

Upper thermal tolerances of key taxonomic groups of stream invertebrates

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Received: 25 June 2012 / Revised: 18 June 2013 / Accepted: 30 June 2013 / Published online: 12 July 2013
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Abstract Southwestern Australia has already undergone significant climatic warming and drying and water temperatures are increasing particularly in small streams where riparian vegetation has been cleared. The ability to predict how freshwater fauna may respond to these changes requires understanding of their thermal tolerances. A review of relevant literature and laboratory testing of four aquatic species from southwestern Australia were used to compare upper thermal tolerance (UTT) among key taxonomic groups. UTT for selected species determined by LT_{50} tests were similar to that of species tested elsewhere. Mean UTT, based on relevant literature and LT_{50} experiments, ranged from 22.3°C for Ephemeroptera to 43.4°C for Coleoptera. Mean UTT for both Coleoptera and Odonata (41.9°C) were significantly higher than those for all the other groups (22.3–31.5°C) with the exception of Planaria. The mean UTT value of 22.3°C for Ephemeroptera was significantly lower than for Decapoda (29.6°C), Trichoptera (30.1°C) and Mollusca (31.5°C). For three insect orders tested, eurytherms had significantly

higher UTT values than stenotherms. The variation in UTT among taxa suggests that additional thermal shifts, caused by riparian disturbance and/or climate change, are likely to create novel assemblages due to the replacement of temperature-sensitive taxa by more tolerant taxa. This has implications for the sustainability of regionally important endemic cool water species.

Keywords Temperature · LT_{50} · Aquatic invertebrates · Stream restoration · Southwestern Australia · Climate change

Introduction

Stream invertebrates are a highly diverse component of aquatic communities and play a critical role in aquatic food webs by providing linkages between primary sources of carbon (e.g. detritus, algae) and higher-order consumers including fish (Bunn et al., 1999). Water temperature is thought to play a role in structuring stream communities (De Deckker, 1986) and may affect aquatic biota either directly (e.g. by exceeding thermal tolerances of species), or indirectly (e.g. through its influence on dissolved oxygen concentrations) (Bunn & Davies, 1992; Horne & Goldman, 1994; Bunn et al., 1999). In small to mid-sized streams, riparian vegetation mediates water temperature by reducing input of solar radiation through shading (Rutherford et al., 2004). However,

Handling editor: Sonja Stendera

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riparian zones are also often sites of intense disturbance and clearing, particularly in agricultural landscapes (Bunn et al., 1999). Removal of riparian vegetation has been widespread in Australian (Bunn et al., 1999; Armstrong et al., 2005), and those streams lacking riparian shading are no longer buffered from temperature extremes (see Davies et al., 2004). Consequently these streams will not be resilient to the additional thermal shifts expected with climate change.

Southwestern Australia has already undergone significant climate change with drying and warming (CSIRO, 2007; Davies, 2010). A further 0.2°C increase per decade is predicted for the next 30 years, resulting in a 2°C increase by 2,050 (Hennessy et al., 2007; Davies, 2010). Unlike other Australian regions, southwestern Australia is surrounded by either ocean or deserts, with low relief, and many of the stenothermic representatives are considered to be approaching the upper limit of their thermal range (Davies, 2010). In effect, the aquatic biota of southwestern Australia is thermally isolated (*sensu* Ward & Stanford, 1982) and with limited available cool refugia to colonise, even if mobility or migration pathways would allow (*sensu* Davies, 2010), their sustainability is at significant risk from climate-forced increases in water temperature.

