

wetlands

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Significance statement

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Acute thermal and asphyxia exposure risks for freshwater fish occupying three tropical wetland typologies were examined. Field water-quality data revealed that fish in wetlands grazed by pigs had the highest exposure risks, because they are shallow and heavily damaged by pig activities. In contrast, with the exception is dissolved oxygen (which still

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reached critical conditions because of aquatic vegetation respiration), deeper permanent and pig-managed wetlands provides the best opportunity for the same fish species to survive in a heavily pig-modified tropical landscape.

KEYWORDS

dissolved oxygen, floodplain, freshwater fish, pigs, thermal tolerance, wetland

Duration and frequency of coastal floodplain connection with primary rivers is an essential element in successful fish production (Bennett & Kozak, 2016; Galib *et al.*, 2018; Górski *et al.*, 2016; Hurd *et al.*, 2016). However, many months after river flow ceases, floodplain wetlands disconnect from primary rivers and progressively become smaller and shallower (Pusey & Arthington, 2003), many drying completely (Datry *et al.*, 2018) because of water loss either through evaporation, groundwater recharge, or consumption from wildlife (McJannet *et al.*, 2014; Pettit *et al.*, 2012). In tropical regions such as northern Australia wetlands continue to retract away from the banks and riparian shade (Pusey & Arthington, 2003), where they become predisposed to reduced water quality conditions and depth (Pettit *et al.*, 2012), but most notably experience high water temperatures (Waltham & Fixler, 2017) reaching acute and chronic thresholds for local aquatic fauna (Wallace *et al.*, 2015; D. Burrows & B. Butler, unpubl. data). In the late dry season, fish are confined to the bounds of the isolated wetland and have very limited avoidance options. Wetland fish must, therefore, exploit available ephemeral aquatic habitats in order to survive until monsoonal rain reconnects the floodplain and again providing the opportunity for those remaining aquatic fauna to move.

Here, three wetland typologies were examined in the Archer River catchment in northern Queensland, Australia (Fig. 1): pig modified [Fig. 1(b)], wetlands where the feeding activity of feral pigs *Sus scrofa* contributes to the loss of vegetation, exposure and turnover of sediments (Baber & Coblenz, 1986) and where they are shallow and suffer poor water quality (Doupé *et al.*, 2010; Waltham & Schaffer, 2017); permanent wetlands [Fig 1(c)], wetlands that are deeper and more permanent (remain through dry season until the next wet season) and are therefore less affected by feral animals (Pettit *et al.*, 2012); fenced wetlands [Fig. (1d)], wetlands where human intervention prevents feral animal access, where submerged aquatic vegetation remains and water quality is usually better with clear, deeper, waters (Waltham & Schaffer, 2017). The aims were first to determine the acute effects temperature (AET) at which freshwater fish occupying these types of wetland habitats in northern Queensland. The

second was to contextualise the AET and hypoxia exposure risks for fish occupying tropical wetlands, among the different levels of disturbance from feral pigs. The second aim was achieved by collecting high frequency water temperature and dissolved oxygen data to generate exceedance frequencies curves, which are then used to define the risk for fish occupying these wetlands.

Calibrated Hydrolabs (OTT Hydromet GmbH; www.ott.com) were deployed in wetlands (0.2 m depth) in the catchment for between 2 and 4 days to record water temperature, dissolved oxygen (%), electrical conductivity and pH every 20mins (electrical conductivity and pH are not analysed here); logging at this frequency provides explicit insight into diel changes in environmental water processes (Wallace *et al.*, 2015, 2017; Waltham *et al.*, 2013; Waltham & Fixler, 2017) (Supporting Information Table S1). Weather was fine with wetlands on the falling stage of the hydrograph, representing the most extreme time of year for fauna occupying these types of wetlands. The water column exhibited pronounced diel temperature periodicity; 1–2 h after sunrise each day near-surface water temperatures began to rise at an almost linear rate for a period of 7.5–8.5 h reaching daily maxima as high as 40.2° C during the middle of the afternoon. The mean daily temperature amplitude was 6.26° C (highest daily amplitude 9.67° C, lowest 4.4° C). For the remaining 16 h of each day near-surface water temperatures (0.2 m) gradually declined reaching a minimum (lowest 24.5° C; maximum 28.9° C) shortly after sunrise.

