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A global review of freshwater crayfish temperature tolerance, preference, and optimal growth

J. T. Westhoff · A. E. Rosenberger

Abstract Conservation efforts, environmental planning, and management must account for ongoing ecosystem alteration due to a changing climate, introduced species, and shifting land use. This type of management can be facilitated by an understanding of the thermal ecology of aquatic organisms. However, information on thermal ecology for entire taxonomic groups is rarely compiled or summarized, and reviews of the science can facilitate its advancement. Crayfish are one of the most globally threatened taxa, and ongoing declines and extirpation could have serious consequences on aquatic ecosystem function due to their significant biomass and ecosystem roles. Our goal was to review the literature on thermal ecology for freshwater crayfish worldwide, with emphasis on studies that estimated temperature tolerance, temperature preference, or optimal growth. We also explored relationships between temperature metrics and species distributions. We located 56 studies containing information for at least one of those three metrics, which covered approximately 6 % of extant crayfish species worldwide. Information on one or more metrics existed for all 3 genera of Astacidae, 4 of the 12 genera of Cambaridae, and 3 of the 15 genera of Parastacidae. Investigations employed numerous methodological approaches for estimating these parameters, which restricts comparisons among and within species. The only statistically significant relationship we observed between a temperature metric and species range was a negative linear relationship between absolute latitude and optimal growth temperature. We recommend expansion of studies examining the thermal ecology of freshwater crayfish and identify and discuss methodological approaches that can improve standardization and comparability among studies.

Keywords Thermal ecology · Temperature preference · Temperature tolerance · Optimal growth · Acclimation · Crayfish

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Introduction

Temperature is the master abiotic factor (Brett 1971) that influences numerous aspects of the biology, physiology, distribution, and behavior of aquatic

ectothermic animals (Narum et al. 2013). Temperature can be a lethal, controlling, limiting, masking, or directive factor related to metabolic processes (Fry 1947), which complicates its physiological role when considered in conjunction with other biotic or abiotic factors. Evolutionary thermal biology, including thermal adaptation, is intricately tied to numerous aspects of how species persist and how they may respond to future climate change (Angilletta 2009). Many aquatic ectotherms, including freshwater crayfish, behaviorally thermoregulate by actively seeking water temperatures suitable for maintaining or maximizing life functions (Diaz et al. 2004). However, ideal temperatures are not always available to the organisms, and altered temperature regimes can result in reduction of species' ranges and an overall loss of biodiversity (Heino et al. 2009).

Given its key importance for biological processes, thermal ecology of organisms and factors that affect the thermal environment of aquatic ecosystems is frequently the focus of applied science and management. Habitat alteration in the form of runoff from urbanized areas or impervious surfaces (Paul and Meyer 2001) and water releases from impoundments (Lessard and Hayes 2003) can alter the thermal characteristics of streams. Provisions of the United States Clean Water Act consider thermal effluent a pollutant requiring regulation from power production facilities and other sources (Gift 1977). Thus, many researchers determined temperature tolerance estimates for indicator species as a way to inform legal proceedings related to thermal pollution (Gift 1977).

Information on thermal ecology is used to parameterize trait-based modelling efforts for broad ecological issues linked to anthropogenic change (Chown 2012). For example, climate change may affect thermal regimes in aquatic systems, and, in turn, affect aquatic organisms at many levels of organization (Pörtner and Farrell 2008; Woodward et al. 2010). Knowledge of thermal requirements of aquatic organisms can be used to predict species range shifts (Heino et al. 2009; Westhoff and Paukert 2014), growth (Elliott and Elliott 2010), or phenology (Parmesan 2006) under future climate scenarios. Further, temperature tolerance values for introduced or potentially invasive species allow prediction of successful establishment (Kolar and Lodge 2002) or the extent of distributional expansion (Kimball et al. 2004). These modeling efforts can be limited by data availability and face other challenges, including the output of

spurious results if accurate and methodically standardized information on the thermal ecology of the animals of interest is unavailable. Finally, an understanding of thermal ecology benefits propagation and production efforts for economically important cultured species.

Thermal ecology can be conceptualized in different ways depending on the context of the research objectives and may be reported as fixed and species-specific; however, it is crucial to evaluate the experimental conditions of the studies that generate these metrics. For instance, the inherent plasticity of organisms in response to temperature (i.e., acclimation) can affect tolerance and preference metrics (Mirenda and Dimock 1985). Without acclimation, alterations of temperature can result in physiological responses that confound experimental outcomes (Claussen 1980; Lutterschmidt and Hutchison 1997). Further, the accuracy of temperature tolerance and preference metrics are vulnerable to other experimental conditions, such as organism condition. The postprandial metabolic increment related to food digestion influences oxygen demand and thus how an organism responds to temperature (Clark et al. 2013). As such, it is important to standardize the amount of time since test organisms were last fed (satiation state) prior to thermal experimentation.

Freshwater crayfish (Malacostraca: Decapoda: Astacidae, Cambaridae, Parastacidae) are one of the most globally threatened taxa (Taylor et al. 2007; Richman et al. 2015). Crayfish losses could have serious consequences on ecosystems; they are among the most ecologically dominant organisms in most streams due to their significant biomass (Huryn and Wallace 1987; Rabeni et al. 1995; Usio and Townsend 2001) and role as prey for >200 other aquatic, terrestrial and avian animals (Probst et al. 1984; DiStefano 2005). Despite this importance, poor understanding of their thermal ecology hinders our ability to manage and conserve them through identification of threats and opportunities for conservation, restoration, or mitigation (Richman et al. 2015). Most early efforts to investigate crayfish thermal ecology focused on cultured species and methods for maximizing growth and production (Frost 1975; Espina et al. 1993). An expanded and comprehensive understanding of crayfish thermal ecology could also assist in conservation efforts and apply to threatened species that could benefit from captive breeding and reintroduction programs (Souty-Grosset and Reynolds 2010; Carey et al. 2013). Compilation of existing knowledge of crayfish thermal ecology

facilitates understanding, application, and advancement of crayfish conservation and ecosystem management.