Many taxonomic insect groups are believed to have a ‘cool water ancestry’ (Ward & Stanford, 1982) and the maintenance of cool water refugia is therefore critical for these aquatic invertebrates (Davies, 2010). This is true for many stream species in Australia (Bunn & Davies, 1990; McKie et al., 2004), particularly those species with ancestral lineages that originated when Australia, as part of ‘Gondwanaland’, was situated over Antarctic latitudes with a cooler, wetter climate than today (McKie et al., 2005). These gondwanic relicts are considered cold stenotherms, intolerant of elevated water temperatures. For mobile species capable of accessing temperature refugia, the response to thermal shifts, particularly increases in temperature, will result in redistribution (usually contraction) of the species range. Some species may also become thermally isolated, due to either reduced dispersal capabilities or the absence of suitable temperature refugia (*sensu* Ward & Stanford, 1982). For these species, *in situ* restoration of rivers and streams is a practical response to riparian degradation and climate change in the short to medium term. Consequently there is a growing interest both in

Australia (e.g. Price et al., 2008) and elsewhere (see Bernhardt et al., 2005) in the restoration of riparian ecosystems.

The control of water temperature, through riparian shading, is an area of restoration where target values can be set and consequently the amount of vegetation required to meet these targets can be specified (Davies et al., 2004). Modelling studies have demonstrated that planting trees on stream banks can reduce daily maximum water temperatures (Theurer et al., 1985; McBride et al., 1993) with some of this research (e.g. Rutherford et al., 1997, 2004) predicting the extent of cover and length of rehabilitation required to restore or maintain stream temperatures within the thermal tolerance of keystone species. These studies consequently rely on thermal tolerance data for stream invertebrates to set these limits. Although thermal tolerances have been determined for aquatic invertebrates occurring in streams in USA (e.g. De Kowzowski & Bunting, 1981; Claussen & Walters, 1982), South Africa (Buchanan et al., 1988) and New Zealand (Quinn et al., 1994), the thermal tolerances of Australian stream invertebrates remain largely unknown (e.g. McKie et al., 2004).

The ability to predict characteristics of future ecosystems is crucial for environmental planning and the development of effective climate change adaptation strategies (Groves et al., 2012). With further thermal shifts in aquatic habitats, we expect novel or hybrid ecosystems (*sensu* Hobbs et al., 2009; Walther et al., 2009; Catford et al., 2012) characterised by altered species assemblages to develop due to taxonomic differences in thermal optima, tolerance and sensitivity (see Ward & Stanford, 1982 and references therein; Jacobsen et al., 1997; Calosi et al., 2010). While the capacity to maintain or reinstate cooler temperatures through riparian restoration has been demonstrated (Rutherford et al., 1997, 2004), the ability to predict ecological response, particularly change in assemblage structure, to those actions is limited by knowledge on the thermal tolerance of key taxonomic groups.

The primary aim of this paper is twofold. Firstly, we review available data on the upper thermal tolerance (UTT) limits of aquatic invertebrates, relating these tolerances to taxonomic groups, acclimation temperatures and temperature regimes at which species occur naturally. Secondly, we present the results of an investigation using standard 96 h LT₅₀ tests of the

thermal tolerances of four key southwestern Australia taxa. This represents the first investigation of thermal tolerances of species from this region. Together, the data from the review and these experiments, will allow the formulation of temperature targets for riparian restoration both in Australia and worldwide.

Materials and methods

Laboratory experiments

In order to facilitate the selection of a range of organisms with a wide variation in UTTs for the LT₅₀ experiments, macroinvertebrate community structure was initially compared among eight sites along Marbellup Brook in the Torbay catchment, Western Australia; four ‘shaded’ sites with intact riparian vegetation, and four ‘unshaded’ sites devoid of riparian trees. At each site, macroinvertebrates were collected by sweeping a 250- μ m mesh net over 10 m² of stream bed, disturbing the top few centimetres of substrate. Leaves, twigs and other debris were rinsed and discarded, and animals were returned to the laboratory where they were identified to family level. Community structure among the sites was compared using the software package PRIMER v5 (Clarke, 1993). After calculating similarities between every pair of the eight samples using the Bray–Curtis coefficient, samples were clustered using the UPGMA algorithm. Significant differences among assemblages were tested using ANOSIM. Species which primarily accounted for the observed assemblage differences were identified by the SIMPER routine, such that the overall percentage contribution each species made to the average dissimilarity between the two groups was calculated, and species were listed in decreasing order of their importance in discriminating the two sets of samples. Based on the results of these analyses and specimen availability, four species were selected for the LT₅₀ experiments: the caddisfly *Cheumatopsyche modica* (family Hydropsychidae) and the mayflies *Offadens soror* (Baetidae) and *Nyungara bunni* (Leptophlebiidae), all ‘typical’ of shaded sites (but poorly represented or absent at unshaded sites), and the dragonfly *Austroaeschna anacantha* (Telephlebiidae), found consistently at both shaded and unshaded sites. Three of these species (*N. bunni*, *A. anacantha* and *C. modica*)