Fish were collected from four of these wetlands using a fyke net (0.8m opening, double 4m wing panels, 1mm stretch mesh) that was soaked overnight (*c.* 1400 hours to 0900 hours) November 2017. In wetlands occupied by feral pigs, Secchi disc depth was < 0.1m and they had no submerged or floating aquatic plants present, while the permanent and fenced wetlands were generally deeper (≤ 1.5 m) and contained submerged aquatic vegetation. Fish were placed in a tub *c.* 90 l) at the station homestead (within 3 h of collection) with water sourced directly from the Archer River. Fish were acclimated ($28^{\circ}\text{C} \pm 1.2$) which is proximal to the daily

water-column average (which is suitable for hyperthermic experiments; D. Burrows & B. Butler, unpubl. data) in the tub for between 4 and 8 h before a programmable thermo-controller (Thermoline, Eurotherm 316 Control; www.thermoline.com.au) increased the water temperature at a linear rate (2.5°C), proximal to the average hourly increase measured in these wetlands (Waltham & Schaffer, 2015). The time at which fish showed lost equilibrium, which is an assumed acute thermal response (Eme *et al.*, 2011; Stewart & Allen, 2014), along with the temperature displayed on the thermocline were recorded. Fish were removed immediately from the experimental tank and placed in a bucket with river water (*c.* 28°C) to recover and then returned to the same wetland the next day. This research was completed under Queensland Animal Care and Protection Act 2001 and James Cook University animal ethics permit number A2239.

The AET determined for each fish species (Table 1) revealed that the empire gudgeon *Hypseleotris compressa* (Krefft 1864) has the widest range (3.5°C between minimum and maximum AET). The lowest (1.0°C) range was northern trout gudgeon *Mogurnda mogurnda* (Richardson 1844). The highest single observed AET (39.9°C) was the sleepy cod *Oxyeleotris lineolata* (Steindachner 1867), while the lowest (36.6°C) was *H. compressa*. For each fish species, there was no significant relationship between fish size and AET ($P > 0.05$).

Contextualising AET findings involved using a frequency distribution plot displaying the range of water temperatures recorded in the wetlands (Fig. 1). The AET for fish were higher than water temperature conditions in the permanent and fenced wetlands, which means that fish probably have no need to be searching for thermal refugia. In contrast, AET thresholds were exceeded in pig-modified wetlands, between 8 and 18% of the logging period and therefore would need to seek thermal refugia for at least part of the day. A review of water temperature data recorded at government-maintained stream-flow gauging stations across northern Australia reported that water temperatures in excess of 50°C are possible in summer during daylight hours (D. Burrows & B. Butler, unpubl. data). The wetlands monitored here

do not experience maximum water temperatures that high, although the daily maximum field temperatures did reach 43°C, which is high enough to be stressful for fish. The fish species here are found in most rivers throughout northern Queensland (Pusey *et al.*, 2017), including off-channel wetlands that become seasonally connected during wet season rainfall (Balcombe *et al.*, 2007). It is not surprising that the ephemeral wetlands affected by feral pigs were prone to rapid water temperature fluctuations and acute hyperthermia periods, given their shallow nature and smaller thermal mass when compared with the more open, deeper, permanent wetlands. Fenced wetlands are intact, maintain more depth and have abundant floating and submerged macrophytes, in addition to riparian vegetation, that provide shade and cooling refugia (Kelleher *et al.*, 2012). Research elsewhere illustrates that freshwater species regulate high water temperature by accessing shaded microhabitat areas along river edges, such as under rocks, or fallen timber (Jones & Bergey, 2007; Larson *et al.*, 2009), which suggests that fencing or deep permanent wetlands with vegetation offers an important thermal safeguard for fish in tropical river catchments.