In this review, we summarize our current understanding of selected aspects of the thermal ecology of freshwater crayfish, in particular, thermal tolerances, preferences, and ranges for optimal growth. To date, we are unaware of any source in the peer-reviewed literature that thoroughly reviews existing knowledge of freshwater crayfish thermal ecology. Nyström (2002) presented a table of thermal ecology data for 14 species of freshwater crayfish, but that list was not intended to be comprehensive. Our goal was to provide a comprehensive review of several aspects of crayfish thermal ecology from which future researchers could better frame hypotheses and design robust and standardized experiments. Our specific objectives were to (1) summarize the existing methodology for elucidating crayfish temperature tolerance, preference, and optimal growth, (2) compile reported values of crayfish temperature tolerance, temperature preference, and optimal growth, (3) investigate temporal and taxonomic trends in the availability of information, (4) define ecological relationships between crayfish distribution and temperature metrics, and (5) propose improvements for methodological standardization. We predicted that published thermal ecology information exists for less than 25 % of all crayfish species, and the rate of publication on the topic has increased over time. We also anticipated that the methodology used to investigate crayfish thermal ecology would vary among studies—a lack of standardization that complicates among-species comparisons. We therefore summarize these methodologies to allow for educated comparisons among different studies and provide suggestions for methodological standardization. Finally, we anticipated that several species would have estimates for multiple metrics, allowing us to look for differences and relationships among metrics. We hypothesized no difference in intraspecific estimates of optimal growth temperature and temperature preference, and upper tolerance temperature would be significantly greater than optimal growth temperature.

Methods

Thermal ecology is an extensive topic, thus we focused our literature search on published studies of temperature tolerance, preference, and range for optimal growth

for all known freshwater crayfish species. These three aspects of thermal ecology are frequently investigated for aquatic organisms and represent metrics that are commonly used to inform modeling efforts and management (Gift 1977; Reynolds and Casterlin 1979; Chown 2012). We did not systematically review the literature on temperature as a driver of life-history events, behavior, or as an environmental correlate in distributional or habitat relationships; nor did we review aspects of thermal ecology related specifically to physiological or metabolic processes. Understanding these additional topics is essential to gain a comprehensive view of crayfish thermal ecology, but was beyond the scope of this review. However, these topics were briefly addressed in the discussion to frame a more complete context for our results.

We obtained literature primarily through targeted Google Scholar® searches of specific terms. First, we searched only within the titles of articles using the criteria "crayfish AND temperature OR thermal" followed by a broader search of titles and text using the criteria "crayfish OR temperature OR thermal". We also targeted specific journals to ensure widespread coverage of our search. We searched the *Journal of Thermal Biology* for the term "crayfish" and manually read through each title from *Freshwater Crayfish* to extract pertinent studies. Finally, we examined the "literature of interest to astacologists" from the archives of all issues of the International Association of Astacology newsletter *Crayfish News* and consulted crayfish-related books and resources. All searches were conducted in August 2014 and were inclusive of all materials published prior to that date.

We examined search results by reading paper titles first, and any paper with a promising title was further examined by reading its abstract. Papers that appeared of interest based on abstract content were then examined to extract pertinent information. We categorized each study based on species examined, type of thermal information contained (lower tolerance, upper tolerance, preference, optimal growth), and methodology used. This resulted in a final master-table containing information from every relevant study. We then summarized the information to determine the total number of papers published, percentages of taxa covered based on family, genus, and species, temporal trends in publication, and variation in methodology.

We also used estimates compiled in the master-table to determine what typical values of each metric were, how metrics were related to one another, and

relationships between each metric and crayfish distributional attributes. The range in values for each estimate was shown as the lowest observed temperature and the highest observed temperature across all species. Mean and standard deviation values for each estimate were calculated by first averaging all estimates within a species across acclimation temperatures, and then across all studies to obtain a single value for each metric and species combination. We calculated the difference between estimates of different metrics to further investigate how metrics were related for those species with multiple metrics. We reported those values for each possible pair of metrics using range, mean, and standard deviation. For two combinations (optimal growth temperature and preferred temperature, and optimal growth temperature and upper tolerance), we used paired, two sample *t* tests to determine statistical differences in estimates.

Finally, we hypothesized that aspects of crayfish distribution could be related to temperature metric values. We tested this using linear regression to examine relationships between absolute latitude (latitude of distributional extent closest to equator) and each of five temperature metrics (upper tolerance, lower tolerance, tolerance breadth, optimal growth, and preferred temperature). Distribution data were obtained from Richman et al. (2015). We also used linear regression to examine the relationship between total range extent (northern extent of latitude–southern extent of latitude) and temperature tolerance breadth. We used the Shapiro–Wilks test to determine normality of data prior to regression analyses.

The estimated number of extant crayfish species ranges from 590 (Sibley et al. 2011) to 644 species (Gherardi 2010). Additionally, new species are continuously described and taxonomic revisions occur with the availability of better information (Crandall and Buhay 2008). For our purposes, we use 628 species (excludes 20 sub-species and two fossil species) to calculate percentages for our analysis (Fetzner Fetzner 2014; Holdich 2014).

Results

Methodological approaches

Metrics describing temperature tolerance, temperature preference, and optimal growth for crayfishes were primarily developed for other ectothermic organisms (mostly fishes) and adapted for use on freshwater crayfish. We briefly review these concepts and their methodological considerations below.

Temperature tolerance

Temperature tolerance is widely studied in aquatic organisms (Firkins and Holdich 1993; Beitinger et al. 2000; Pandolfo et al. 2010) and can be considered the temperature range within which survival is not limited directly by temperature (Reynolds and Casterlin 1979). Estimates of temperature tolerance can be obtained from field data by matching collection records with temperature data from collection locations (Eaton et al. 1995), but we did not locate any studies that used this method for crayfishes. Estimation of temperature tolerance in laboratory settings focuses on reducing the effects of behavioral adaptation and acclimation by testing the physiological limits of organisms (Reynolds and Casterlin 1979). We highlighted essential aspects for determining temperature tolerance of aquatic ectotherms, but interested readers may consult Reynolds and Casterlin (1979) and Beitinger et al. (2000) for more in-depth reviews of these concepts and methods.

Determination of temperature tolerance was often achieved using either "static" or "dynamic" methods (Lutterschmidt and Hutchison 1997). Static methods typically measured the time to death for organisms acclimated at set temperatures and then introduced (i.e., plunged) to different, yet constant, temperatures (Fry 1947). Static-type scenarios may exist in the environment for some species whereby temperature changes occur rapidly, and acclimation is dependent on prior experience (Norin et al. 2014). This method was exemplified by the LT_{50} metric (temperature estimated to cause 50 % mortality within a specific time frame) and estimated upper incipient lethal temperature (UILT), ultimate upper incipient lethal temperature (UUILT), and lower incipient lethal temperature (LILT) (Reynolds and Casterlin 1979; Claussen 1980; Lutterschmidt and Hutchison 1997). The UILT and LILT represent boundaries for the thermal tolerance breadth and are relative to acclimation temperature, whereas UUILT represents a plateau of UILT where temperatures are lethal to the organism regardless of acclimation (Reynolds and Casterlin 1979).