are endemic to southwestern Australia and are considered to be gondwanic relicts.

Individuals of the selected taxa were collected from Marbellup Brook using the same methodology described above and then transferred to aerated buckets using wide-mouthed pipettes. On return to the laboratory, animals were transferred to 200 ml plastic containers (five individuals in each) containing pre-conditioned, filtered river water, and for each species, five replicate, aerated containers were placed in constant temperature water baths. The baths were initially set to 15°C, and the animals were acclimated for 4 days at this temperature. In previous investigations aquatic invertebrates have been acclimated for between 3 (Gaufin & Hern, 1971; De Kowzowski & Bunting, 1981; Moulton et al., 1993) and 12 days (Claussen & Walters, 1982). As is commonplace in investigations of this type, animals were not fed during experiments (e.g. Claussen & Walters, 1982; Buchanan et al., 1988). All experiments were conducted in a laboratory with a natural diurnal light regime (due to the presence of large, external windows) and baths subjected to treatments were randomly positioned. Thermal tolerance at one control (15°C) and five different test temperatures (25, 29, 33, 37 and 41°C) were assessed for the dragonfly and caddisfly species, and four test temperatures (21, 25, 29 and 33°C) for the two mayfly species. Acclimation temperatures were chosen to reflect likely environmental temperatures to which wild populations are exposed in both shaded and unshaded streams. To avoid thermal shock, temperatures in the individual water baths were manually raised by 2–3°C/h until the desired experimental temperatures were maintained to within 0.5°C. Submersible pumps in each bath ensured that the temperature was evenly distributed, and temperatures in each container were constantly monitored to ensure that they remained at the target level. Survival was recorded at three endpoints (24, 48 and 96 h) after the target temperature was reached. The temperature at which 50% of the organisms died (LT₅₀ values) and 95% fiducial limits were calculated for each time period by probit analysis following the EPA flowchart procedure outlined in ToxCalc, a toxicity data analysis and database software package (Tidepool Scientific Software and Micheal A. Ives, 1994–1996). A trimmed Spearman–Karber analysis was used to estimate LT₅₀ values where data did not fit the probit model.

Review of upper thermal tolerance levels

A comprehensive search revealed a limited literature on UTT of aquatic invertebrates, with 19 papers on thermal tolerance of aquatic invertebrates published in the period 1968 to 2008. For each study, we noted the procedures and methods used (LT method or CTM_{ax}), species tested and geographical location of specimen collection. We also recorded acclimation temperatures as a species' thermal history immediately prior to testing is known to influence thermal tolerances (Lutterschmidt & Hutchison, 1997). A total of 11 of the 19 studies assessed (58%) used the LT method; six studies used CTM_{ax} (32%) and two studies used both methods.

Traditionally, UTT has been determined in the laboratory using either time to death at constant test temperatures (the lethal temperature, or LT method), or the critical thermal maximum (CTM_{ax}) method which involves increasing test temperatures until an end point is reached. Of these two approaches, the use of the LT methodology has been favoured for invertebrates, although there has been a general trend across all major faunal groups to move from using LT methods to CTM_{ax} methods (Lutterschmidt & Hutchison, 1997). Only 22% of invertebrate studies reviewed by Lutterschmidt & Hutchison (1997) used CTM_{ax} methods, and these authors suggested that this might be due to the fact that the onset of muscular spasms (common endpoint in CTM_{ax} studies) is difficult to observe in many invertebrates. Working on fish, Kilgour & McCauley (1986) constructed a heuristic model which showed that these two experimental procedures are closely related, and that data from either can provide a reasonable prediction of results from the other approach. Similarly, in an investigation of upper thermal temperatures for dragonfly nymphs, Garten & Gentry (1976) found that LT estimates were significantly correlated with CTM_{ax} values for the species examined.