In addition to floating macrophytes, evidence from northern Australia shows that the bottom waters of thermally stratified fresh waters provide thermal refugia for fish, provided that the bottom strata contains sufficient dissolved oxygen to meet respiratory needs (Wallace *et al.*, 2017). The latter proviso is not always met, as deep waters in tropical wetlands experience critically low dissolved oxygen concentrations, often below 10% saturation (Waltham *et al.*, 2013); nevertheless, vertical migration between cool oxygen-depleted deep waters to warm oxygen-rich surface waters has been an effective thermoregulatory behaviour elsewhere (Elliott, 2000). Diel stratification can provide ideal conditions to support this kind of regulatory behaviour because the cool (but poorly aerated) bottom stratum forms only during the heat of the day (when a thermal refuge is most needed) and then mixes with the oxygenated surface water each night thus preventing the development of oxygen deficits (B. Butler, D. Burrows & R. Pearson, unpubl. data). When deep waters become stably stratified,

the bottom waters can remain unaerated for prolonged periods, increasing the risk of becoming too hypoxic to be utilized as thermal refugia for aerobic organisms. The depth required for stratification to occur is contingent on numerous site-specific variables such as flow characteristics, the size and aspect of the wetland, the degree of wind exposure and the composition and clarity of the water (Wallace *et al.*, 2017). These data for pig-modified wetlands suggest that water depth of < 1 m is not adequate to sustain diel stratification, particularly during the late dry season when tropical conditions are extreme.

The solubility of dissolved oxygen in water is strongly affected by temperature (*i.e.* high temperature reduces dissolved oxygen solubility (Diaz & Breitburg, 2009). Data on hypoxia tolerances of local freshwater fish species in northern Queensland is available (B. Butler & D. Burrows, unpubl. data) and while tolerance varies between species and life stages, for the purposes here, the chronic (62%) and acute (24%) threshold limits for *H. compressa* are shown for the three wetlands (Fig. 2) and indicate that this fish must regulate breathing many hours during the day. Regulating breathing results in increased ventilation rate (Collins *et al.*, 2013); hence the lower the dissolved oxygen level, the greater the amount of energy expended in order to breathe. In the wetlands here, exposure risk was highest in the pig-modified wetland [Fig. 2(a)], where the chronic threshold is exceeded 98% of the logging time and 48% of the acute threshold. While these data cover a few days, it reflects the hottest period of the year and thereby long-term exposure at this time of the year could result in energy deficits and reduction in growth rates and fecundity (Flint *et al.*, 2018). Nevertheless, many fish species successfully exploit waters with dissolved oxygen concentrations significantly lower than that. Regulatory failure and potential asphyxiation occurs at about 30% in the most sensitive local fish species and around 10% to 15% in sensitive invertebrates (B. Butler & D. Burrows, unpubl. data). Below those concentrations, the number of species affected increases with declining dissolved oxygen concentrations. Some fish in the wild survive regular exposure to concentrations below thresholds by rising to the surface to utilise aquatic surface respiration or

air gulping [*e.g.* tarpon *Megalops cyprinoides* (Broussonet 1782)]. Their capacity to do that safely depends on the timing of the oxygen sag and antecedent conditions, though maybe inhibited outright by the presence of dense floating weed mats (Waltham & Fixler, 2017). Notably it appears that most of the mortality associated with hypoxia-induced fish kills is due to exposure (*e.g.* thermal stress and sunburn) resulting from the animals' need to remain at the surface during the heat of the day to access available oxygen for respiration. In addition, predation risk probably increases as wetlands become shallower, or indeed, as fish respond to low oxygen availability and commence surface respiration.