Dynamic approaches involve altering water temperature at a steady rate (e.g., 1 °C/min) until a defined endpoint such as onset of spasms (OS) or loss of righting response (LRR) is reached, whereby an organism would be unable to escape lethal conditions (Lutterschmidt and Hutchison 1997). Loss of righting response was a common stress event used to define temperature tolerance in crayfishes and occurred when a test organism was placed on its dorsal surface and was unable to right itself (flip to its ventral surface) within a given time. To achieve this response, many studies altered water temperature in a test chamber at a rate of approximately 1 °C/min until LRR was observed for a minimum of 30 s (Layne et al. 1985; Mirenda and Dimock 1985). Unlike the static approach, this dynamic approach was generally not lethal to the test organisms. The most common metric estimated using dynamic methods was critical thermal maxima (CTM) and can be defined for a minimum (CTMin) or maximum (CTMax) temperature (Beitinger et al. 2000). We encountered multiple definitions of CTM, but the most common referred to the thermal landmarks for which the animals' disorganized activity indicates that it would be unable to escape from conditions that would eventually lead to mortality when heated (or cooled) from its acclimation temperature at a rate that allows whole body temperatures to change concurrently with the environment (Cox 1974).

The above methods used to determine temperature tolerance exposed test organisms to artificial conditions, whereby the physiological limits translate in an ecological sense to conditions that result in death. Other approaches termed acclimated chronic exposure (ACE) and chronic lethal method (CLM) created a more natural thermal environment, whereby test organisms were exposed to slow changes in water temperature (e.g., 1 °C/day). The ACE method is a static method that used a system that acclimated test organisms by raising temperatures at a rate of ≈1 °C/day until a target temperature was reached, and then held at that temperature to observe mortality using LT_{50} methods (Selong et al. 2001; Recsetar et al. 2014). The CLM method is dynamic, whereby temperatures were raised at a defined rate (e.g., 1 °C/day) until the experimental endpoint was reached (generally mortality; Beitinger et al. 2000). These methods allowed for physiological acclimation to thermal conditions, which may generate higher tolerance values, but, conversely, may also allow for chronic accumulation of thermal stress that could lower tolerance values compared to other methods (Beitinger et al. 2000).

Temperature preference

Temperature preference was generally represented by the final preferendum (Fry 1947) and is the temperature to which an organism will gravitate if given adequate access. This temperature often coincides with the optimum temperature at which an organism can maximize its energy efficiency (Beitinger and Fitzpatrick 1979; McCauley and Casselman 1981; González et al. 2010).

Estimation of temperature preference for aquatic ectotherms was performed using multiple methods and experimental setups that include electronic shuttle boxes, rosette devices, and vertical or horizontal linear gradients (McCauley 1977). Although commonly used, estimates from linear gradient devices can be biased by the amount of time organisms are observed within the gradient (García-Guerrero et al. 2013). Acute (approximately 2 h of observation) and gravitational (≥24 h of observation) methods were common for determining temperature preference (Reynolds and Casterlin 1979), but it is less common that both methods were used in the same study (González et al. 2010). Often the reported metric was a measure of central tendency and variation for temperatures selected by the test organism. Performing both acute and gravitational methods allowed researchers to compare results and account for temporal responses to in situ acclimation. Electronic shuttlebox experiments can eliminate the potential that a crayfish is simply exploring its surroundings and forces active selection based on temperature by increasing or decreasing temperature, eliciting active avoidance of unfavorable temperatures (Tattersall et al. 2012).

Temperature preference can also be estimated using field techniques by observing marked animals in wild settings (Coutant 1977; Coutant et al. 1984). However, determination of temperature preference in field settings can be complicated by interacting effects from other factors not related to temperature (Coutant et al. 1984). We did not encounter any estimates of crayfish temperature preference based on field observations.

Optimal growth temperature

The optimal growth temperature represents the temperature at which an organism can achieve greatest potential somatic growth when excess food resources are available (Jobling 1981). This temperature, or range of temperatures, occurred within a broader range of temperatures where positive growth was possible. Growth can be limited on the low end by inactivity or inability to consume food (Söderbäck et al. 1988). On the high end, metabolic costs may exceed the organism's ability to add mass, regardless of food consumption or oxygen availability (Meade et al. 2002). Bioenergetic approaches that estimate scope for growth (consumption–respiration) can also estimate optimal growth temperature and require much shorter experimental duration than traditional approaches (Whitledge and Rabeni 2002). Optimal growth was typically estimated by holding individuals in enclosures representing a range of static temperatures for a set period of time and determining at what temperature growth was greatest (Carmona-Osalde et al. 2004; Policar et al. 2010). Experimental endpoints were related to growth in length or mass, growth rate, or number or frequency of molts.

Summary of thermal ecology studies on freshwater crayfish

We identified 56 pertinent studies, which reported a total of 116 estimates of crayfish temperature tolerance, preference, or optimal growth covering 37 (5.9 %) of the 628 known crayfish species (Table 1). At least one species from each of the families Astacidae, Parastacidae, and Cambaridae was represented in each of the four categories (lower tolerance, upper tolerance, preference, and optimal growth) of thermal ecology information (Table 2). At the genus level, all three genera of Astacidae, 4 of the 12 genera of Cambaridae, and 3 of the 15 genera of Parastacidae were represented (Table 1). Astacidae was the most completely studied family, with 33.3 % (4 of 12 species) of its members represented, followed by Cambaridae at 6.3 % (27 of 429 species), and Parastacidae at 3.2 % (6 of 187 species). Publication dates ranged from 1955 to 2014, with no more than 13 studies published over any 5-year span during that time and a peak in publications during the 1990s (Fig. 1).

All but one, *Procambarus acutus*, of the 12 most important culture species around the world (Huner

1988), have published estimates of optimal growth temperature (Table 3). Of these 12 species, temperature tolerance estimates exist for 9 and temperature preference values for 5 (Table 3). We located published information on temperature tolerance, temperature preference, and optimal growth temperature for *Procambarus clarkii*, *Orconectes rusticus*, *Astacus astacus*, and *Cherax quadricarinatus*. No other species in our analysis had information on all three of these metrics.