Significant differences in UTT among broad taxonomic groups (usually order or class level), and between acclimation temperature categories (acclimated at temperatures below 15°C or at temperatures of 15°C or above) and stenotherm and eurytherm species within the major taxonomic groups were detected using analysis of variance (ANOVA) and Tukey's post hoc multiple comparison tests (Tukey, 1977). Species were classified as stenotherms if they were either known to occur

naturally in cold streams, or were known to emerge in early spring prior to elevated summer water temperatures. Those species classified eurytherms in our study were either known to inhabit warmer, slow moving streams, or had longer life cycles emerging after exposure to elevated summer water temperatures.

Results

Laboratory experiments

Control mortality in laboratory procedures was low and varied from 0 to 4% in all experiments. Dragonflies were the least sensitive to high temperatures with a LT_{50} value of 33.5°C after 96 h exposure (Table 1). Few deaths were recorded at either 25 or 29°C after 96 h (Fig. 1). Mortality increased at 33°C, and at 37°C, 48% of animals had died after 24 h, and by 48 h, all remaining animals had died. At 41°C, all animals died within 24 h. Caddisflies were more sensitive to high water temperatures than dragonflies. Although few animals died at 25 and 29°C, significant mortality (96%) occurred at 33°C after only 24 h. An LT_{50} value of 30.7°C after 96 h exposure was calculated for this species. The two species of mayflies tested were the most sensitive to high water temperatures, with LT_{50} values of 20.5°C estimated for the baetid *O. soror*, and 21.9°C for the leptophlebiid *N. bunni* after 96 h exposure.

Review of upper thermal tolerance levels

Review of published literature (including laboratory results from this study) revealed UTT data for 81 species in 40 invertebrate families (or subfamilies) (Table 2). Mean UTT among the major macroinvertebrate taxonomic groups, tested in laboratory studies worldwide (including results from this study) ranged from 22.3°C for Ephemeroptera (mayflies) to 43.4°C for Coleoptera (beetles) (Fig. 2; Table 3). Mean thermal tolerance levels for Coleoptera (43.4°C) and Odonata (41.9°C) were similar (ANOVA, $P > 0.05$), but significantly higher than mean values for all the other groups assessed (range from 22.3 to 31.5°C) with the exception of Planaria (ANOVA, $P < 0.05$). The mean value of 22.3°C for Ephemeroptera was significantly lower than for Decapoda (29.6°C), Trichoptera (30.1°C) and Mollusca (31.5°C) (ANOVA, $P < 0.05$).

Table 1 LT₅₀ values with associated 95% fiducial limits (where given by probit analysis) and 95% confidence limits (where given by Spearman–Karber analysis) for four southwestern Australian species of aquatic invertebrates at 24, 48 and 96 h

Taxa	24 h		48 h		96 h	
	LT ₅₀	95% limits	LT ₅₀	95% limits	LT ₅₀	95% limits
<i>Offadens soror</i>	26.6	25.5–27.6	23.7	22.7–24.7	20.5	–
<i>Nyungara bunni</i>	–	–	–	–	21.9	–
<i>Austroaeschna anacantha</i>	36.8 ^a	35.9–37.7	34.3 ^b	33.6–34.9	33.9 ^b	33.1–34.6
<i>Cheumatopsyche modica</i>	30.7	29.7–31.6	30.6	29.6–31.5	30.7	29.5–31.6