Efforts to control effects of feral pigs on coastal wetlands are underway in northern Australia and we advocate here that the return for the financial investment, in terms of reducing thermal exposure to fish, similar to permanent wetlands, means that these interventions should continue. These data support a model that damage to wetlands from pig activities not only contributes to reduced aquatic habitat, through loss of aquatic vegetation communities, but also probably has secondary consequences, including water temperature and asphyxiation risks for many hours each day. The cultural and ecological value of coastal wetlands means that management intervention is increasingly necessary to ensure they remain productive and viable habitat (Creighton *et al.*, 2015). Here, permanent wetlands are probably the most critical aquatic habitat in terms of management priority (followed by managed wetlands) given the reduced thermal and hypoxic risks for fish without the expensive fence costs. Further research is necessary to examine climate change resilience on permanent wetlands (and managed wetlands) particularly whether they provide a similar level of refugia (James *et al.*, 2017).

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SUPPORTING INFORMATION

Supporting information can be found in the online version of this paper.

List of Figures

FIGURE 1 The three wetland typologies: (a) pig modified, wetlands that are shallow (typically < 0.5m deep), without submerged aquatic vegetation, turbid and eutrophic; (b) permanent wetland that is deeper (typically < 2m deep) and steep sided, which limits pig access, and clear with submerged aquatic vegetation present; (c) fenced wetland that prevents pig access, are deeper (typically < 2m deep), clear with submerged aquatic vegetation present, which is dominant in (d) the Archer River catchment. (e) Surface (0.2m) water temperature time-frequency distribution logged 12–22 November 2017 in the three wetland types: —, pig modified; ····, permanent; - - -, fenced. Horizontal lines show minimum acute effects temperature (AET) of freshwater fish present in wetlands to illustrate percentage of time above the water thresholds. Fish images courtesy of B. Hutchins, Western Australia Museum (*Hypseleotris compressa*), Department of Primary Industry, Government of New South Wales (*Mogumda mogumda*); www.fishesofaustralia.net.au (*Melanotaenia inomata*); www.ecogrow.ca (*Oxyeleotris lineolata*).

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- 1 Change A), B), etc to (a), (b) etc on each panel.
- 2 Change y-axis to read Time above AET (%).
- 3 Delete pig impacted wetland , persistent wetland , fenced wetland , (photo B Hutchins, Western Australian Museum) , (photo DPI NSW government) , (photo modified from fishesofaustralia.net.au) , (photo www.ecogrow.ca) .

FIGURE 2 Dissolved oxygen concentrations logged at (a) pig-modified, (b) permanent and (c) fenced wetland sites. Trigger guideline shown are 80% percentile peak ventilation rate (—) for eastern rainbow fish (*Melanotaenia s. inornata*) and 5% effect concentrations (- - -), after Butler *et al.* (2007).

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- 1 Change A), B), C) to (a), (b), (c).
- 2 Delete Day/time from (a) and (b).

- 3 Change Date/time below (c) to read Date and time (hours).
- 4 On each x-axis change 0:00 to 0000.
- 5 Delete Dissolved oxygen (%) from (a) and (c).