Temperature tolerance

We identified 26 studies that reported upper temperature tolerance values for a total of 21 species, which represents 3.3 % of all crayfish taxa (Table 2). Nine of these studies also reported lower temperature tolerance values covering 15 (2.4 %) total taxa. No studies estimated only lower tolerance values, but 17 investigated only upper tolerance values. Several species had multiple estimates of tolerance values from different sources and, in all, 40 estimates of upper tolerance and 21 estimates of lower tolerance exist. Of those 40 estimates, 18 were based on adult crayfish, nine on juveniles, one on both juveniles and adults, and 12 on studies that did not report information on crayfish size or state of sexual maturity. Twelve studies used more than one acclimation temperature, including two studies (Mundahl 1989; Mundahl and Benton 1990) that used crayfish acclimated to in situ seasonal conditions by testing crayfish caught during different times of year and tested immediately after removal from the field.

We categorized methods used to estimate temperature tolerance as static (plunge, ACE or LT50, other), dynamic (CTM or CLM), or unknown (Table 4). Static methods were the least common (11 studies covering eight species) and dynamic methods the most common (12 studies covering 17 species). Two studies estimated temperature tolerance using both static and dynamic methods (Mirenda and Dimock 1985; Claussen 1980). We were unable to locate details to determine the methods used in 5 studies. No single approach dominated the static methods. The plunge approach was used in 3 studies, the LT_{50} or a variant of the ACE method was used in 5 studies, and 3 studies used methods based on extrapolation of results from optimal growth studies. None of the studies that used LT_{50} or ACE methods referred to the methodology as

Table 1 Published thermal ecology information for all species of freshwater crayfish obtained in the literature search

Species	Lower tolerance (°C)	Upper tolerance (°C)	Optimal growth (°C)	Preference (°C)	Method	Life stage	Source
Astacidae							
Astacus astacus			15–25		OG.3	J	Cukerzis (1973)
Astacus astacus				11.9–18	P.1.2(A)	A	Kivivuori (1994)
Astacus astacus[a]		28			T.4	U	Rognerud et al. (1989)
Astacus astacus[a]			16–24		OG.1	B	Söderbäck et al. (1988)
Astacus leptodactulus			17–27		OG.3	J	Cukerzis (1973)
Astacus leptodactulus[a]	9	36	21.8		T.2.4(A); OG.1	A	Firkins and Holdich (1993)
Astacus leptodactulus[a]	4	32			T.4	U	Köksal (1988)
Astacus leptodactulus			23–25		OG.1	A	Hesni et al. (2009)
Austropotamobius pallipes		32–34.5			T.1.2(A)	U	Bowler et al. (1973)
Austropotamobius pallipes			20.3		OG.1	J	Policar et al. (2010)
Austropotamobius pallipes[a]	8	34	21.4		T.2.4(A); OG.1	B	Firkins and Holdich (1993)
Pacifastacus leniusculus		31.1			T.2.5	A	Nakata et al. (2002)
Pacifastacus leniusculus			20–26; 22		OG.2	A	Simčič et al. (2014)
Pacifastacus leniusculus[a]		32–33			T.1.1(A)	U	Becker et al. (1975)
Pacifastacus leniusculus[a]	7.5	38	22.8		T.2.4(A); OG.1	B	Firkins and Holdich (1993)
Cambaridae							
Cambaroides japonicus		27			T.2.5	A	Nakata et al. (2002)
Cambarus acuminatus	1.5; 1.3–10.7	33; 26.6–36			T.1.1(A); T.2.4(A)	A	Mirenda and Dimock (1985)
Cambarus bartoni				22.1	P.2.2	U	Casterlin and Reynolds (1977)
Cambarus bartoni		32.5			T.1.2(A)	J	Cox and Beauchamp (1982)
Cambarus bartoni		33.8			T.4	U	Mirenda (1975)
Cambarus cryptodytes	4.7 ± 0.9	33.2 ± 1.1			T.2.5	A	Caine (1978)
Cambarus latimanus				16.8	P.1.3	U	Taylor (1984)
Orconectes causeyi				14–29	P.1.1(A)	U	Loring and Hill (1976)
Orconectes eupunctus			22		OG.2	A	Whitledge and Rabeni (2002)
Orconectes hylas			22		OG.2	B	Whitledge and Rabeni (2002)
Orconectes immunis				18–22	P.1.2	A	Crawshaw (1974)
Orconectes immunis				21.5	P.1.2(A)	A	Crawshaw (1983)
Orconectes immunis			25		OG.1	J	Wetzel and Brown (1993)
Orconectes limosus			24–25; 26		OG.2	A	Simčič et al. (2014)
Orconectes luteus			26		OG.2	A	Whitledge and Rabeni (2002)