^a Estimated using probit analysis

^b Estimated using Spearman–Karber analysis

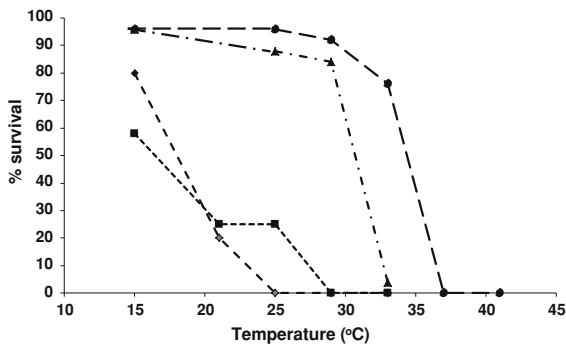


Fig. 1 Plot of temperature versus % survival after 96 h exposure for four species of aquatic invertebrates from southwestern Australia. Symbols are as follows: diamond, *Offadens soror*; square, *Nyungara bunni*; triangle, *Cheumatopsyche modica*; circle, *Austroaeschna anacantha*

Mean UTT values did not vary significantly between acclimation categories (those acclimated at temperatures below 15°C versus those acclimated at 15°C and above) for each of the orders Ephemeroptera, Plecoptera and Trichoptera (ANOVA, P ranging from 0.1 to 0.86). However, when mean UTT for stenotherms versus eurytherms were compared in these three insect orders, these were found to be significantly different at the 5% level in the Ephemeroptera and Trichoptera (Student's t test; $P < 0.05$), and marginally significantly different in the Plecoptera ($P = 0.07$) (Table 4).

Discussion

Early studies of the UTTs of aquatic invertebrates mainly centred in the USA due to a concern that heated water from steam-electric power generating facilities would have a detrimental effect on the biota (e.g.

Gaufin & Hern, 1971). Since then, the literature on thermal tolerance has grown to include a variety of invertebrate taxa from a range of regions, presenting the opportunity for review of broad patterns in UTT of aquatic invertebrates. The results of our laboratory experiments and review of the literature confirm considerable taxonomic differences in ability to tolerate high water temperatures. Mayflies (Ephemeroptera) and Stoneflies (Plecoptera) were shown to be particularly sensitive (e.g. Ward & Stanford, 1982; Quinn et al., 1994), supporting the use of this group as a part of the commonly used EPT (Ephemeroptera, Plecoptera and Trichoptera) index for testing of ecological water quality. These taxa contrast with the higher tolerance levels of beetles (Coleoptera), dragonflies (Odonata), and to a lesser extent, planarians. While thermal tolerance studies on dragonflies are limited, it does appear that these animals are able to tolerate higher temperatures than many other components of the freshwater fauna (e.g. Martin & Gentry, 1974). In the case of the planarians, Claussen & Walters (1982) suggested that the high thermal tolerances of these animals corresponded with their widespread and eurythermic distributions.

The Ephemeroptera is likely to be adversely affected by significant increases in stream temperatures, which might arise as a consequence of climate change (see Davies, 2010) and/or land use practices (see Horwitz et al., 2008). Although the order Ephemeroptera is relatively species poor in southwestern Australia (only 12 species) when compared to other parts of Australia (over 140 species), the fauna in the region is unique, with 58% of these species being endemic to southwestern Australia, and 83% being endemic to Western Australia (Davies & Stewart, submitted).

Table 2 Mean upper thermal tolerances (UTT) for families of aquatic macroinvertebrates as determined in a review of laboratory experiments using either lethal temperature (LT) or critical thermal maximum (CTM) approaches

