural diel temperature periodicity of the animals’ environment during acclimation (Coulter et al., 2016). We advocate here that fluctuating acclimation temperatures are probably most appropriate in laboratory experiments, however, based on our field measured temperature data, determining what diel range to simulate would be difficult.

3.3 Modelling lake water temperature

The water temperature model used here predicted measured temperature to within 1°C during periods when the lake was well mixed (Supplementary Fig S2 and S3). Underestimation of water temperature in the modelling has been shown in other studies McJannet et al., (2008) and Wallace et al., (2017), where those studies attributed the underestimation in wind speed (which may be different to the 1.3 m/s applied here in the model; increasing the wind speed to 2 m/s (as applied in freshwater waterholes in northern Australia; Wallace et al., 2015; Wallace et al., 2017) contributed to further model underestimation ($R^2 = 0.81$). For this reason the absolute accuracy of the modelling when using readily available government weather climate data is probably between 1 and 2°C, however, precision could be improved with installation of weather stations, recording continuous weather conditions, that are located immediately adjacent to water body of interest.

Concern about the potential impacts of climate change on coastal transitional waters is widespread. For example, authors of studies in the US and Europe have found that climate-warming increases may reduce habitat availability, while for others it will increase leading to
shifts in species distributions (Buisson et al., 2008; Eaton and Scheller, 1996; Robins et al.,
2016; Sinokrot et al., 1995). Future changes in climate in northern Queensland could affect the
thermal environment of constructed urban tidal lakes. For the proposed increase in air
temperature of 2.7°C by 2100 (Hennessy et al., 2008), the model predicts water temperature will
increase accordingly by 1.3 °C. The modelling suggests that the period of exposure to acute
thermal conditions increases, particularly at the near-surface water layer. It seems that deeper
lake areas might provide important thermal refugia, where water temperatures under future
climate conditions remain below the thermal threshold for the fish species examined here. On
this basis it seems probable that fish occupying the deep waters are shielded from future climate,
however, fish species associated with near-surface waters may need to migrate down the water
column, more often, to find thermal relief. In the future, vertical migration in the water column
may increase expose to critically low dissolved oxygen (Marshall and Elliott, 1998; O’connell et
al., 2000). Fish in estuaries may be also subjective to salinity which can vary seasonally, tidally
The interaction between salinity and water temperature has been previously shown to influence
thresholds in estuarine fish (including for analogous Ambassidae species) (Blaber, 1973; Martin,
1988), and should be investigated in future research.

4. Conclusions

Once in a constructed artificial urban lake, at least some estuarine fish species are faced with
acute thermal exposure stress during summer months, and in response, would need to actively
search for thermal refugia, including potentially accessing the cooler, lake, bottom waters.
Using a water energy balance model, it seems that fish occupying the near-surface waters will
spend more hours of the day searching for thermal refugia under future climate change, in some
cases up to twice the amount of time each day that they currently invest. Whether fish can
successfully achieve this will be influenced by other factors, such as available oxygen, salinity
or prey abundance, but would indeed still require fish to be continually moving in the water column. We believe that the methodology presented here is transferable to other transitional water locations.

Acknowledgements

Funding for this project was provided by TropWATER (Centre for Tropical Water and Aquatic Ecosystem Research), and College of Science and Engineering, James Cook University, internal grant awarded to NW. We thank Prof J Wallace (TropWATER) for assistance with climate change modelling, M Kuehlcke for laboratory assistance, and staff from MARFU (Marine Aquaculture Research Facility Unit), James Cook University. This study was completed under ethics approval (A2150) and general fisheries permit (151660).

References


Table 1. Temperature tolerance experiments for each species examined. Summary statistics provided demonstrating the range in AET. Current and future climate threshold exceedance (%) for both surface and bottom logger data.

<table>
<thead>
<tr>
<th>Family/species</th>
<th>Number</th>
<th>Size range (TL, mm)</th>
<th>Statistic</th>
<th>28°C acclimation experiment</th>
<th>Current climate threshold exceedance (%)</th>
<th>Future climate threshold exceedance (%)</th>
<th>Current climate threshold exceedance (%)</th>
<th>Future climate threshold exceedance (%)</th>
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List of figures

Figure 1. A) Curralea Lake (Lake 1) and Keyatta Lake (Lake 2), and connecting channels adjacent to Ross Creek, Townsville, Australia. Dark grey fill indicates urban, industrial or commercial areas. B) Photo illustrating limited riparian shading provided around these lakes.

Figure 2. High frequency of water temperature recorded at the surface (~0.2m; black) and bottom (~2.4m; grey) in Lake 1. A) full data set; and B) subset of the logging data from (A), along with rainfall data for this logging period.

Figure 3. The percentage of time (based on 20 min data between 31 October 2015 and 31 March 2016) water temperature in Lake 1. In both graphs, black curve line is measured water temperature for the current survey period, broken black curve line is the future modelled climate change data for the same time period. (a) lake near surface; and b) lake bottom waters. Threshold lines present minimum Ambassis vachelli AET (black line), and maximum AET (grey line measured temperature (not shown given <1%; Table 1)).
Fig 1.
Fig 2.
Fig 3.