Table 1 continued

Species	Lower tolerance (°C)	Upper tolerance (°C)	Optimal growth (°C)	Preference (°C)	Method	Life stage	Source
Orconectes nais			24–28		OG.1	J	Hellman (1992)
Orconectes obscurus				30	P.1.1(A)	U	Hall et al. (1978)
Orconectes obscurus				29.8–33.9	P.1.1	U	Mather et al. (1982)
Orconectes palmeri				26.2	P.1.2	A	Sargent et al. (2011)
Orconectes propinquus				21	P.1.1	A	Keller and Hazlett (2010)
Orconectes punctimanus			22		OG.2	A	Whitledge and Rabeni (2002)
Orconectes rusticus		38.5–41.5[b]			T.1.2(A); T.2.4(A)	U	Claussen (1980)
Orconectes rusticus				22	P.1.1	A	Keller and Hazlett (2010)
Orconectes rusticus	0.9–6.1	30.2–36.2			T.2.4(A)	U	Layne et al. (1985)
Orconectes rusticus	5.9–6.3	34.5–35.4			T.2.4(A)	U	Layne et al. (1987)
Orconectes rusticus	8.5–12.5[b]	32.5–39.5[b]	26–28	22	T.2.4 (A); P.1.1 (A); OG.1	B	Mundahl and Benton (1990)
Orconectes rusticus		36.6			T.1.2(A)	A	Spoor (1955)
Orconectes rusticus[a]		27.4–38.2			T.2.4(A)	A	Mundahl (1989)
Orconectes virilis		38.5[b]			T.1.2(A); T.2.4(A)	U	Claussen (1980)
Orconectes virilis				21	P.1.1	A	Keller and Hazlett (2010)
Orconectes virilis				24	P.1.2(A)	A	Peck (1985)
Orconectes virilis			25		OG.1	J	Wetzel and Brown (1993)
Orconectes virilis			26		OG.2	A	Whitledge and Rabeni (2002)
Procambarus clarkii				24–26.7	P.1.2	A	Bückle-Ramírez et al. (1994)
Procambarus clarkii				23.4	P.1.1(A)	U	Espina et al. (1993)
Procambarus clarkii			22–30		OG.3	U	Huner (1988)
Procambarus clarkii				21.8–25.9	P.2.1	J	Tattersall et al. (2012)
Procambarus clarkii				22	P.1.3	U	Taylor (1984)
Procambarus clarkii[a]		35			T.4	U	Huner and Barr (1991)
Procambarus horsti	6.6 ± 0.7	28.6 ± 1.6			T.2.5	A	Caine (1978)
Procambarus kilbyi[a]	1	38.4 ± 1.2			T.2.5	A	Caine (1978)
Procambarus leonensis[a]	1	38.9 ± 0.6			T.2.5	A	Caine (1978)
Procambarus llamasi			26		OG.1	J	Carmona-Osalde et al. (2004)
Procambarus orcinus	4.0 ± 0.6	33.1 ± 1.2			T.2.5	A	Caine (1978)
Procambarus paeninsulanus[a]	4.7 ± 0.7	37.1 ± 1.2			T.2.5	A	Caine (1978)
Procambarus simulans				22.1	P.1.2	A	Dupré and Wood (1988)
Procambarus spiculifer				23.4	P.1.2	A	Sargent et al. (2011)

Table 1 continued

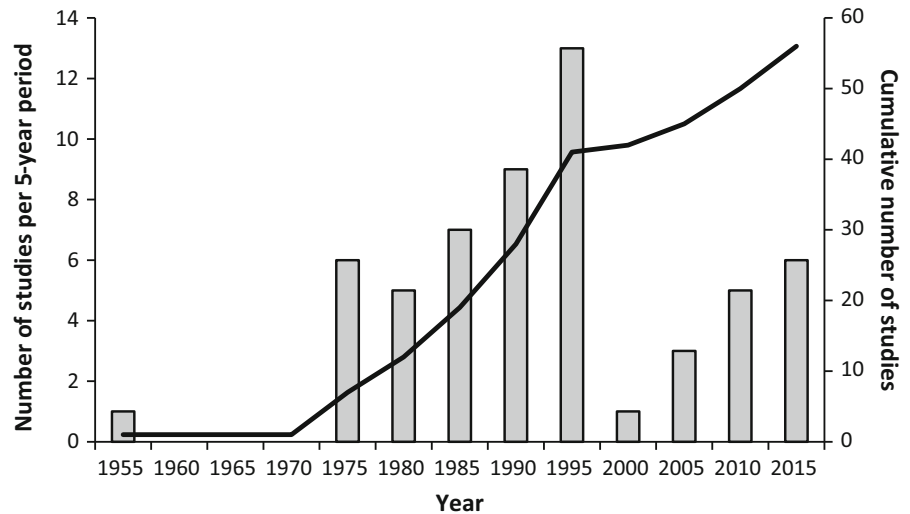| Species	Lower tolerance (°C)	Upper tolerance (°C)	Optimal growth (°C)	Preference (°C)	Method	Life stage	Source
Procambarus spiculifer				23.4	P.1.3	U	Taylor (1984)
Procambarus spiculifer[a]	8.1 ± 1.1	33.3 ± 0.9			T.2.5	A	Caine (1978)
Parastacidae							
Cherax destructor			20–25		OG.3	U	Frost (1975)
Cherax destructor		36	28		T.4; OG.3	U	Mills et al. (1994)
Cherax destructor[a]	7	34			T.1.2	A	Semple et al. (1995)
Cherax quadricarinatus			28	23–26	P.1.2(A); OG.1	J	García-Guerrero et al. (2013)
Cherax quadricarinatus		34	28		T.1.3; OG.1	J	Jones (1995)
Cherax quadricarinatus	22	32	30		T.1.3; OG.1	J	King (1994)
Cherax quadricarinatus			28		OG.1	J	Meade et al. (2002)
Cherax quadricarinatus		40.1 ± 0.4, 39.7 ± 0.3			T.2.4 (A)	J	Richwell (2013)
Cherax quadricarinatus	7	34			T.1.2	A	Semple et al. (1995)
Cherax quadricarinatus			25–28		OG.1	J	Verhoef et al. (1998)
Cherax quadricarinatus[a]	4	40	25–30		T.1.1; OG.1	J	Austin (1995)
Cherax tenuimanus		37			T.2.5	J	Geddes et al. (1993)
Cherax tenuimanus		31.5	15–20		T.4; OG.3	U	Mills et al. (1994)
Cherax tenuimanus	11	30	24		T.1.3; OG.1	J	Morrissy (1990)
Cherax tenuimanus	4	28			T.1.2	A	Semple et al. (1995)
Euastacus armatus[a]		30			T.2.5	J	Geddes et al. (1993)
Euastacus sulcatus		27			T.2.5	J	Bone et al. (2014)
Paranephrops zealandicus			16		OG.1	J	Hammond et al. (2006)

Alphabetic codes in life stage column indicate if crayfish were adult (A), juvenile (J), both adult and juvenile (B), or unknown (U). Codes in the methods column indicate specific methodologies used in each study. The first part of each code indicates if the study contained methods intended to estimate temperature tolerance (T.x.x), temperature preference (P.x.x), or optimal growth (OG.x). The "x" values in these descriptions serve as placeholders for numbers that indicate additional methodological detail. For temperature tolerance studies, studies were classified as static (T.1.x), dynamic (T.2.x), both static and dynamic (T.3.x), or unknown methods (T.4.x). Studies were further classified as plunge (T.x.1), LT50 or acclimated chronic exposure (T.x.2), other static method (T.x.3), critical thermal method (T.x.4), or chronic lethal method (T.x.5). For temperature preference studies, numbers relate to use of a horizontal gradient (P.1.x) or a shuttlebox (P.2.x), followed by an indication if the test was acute (P.x.1) or gravitational (P.x.2). In cases when both gravitational and acute methods were used, the study was classified P.x.3). For optimal growth studies, OG.1 indicates the endpoint was a measurement of growth (weight, length, or molts), OG.2 indicates the endpoint was growth scope predicted from consumption and respiration, and OG.3 indicates the endpoint was not reported. Studies that used multiple acclimation temperatures are further designated by (A) following the methodological codes described above