Group	Family/ subfamily	UTT (°C)	SE	Localities	Source
Planaria	Dugesiidae	32.2	0.3	USA	Claussen & Walters (1982)
Oligochaeta	Lumbriculidae	26.7	–	New Zealand	Quinn et al. (1994)
Mollusca	Hydrobiidae	31.8	0.4	New Zealand	Winterbourn (1969), Cox & Rutherford (2000)
	Sphaeriidae	30.5	–	New Zealand	Quinn et al. (1994)
Amphipoda	Eusiridae	24.1	–	New Zealand	Quinn et al. (1994)
	Gammaridae	14.6	–	USA	Gaufin & Hern (1971)
	Paramelitidae	34.1	–	South Africa	Buchanan et al. (1988)
Decapoda	Astacidae	30.6	0.9	New Zealand, Japan	Simons (1984), Nakata et al. (2002)
	Atyidae	25.8	0.1	New Zealand	Davenport & Simons (1985), Quinn et al. (1994)
	Cambaridae	32.3	2.7	USA, Japan	Claussen (1980), Nakata et al. (2002)
Ephemeroptera	Baetidae	20.1	–	Australia	Present study
	Ephemerellidae	20.4	1.7	USA	Nebeker & Lemke (1968), Gaufin & Hern (1971), De Kowzłowski & Bunting (1981)
	Ephemeridae	26.6	–	USA	Gaufin & Hern (1971)
	Heptageniidae	23.0	5.9	USA	Nebeker & Lemke (1968), Gaufin & Hern (1971)
	Leptophlebiidae	23.1	0.5	Australia, New Zealand	Quinn et al. (1994), Cox & Rutherford (2000), Present study
Odonata	Aeshnidae	33.2	0.7	Australia, USA	Nebeker & Lemke (1968), Present study
	Corduliidae	41.1	1.1	USA	Garten & Gentry (1976)
	Gomphidae	33.0	–	USA	Nebeker & Lemke (1968)
	Libellulidae	43.7	0.5	USA	Martin & Gentry (1974), Garten & Gentry (1976)
	Macromiidae	41.0	2.2	USA	Garten & Gentry (1976)
Plecoptera	Capmidae	23.0	–	USA	Nebeker & Lemke (1968)
	Gripopterygidae	25.5	–	New Zealand	Quinn et al. (1994)
	Nemouridae	31.5	–	USA	Ernst et al. (1984)
	Perlidae	31.7	0.9	USA	Nebeker & Lemke (1968), Heiman & Knight (1972), Ernst et al. (1984)
	Perlodidae	24.1	4.9	USA	Nebeker & Lemke (1968), Gaufin & Hern (1971), Ernst et al. (1984)
	Pteronarcyidae	27.0	1.5	USA	Nebeker & Lemke (1968), Gaufin & Hern (1971)
	Taeniopterygidae	21.0	–	USA	Nebeker & Lemke (1968)
Trichoptera	Brachycentridae	30.5	1.2	USA	Nebeker & Lemke (1968), Gaufin & Hern (1971), De Kowzłowski & Bunting (1981)
	Conoesucidae	28.7	3.7	New Zealand	Quinn et al. (1994)
	Hydropsychidae	30.4	1.7	Australia, New Zealand, USA	Gaufin & Hern (1971), De Kowzłowski & Bunting (1981), Moulton et al. (1993), Quinn et al. (1994), Present study
	Limnephilidae	26.1	1.3	USA	Gaufin & Hern (1971)
	Philopotamidae	33.8	1.5	USA	Moulton et al. (1993)
	Uenoidae	25.9	–	USA	Gaufin & Hern (1971)
Diptera	Athericidae	32.2	0.2	USA	Nebeker & Lemke (1968), Gaufin & Hern (1971)
	Chironominae	24.1	–	Australia	McKie et al. (2004)
	Orthoclaadiinae	27.2	2.4	Australia	McKie et al. (2004)
	Simuliidae	25.1	–	USA	Gaufin & Hern (1971)
	Tanypodinae	25.3	3.5	Australia	McKie et al. (2004)

Table 2 continued

Group	Family/ subfamily	UTT (°C)	SE	Localities	Source
Coleoptera	Dytiscidae	44.8	0.4	UK	Calosi et al. (2008)
	Elmidae	32.6	–	New Zealand	Quinn et al. (1994)

Literature sources from which the data were extracted are indicated. Families in bold include LT₅₀ data from this study
SE standard error