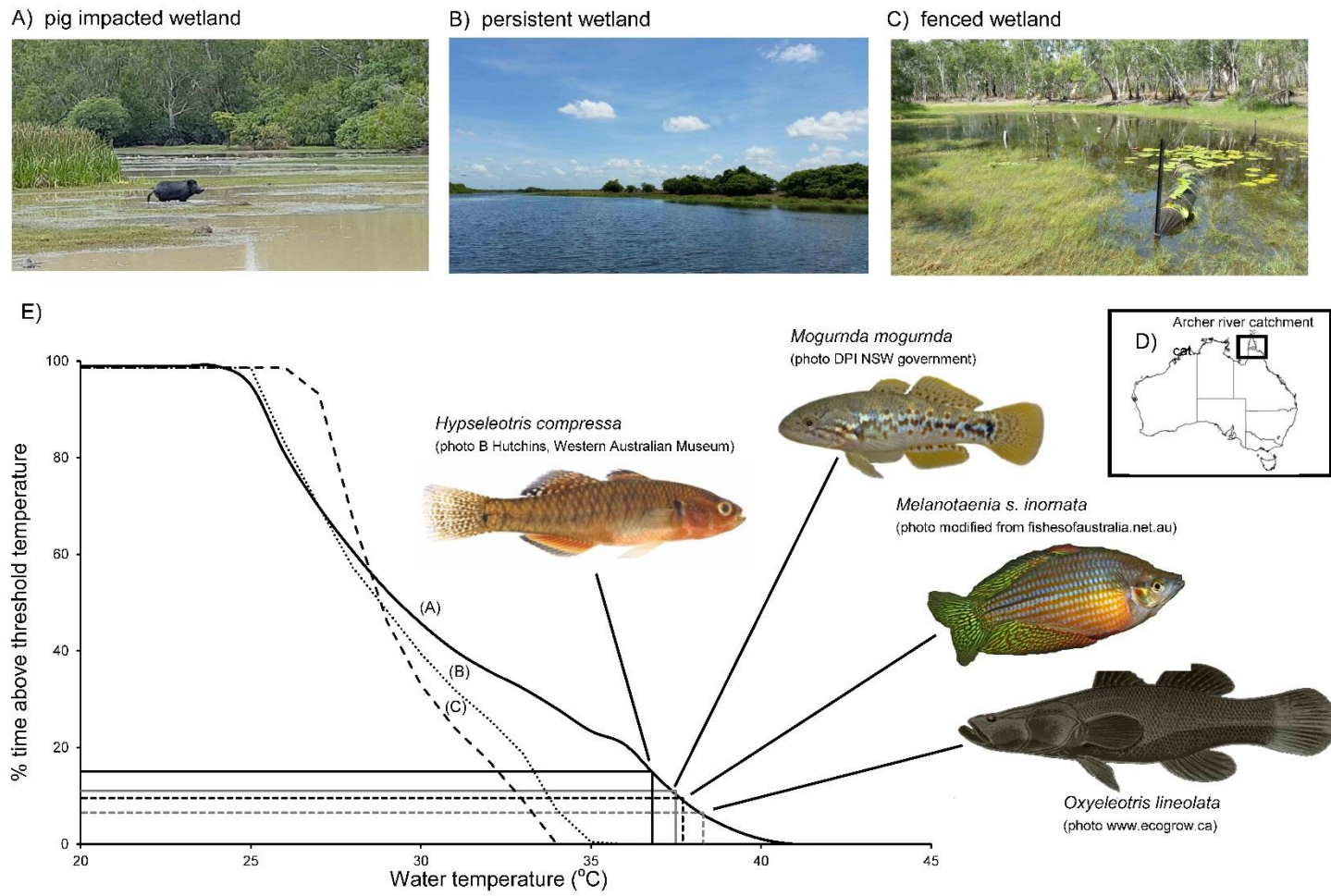


Fig 1.