[a] Studies identified in Nyström (2002)

[b] Values were estimated from figures in the source study

Table 2 The number of species (percentage of total) in each of the three families of freshwater crayfish with published thermal ecology information identified in our review of the literature

	Lower tolerance	Upper tolerance	Optimal growth	Preference
Astacidae	3 (25.0)	4 (33.3)	4 (33.0)	1 (8.3)
Parastacidae	3 (1.6)	5 (2.7)	4 (2.1)	1 (0.5)
Cambaridae	9 (2.1)	12 (2.8)	12 (2.8)	12 (2.8)
Total	15 (2.4)	21 (3.3)	20 (3.2)	14 (2.2)

Fig. 1 Frequency of publication identified in our review of the literature for information on the thermal ecology for all known freshwater crayfish species. Numbers represent only studies that reported values for temperature tolerance, temperature preference, or optimal growth temperature for freshwater crayfishes

Table 3 Prevalence of thermal ecology metrics published for the 12 most important commercial freshwater crayfishes

Commercially important species	Tolerance	Preference	Optimal growth
Astacus astacus	x	x	x
Astacus leptodactylus	x	–	x
Austropotamobius pallipes	x	–	x
Cherax destructor	x	–	x
Cherax tenuimanus	x	–	x
Cherax quadricarinatus	x	x	x
Orconectes immunis	–	x	x
Orconectes rusticus	x	x	x
Orconectes virilis	–	x	x
Pacifastacus leniusculus	x	–	x
Procambarus acutus	–	–	–
Procambarus clarkii	x	x	x

"x" indicates at least one estimate was found and "–" indicates no estimates were found

ACE, and the experimental duration ranged from 1 to 96 h.

Similar to static methods, no single approach dominated the dynamic methods (Table 4). The CTM approach was used in 8 studies, where 11 total estimates were reported covering 6 different species. However, 6 of the 11 CTM estimates focused on one species, *O. rusticus*. Most (6) of the CTM studies used a heating rate of 0.6–0.8 °C/min, whereas one (Mirenda and Dimock 1985) used 1 °C/min and two (Firkins and

Table 4 Summary of methodological approaches for the study of freshwater crayfish temperature tolerance displayed by the number of studies conducted, the number of estimates within those studies, and the number of crayfish species covered

Method	Studies	Estimates	Species
Static	11	14	8
Plunge	3	3	3
LT50/ACE	5	9	7
Other	3	3	2
Dynamic	12	23	17
CTM	8	11	6
CLM	4	12	12
Unknown	5	6	6

Abbreviated methods include lethal time at 50 % mortality (LT50), acclimated chronic exposure (ACE), critical thermal method (CTM), and chronic lethal method (CLM)

Holdich 1993; Richwell 2013) used slower rates. Loss of righting response was the experimental endpoint for all of the CTM estimates, with the exception of Richwell (2013). For those studies that used LRR, crayfish were given 30 s to right themselves except Claussen (1980), who allowed 60 s.

The other dynamic method, CLM, was used in 4 studies covering 12 species. However, none of the authors of these studies used the terminology of CLM. Our designations were based on the criteria of raising water temperature at rates ≤1 °C/day. The slowest rate of water temperature manipulation was 1 °C/week. Confusingly, the resulting metrics from these varied efforts were referred to as UUILT, LC50, or only referred to as temperature tolerance values. Additionally, multiple experimental endpoints were used, including LRR and survival percentage.

Among all species, *O. rusticus* had the highest upper tolerance of 41.5 (Claussen 1980) and *C. quadricarinatus* had the second highest upper tolerance at 40 °C (Austin 1995). *Cambaroides japonicus* and *Euastacus sulcatus* had reported upper tolerance values of 27 °C, which were the lowest noted (Table 1). Tolerance values varied within species with multiple estimates. For example, *O. rusticus* had upper tolerance values that ranged from 27.4 to 41.5 °C and *C. quadricarinatus* upper tolerance values ranged from 32 to 40.1 °C. Additionally, a 6.9 °C discrepancy existed between upper tolerance limit estimates for *Pacifastacus leniusculus* (Firkins & Holdich 1993; Nakata et al. 2002). Lower tolerance values also varied, whereby

0.9 °C was the lowest reported value (*O. rusticus*) and 22 °C the highest (*C. quadricarinatus*). Nineteen of the 21 estimates of lower tolerance limits were below 10 °C. Further evidence of intraspecific variation in estimates was shown by the tolerance breadth for *Astacus leptodactulus*, which was estimated at 4–32 °C by Köksal (1988) and from 9 to 36 °C by Firkins and Holdich (1993).

Temperature preference

We located 17 published studies of crayfish temperature preference, which reported 22 total estimates covering 14 species (2.2 % of all extant species). Ten estimates used gravitational methods, which we defined for our purposes as any study where observations occurred after at least 4 h. Of these, the shortest duration was 4 h and 10 days the longest. Nine estimates were based on acute methods, which we defined as based on observations over 4 or fewer hours. These included estimates taken after as little as 10 min to almost 4 h. Frequency of observation and criteria for including observations in the final estimate were not consistent among studies. Some studies allowed for habituation (Peck 1985), some considered the frequency of use of different temperatures (García-Guerrero et al. 2013), and some collected data at multiple intervals, from every 2 min (Hall et al. 1978) to every hour (Bückle-Ramírez et al. 1994). Only Taylor (1984) reported temperature preference values based on both acute and gravitational methods. We encountered no studies that used field methods to estimate temperature preference for crayfish.

Of the 22 temperature preference estimates, 20 used horizontal temperature gradients to define the preference value and two used a shuttlebox design. The temperature range covered by gradient devices varied by study, but ranged from 4 °C to a 46 °C spread. On average, the gradients covered a 25 °C range from 9 to 34 °C. The lowest available temperature in any gradient was 3 °C, and the highest was 50 °C.

Acclimation procedures and the age of experimental crayfish varied among studies. Eight of the temperature preference estimates used crayfish acclimated at multiple temperatures prior to experimentation. These acclimation temperatures ranged from 6 to 33 °C, and no two studies used the same set of acclimation temperatures. The two most common acclimation temperatures were 14 and 20 °C, which

appeared in three studies. Two of the estimates were obtained using juvenile crayfish, 11 from adults, one from both juveniles and adults, and crayfish size or maturity information was not reported for 8 other estimates. Gender of crayfish was rarely reported.