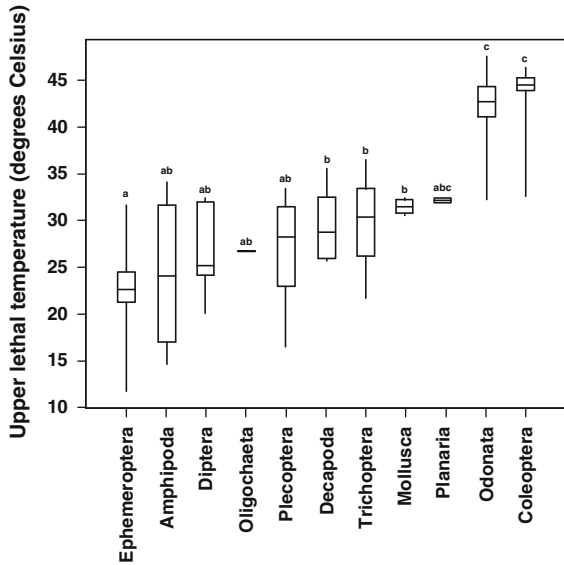


Fig. 2 Box-whisker plots of upper lethal temperatures (UTT) for major taxonomic groups of aquatic invertebrates. Lower case letters indicate results of statistical tests with different letters indicating significant differences at the 5% level

Our study clearly showed that mean UTTs can differ within taxonomic groups. For example, mean UTTs of eurythermic species were significantly higher than that of stenothermic species within the Ephemeroptera, Plecoptera and Trichoptera. The stenotherm species included in our analysis were either restricted to cold headwater streams, or were known to emerge in early spring prior to the occurrence of elevated water temperatures that occur during summer. Eurytherm species were usually more widespread in distribution and had longer life cycles and thus were present in streams at elevated water temperatures. These observations are consistent with those of Calosi et al. (2008, 2010), who found that widespread European diving beetle taxa have significantly higher UTTs than restricted taxa.

The present study has provided the first estimates of UTT of southwestern Australian species. The data

Table 3 Mean upper thermal tolerance levels (UTT) as determined in a review of laboratory experiments using either lethal temperature (LT) or critical thermal maximum (CTM) approaches for selected macroinvertebrate groups

Taxonomic group	Mean UTT (°C)	N	SE	Minimum–maximum (°C)
Planaria	32.2 ^{abc}	2	0.3	31.9–32.4
Oligochaeta	26.7 ^{ab}	1	–	–
Mollusca	31.5 ^b	4	0.4	30.5–32.4
Amphipoda	24.3 ^{ab}	3	5.6	14.6–34.1
Decapoda	29.6 ^b	9	1.3	25.7–35.6
Ephemeroptera	22.3 ^a	13	1.4	11.7–31.8
Odonata	41.9 ^c	27	0.7	32.5–47.6
Plecoptera	27.2 ^{ab}	14	1.4	16.5–33.4
Trichoptera	30.1 ^b	19	0.9	21.7–36.5
Diptera	27.2 ^{ab}	10	1.4	20.1–32.4
Coleoptera	43.4 ^c	9	1.4	32.6–46.4

Lower case letters indicate results of statistical tests with different letters indicating significant differences at the 5% level
N sample size, SE standard error

Table 4 Mean upper thermal tolerance levels (UTT) as determined in a global review of laboratory experiments using either lethal temperature (LT) or critical thermal maximum (CTM) approaches for species of Ephemeroptera, Plecoptera and Trichoptera

Order	Group	Mean UTT (°C)	SE	n	P value
Ephemeroptera	Stenotherms	21.04	1.21	11	0.02
	Eurytherms	29.2	2.60	2	
Plecoptera	Stenotherms	24.74	2.22	7	0.07
	Eurytherms	29.69	1.20	7	
Trichoptera	Stenotherms	28.35	1.13	12	0.01
	Eurytherms	33.06	0.95	7	