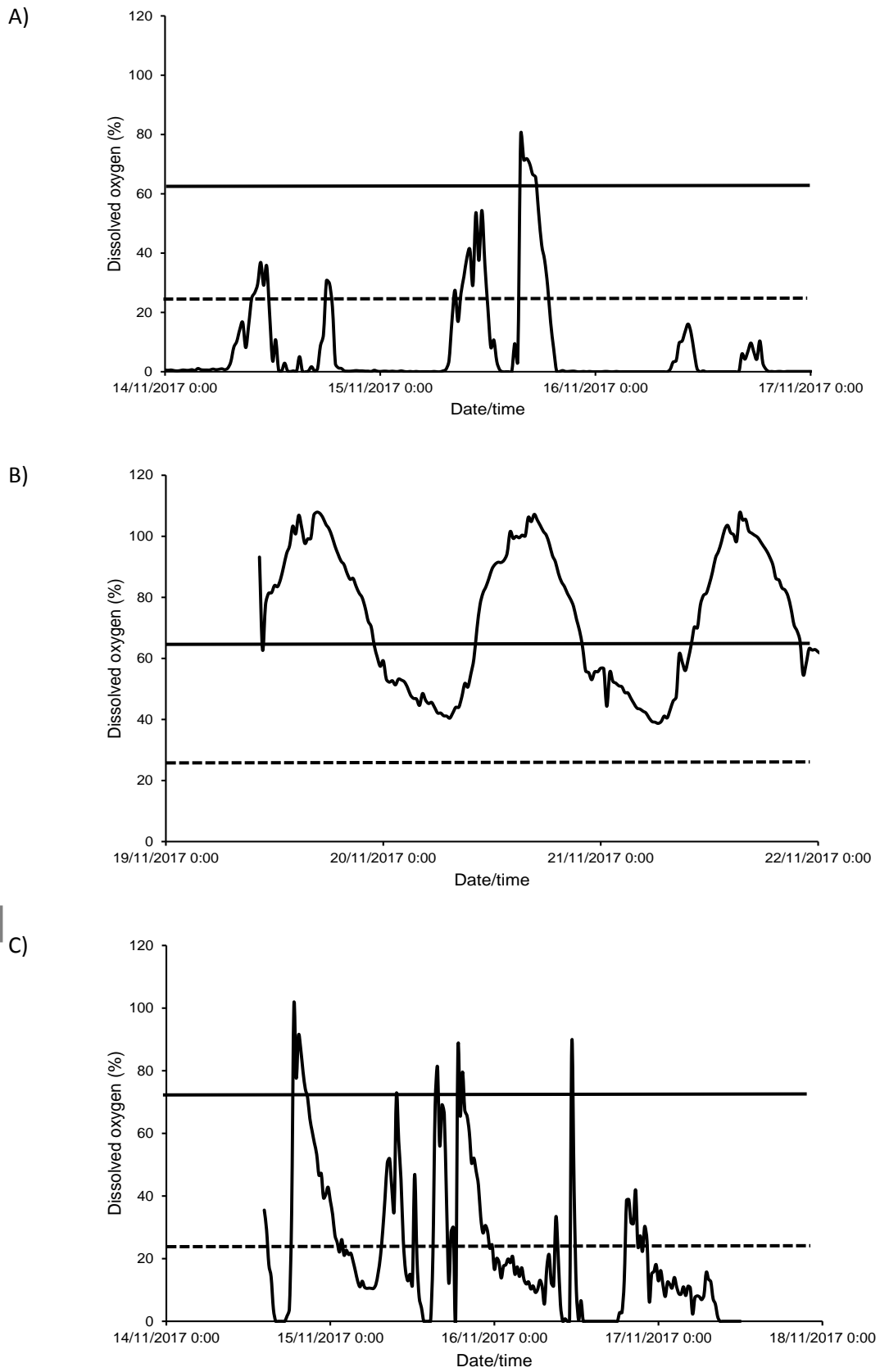


Fig 2.

TABLE 1 Thermal acute effect temperature (AET) results for fish tested in this study with the AET 10th, 50th and 90th percentiles calculated for each fish species, where possible.

Scientific name	Common name	Count	Standard length, range (mm)	AET ₁₀	AET ₅₀	AET ₉₀	Highest Observed AET
<i>Mogurnda mogurnda</i>	Northern trout gudgeon	13	28 - 40	37.5	38.3	38.4	38.5
<i>Iriatherina wernerii</i>	Threadfin rainbow fish	1	19	–	–	–	38.3
<i>Hypseleotris compressa</i>	Empire gudgeon	9	40–51	36.8	38.4	38.7	39.1
<i>Ambassis macleayi</i>	Glass perch	18	20–35	37.8	38.75	39.33	39.6
<i>Melanotaenia nigrans</i>	Black banded rainbowfish	6	48–80	39.1	39.3	39.4	39.4
<i>Melanotaenia s. inornata</i>	Eastern rainbow fish	6	33–40	37.7	38.5	38.7	38.7
<i>Pseudomugil tenellus</i>	Delicate blue eye	8	30–40	37.7	38.05	39.18	39.6
<i>Oxyeleotris lineolata</i>	Sleepy cod	10	60–85	38.3	38.5	39.72	39.9
<i>Porochilus rendahli</i>	Rendahl's catfish	2	75–90	–	38.65	–	38.7