Orconectes obscurus had the highest temperature preference range at 29.8–33.9 °C (Mather et al. 1982) and *A. astacus* had the lowest at 11.9–18 °C (Kivivuori 1994). Estimates for a single species varied (e.g., range of 21.8–26.7 °C for *P. clarkii* obtained from four different studies; Table 1). However, estimates were not always conflicting (e.g., range of 18–22 °C for *Orconectes immunis*, Crawshaw 1974 and 21.5 °C, Crawshaw 1983; or *Procambarus spiculifer* at 23.4 °C, Taylor 1984; Sargent et al. 2011).

Optimal growth

We located 22 published studies of crayfish optimal growth temperatures, consisting of 33 total estimates covering 20 species (3.2 % of all extant species). Most (n = 19) estimates were developed based on juvenile crayfish, but 10 were based on adults, and four estimates could not be classified. Similar to the other metrics, methodology varied among estimates of optimal growth. Estimates were based on as few as 3 to as many as 11 different rearing temperatures. These ranged from 4 to 35 °C, but all included at least one temperature above and below 20 °C. Most estimates were based on data collected from 4 or 5 different temperatures. The duration of the studies varied from 21 to 112 days and used endpoints such as specific growth rate, overall growth in length or mass, or molt frequency. Studies also varied in diet and feeding regimen, which may limit comparability among studies. Two monitored crayfish food consumption and respiration at different temperatures to estimate growth scope as the metric of optimal growth temperature (Whitledge and Rabeni 2002; Simčič et al. 2014).

The lowest reported optimal growth temperatures were 15 °C for *Cherax tenuimanus* and 16 °C for *Paranephrops zealandicus* and *A. astacus* (Table 1). The highest optimal growth temperature reported was 30 °C for *C. quadricarinatus* (King 1994). Some authors reported optimal growth values as a range of up to eight or ten degrees (Cukerzis 1973; Söderbäck et al. 1988), whereas 22 estimates were reported as a single value.

Metric comparison and crayfish distributional relationships

The average tolerance breadth was 28.6 °C across the 15 species with estimates of both metrics (Table 5). Upper tolerance temperature was statistically higher than optimal growth temperature [$t(9) = 17.3$, $p < 0.001$] by an average of 10.3 °C (range 8.0–13 °C), and the metrics were somewhat correlated (Pearson Correlation = 0.78). Surprisingly, optimum growth temperature was statistically higher than preference temperature [$t(4) = 7.0$, $p < 0.001$] by an average of 3.8 °C (range 2.3–5 °C), and highly correlated (Pearson Correlation = 0.96).

All data used in regression models met assumptions of normality. Increasing absolute latitude was negatively associated with increasing optimal growth temperature (p value = 0.01; $R^2 = 0.33$; Fig. 2). Regression analyses relating absolute latitude of species range to upper tolerance, lower tolerance, tolerance breadth, and preferred temperature were not significant (p values >0.10) and failed to explain much variation in the data ($R^2 < 0.15$). Distributional range was not a significant predictor of temperature tolerance for crayfishes (p value >0.15).

Discussion

Our findings that approximately 94 % of crayfishes worldwide lack basic information on their thermal ecology highlight an important knowledge gap that may hinder broad ecological insight. However, crayfish are not the only aquatic taxa that lack widespread investigation into thermal ecology. We were unable to locate reviews similar to ours that examined the overall state of knowledge for other aquatic taxon either globally or regionally, with the exception of two studies on North American fishes. Coutant (1977) compiled a table containing temperature preference data for 111 species of marine and freshwater North American fish, and Beitinger et al. (2000) summarized temperature tolerance data for 116 species ($\sim$ 15 %) of North American freshwater fish. Aspects of thermal ecology for freshwater mussels have been investigated (Pandolfo et al. 2010; Galbraith et al. 2012; Carey et al. 2013), but no taxon-wide summaries exist. Similarly, the thermal ecology of select marine and estuarine crustaceans was investigated (see for

Table 5 Range and mean (SD) of thermal ecology metrics obtained from a literature review of all freshwater crayfish species

	Range (°C)	Mean (SD) °C	n
Metric			
Lower tolerance	0.9–22.0	5.7 (2.9)	15
Upper tolerance	26.6–41.5	33.4 (3.5)	22
Optimal growth	15.0–30.0	23.6 (3.0)	19
Preference	11.9–33.9	22.3 (3.8)	14
Comparisons			
Tolerance breadth	22.0–37.9	28.6 (4.6)	15
Upper tolerance/optimal growth	8.0–16.0	10.3 (1.9)	10
Upper tolerance/preference	9.9–16.0	12.3 (2.0)	7
Lower tolerance/optimal growth	12.9–20.3	16.1 (2.7)	7
Lower tolerance/preference	13.5–15.3	14.7 (1.0)	3
Optimal growth/preference	2.3–5	3.8 (1.2)	5

Ranges for the four primary metrics were derived from estimates based on independent studies and unique acclimation temperatures. For species with multiple acclimation temperatures and/or multiple estimates for a single metric, we averaged across acclimation temperatures within a study and then averaged across all estimates to produce as single value of each metric for the species. This was done for the ranges and means for the comparative summary metrics, along with means for the primary metrics. Counts (n) are based on the averaged data and represent the number of species used to calculate means and standard deviations
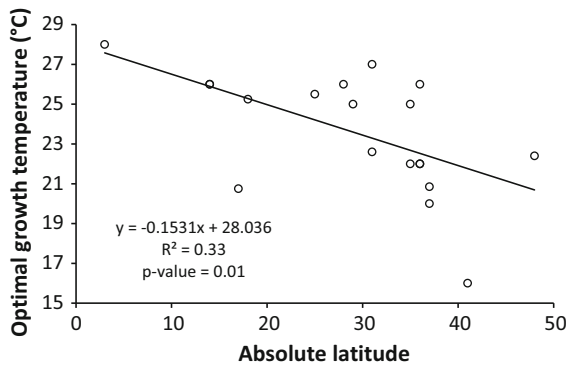

Fig. 2 Significant linear relationship between optimal growth temperature and absolute latitude (latitude of distributional extent closest to equator) for the 19 crayfish species with optimal growth estimates

instance Dove et al. 2005; González et al. 2010), but not summarized across taxa. We contend that compilation of thermal ecology data for all of these taxa would allow researchers to more easily identify regional and taxonomic gaps in knowledge and better standardize their approaches for future investigations.