Stenotherms species occurring in naturally cold streams, *Eurytherms* species occurring in warmer streams with variable temperature regimes, n sample size, SE standard error, P value probability that means are significantly different

generated for four species (representing the insect orders Odonata, Trichoptera and Ephemeroptera) were in agreement with those obtained for other mayfly, dragonfly and caddisfly species from New Zealand (Quinn et al., 1994; Cox & Rutherford, 2000) and USA (Nebeker & Lemke, 1968; Gaufin & Hern, 1971; Martin & Gentry, 1974; Garten & Gentry, 1976; De Kowzlowski & Bunting, 1981). Published estimates of UTT of Australian species of aquatic invertebrates are very limited, with only the Chironomidae receiving attention (McKie et al., 2004) to date. Our data thus makes a significant contribution to our knowledge of UTTs of Australian species. Since results for Australian species are similar to those obtained for related taxa worldwide, data can be combined to form a substantial body of information that can be used both in Australia and elsewhere to set restoration targets for controlling temperature in aquatic ecosystems.

The thermal tolerance of the fauna of southwestern Australia determined here suggests 21°C as the UTT for range of sensitive freshwater insect taxa. This critical threshold temperature was also suggested for a range of temperate species from studies elsewhere (e.g. De Kowzlowski & Bunting, 1981; Quinn et al., 1994; Cox & Rutherford, 2000). In southwestern Australia, this threshold temperature is often exceeded in upland streams flowing through cleared catchments (Rutherford et al., 2004) where the lack of riparian vegetation increases the irradiance into streams (Davies et al., 2004, Davies, 2010) and particularly in reaches running east–west (Davies et al., 2008) where light inputs are maximised (see Osborne & Kovacic, 1993).

Additional thermal shifts, due to continued removal of riparian zones or climate change, are expected to result in novel or hybrid ecosystems (*sensu* Hobbs et al., 2009; Walther et al., 2009; Catford et al., 2012) characterised by altered freshwater species assemblages. We predict that the structure of these assemblages will be largely determined by taxonomic differences in thermal tolerance. Elsewhere, elevated temperatures due to climate change has led to movement of species to cooler regions either at higher latitudes or altitudes (Jacobsen et al., 1997; Davies, 2010). In southwestern Australia, low relief, and surrounding ocean and desert limit the availability of cool water refugia. Consequently, assemblage changes may be characterised by a progressive loss of temperature-sensitive species and the filling of elevated temperature niches by more tolerant taxa. This has

implications for the sustainability of regionally important endemic cool water species (Horwitz et al., 2008). Based on the analysis of UTTs presented here, we expect that mayflies may become more restricted in distribution, whereas those species more tolerant of elevated temperatures (e.g. Coleoptera and Odonata) may become more abundant, or increase in geographical range (where migration and recolonisation pathways allow). Although not addressed in this study, sublethal effects of elevated water temperatures may also be important and lead to changes in community structure. These sublethal effects could include changed behavioural responses. For example, for caddisflies with upper thermal limits around 31°C, Gallepp (1977) found a decrease in filtering rate at temperatures above 24°C and suggested that these larvae were unlikely to thrive and reproduce at higher water temperatures, well below UTT levels.

By identifying UTTs of the aquatic fauna, modelling approaches that predict the extent of cover and length of rehabilitation required to restore or maintain stream temperatures within the thermal tolerance of keystone species (e.g. Rutherford et al., 1997, 2004) can be directly applied, at a regional scale, to prioritise areas for restoration. The values for UTTs determined in this study provide a starting point for such an approach.

Acknowledgments We thank the Department of Agriculture and Food, Western Australia for laboratory facilities and The University of Western Australia, Centre of Excellence in Natural Resource Management for administrative support. This work (Project Number FW-11-01) was financially supported by the National Climate Change Adaption Research Facility (NCCARF) under the Climate Change Adaption Research Grants Program (ARGP) 2011. We thank two anonymous reviewers for their helpful comments.

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