It is likely that our search did not identify all known thermal ecology information for crayfishes. We suspect information on thermal relationships exists in non-peer reviewed sources, gray literature, and non-English language journals. It is also possible that information existed in literature sources not identified by our search terms and strategy. However, we believe we identified the majority of available sources and accurately captured trends and biases in available information.

A negative relationship between optimal growth temperature and absolute latitude was the only expected relationship we observed between thermal ecology of crayfish and their distributional characteristics. Chucholl (2011) observed this same relationship within a single crayfish species, *P. clarkii*, for populations at different latitudes. Similar relationships exist between absolute latitude and temperature tolerance and tolerance breadth for other ectotherms (Sunday et al. 2011); however, our data did not provide evidence for these relationships in crayfish. Physiological traits of species' fundamental niche breadth, especially temperature tolerance breadth, are commonly linked to distributional extent as explained by Rapoport's Rule (Stevens 1989; Calosi et al. 2010). There is mixed support for Rapoport's Rule across taxa, and it is only supported for freshwater fishes in latitudes above 40°N (Rohde et al. 1993). Our data provided no support for the acceptance of Rapoport's Rule for crayfishes; however, it is unclear if this is due to violation of the rule or the limitation of available

information. We explored these relationships despite small sample sizes, varied methodology in metric estimation, coarse grain distributional data, and a potentially biased species pool. Further, other covariates affect species distributions (Calosi et al. 2010) that we could not include in our analyses. Our results highlight the need for additional study of basic temperature relationships for freshwater crayfish to facilitate exploration of broad thermal relationships.

Each of the four metrics we summarized received different levels of attention from researchers, with upper temperature tolerance as the most commonly reported metric for crayfish. Information on upper temperature tolerance is often used in modeling efforts to predict range expansion capabilities (Eaton and Scheller 1996) and resilience to climate change (Kelly et al. 2012) for aquatic organisms. However, some researchers argue that temperature tolerance estimates have little utility for understanding ecological relationships (Lutterschmidt and Hutchison 1997; Pörtner and Peck 2010). Knowing the lower temperature tolerance of crayfishes may be important in predicting invasion success of individual species at different latitudes or in climactically different environments (Usio et al. 2005). Temperature preference values have utility for predicting the optimum temperature for energy maximization and thus, growth and reproduction (Beitinger and Fitzpatrick 1979; González et al. 2010). Not surprisingly, optimal growth estimates exist for almost all of the crayfishes used in large-scale aquaculture to maximize production of rearing environments (Meade et al. 2002). However, non-commercial species of conservation concern that require propagation for reintroduction efforts could benefit from this information. The decision of which temperature metric to estimate is dependent on the ultimate use of the information.

The large average difference (10.3 °C) we observed between upper tolerance and optimal growth temperatures was surprising, as both optimal growth and preference temperatures are often hypothesized to be near upper tolerance limits (Reynolds and Casterlin 1979; Clark et al. 2013; Ern et al. 2014). Optimal growth temperatures always exceeded temperature preference and were highly correlated. A similar relationship was observed for Arctic Charr (*Salvelinus alpinus*) and hypothesized to result from the species optimizing growth efficiency instead of growth rate (Larsson 2005). Kellogg and Gift (1983) examined

four species of fish and found the preferred temperature was always within 2 °C of the optimal growth temperature, with only one of the species selecting temperatures above its optimal growth estimate. It is possible that crayfish have a different relationship between these two metrics than fish, or that the lack of standardization in published crayfish studies introduced bias into our analysis. We collapsed all estimates into a single value for a given species and metric, but others contend that thermal preferendum and optimal growth temperatures are best represented by zones (Jobling 1981; Kellogg and Gift 1983).

Determination of thermal ecology metrics can be costly and time consuming. The ability to estimate and use one metric to predict values for other metrics would reduce costs and effort needed to address multiple species. Jobling (1981) compiled data from 19 species of fish and used linear regression to determine the relation between temperature preference and optimal growth temperature and described a strong relationship with a correlation coefficient of 0.94. We observed a similarly high correlation between these metrics for crayfish, but further research is required to determine how reliable the relationship, given the significant difference between estimates for the two metrics. Jobling (1981) also noted issues with a lack of methodological standardization. Cooper et al. (2008) created a model to predict temperature tolerance of a terrestrial isopod and found that a static method of estimating tolerance could predict the outcome of a dynamic method for estimating tolerance. Similarly, Dallas and Ketley (2011) used CTM and LT_{50} methods to estimate temperature tolerance of 10 aquatic macroinvertebrates and determined that the CTM method resulted in higher values of upper tolerance, but a linear model could reliably predict LT_{50} values. The sparsity of reported temperature metrics prevents development of similar relationships for crayfishes. Improved methodological standardization and coverage of additional species may allow for development of statistical relationships for species lacking a full complement of thermal investigations and endpoints. Calls for standardization of methodology to determine thermal ecology metrics began as far back as 1977 (Richards et al. 1997), but the need remains.

Estimates of the same metric for a single species varied. It is possible that this variation could be related to underlying genetic variation or physiological

gradients related to temperature that span species' distributions (Fangue et al. 2006; Kelly et al. 2012). This source of variation could be investigated by simply using the same methods to test different populations of a given crayfish species. Kelly et al. (2012) demonstrated this phenomenon for a widely-distributed marine copepod and concluded that local thermal adaptation may preclude adaptation to altered thermal conditions.

Although natural variation within populations likely accounts for some variation in thermal metrics, we believe the largest source of variation among studies resulted from methodological differences used to estimate temperature relationships for crayfishes. This was not surprising, as our review covered species from multiple continents and over 60 years. However, the lack of methodological standardization impaired our ability to make broad inferences from reported data. Context-driven considerations ultimately drive experimental design for many studies; however, adherence to basic standardized methods in the future may increase the applicability of findings (Lutterschmidt and Hutchison 1997). For example, Mora and Maya (2006) found that differences in the length of time a blenny species *Acantemblemaria hancocki* were held in captivity and the heating rate of water in CTM tests resulted in statistically different temperature tolerance estimates.

We propose methodological considerations for future studies of crayfish temperature tolerance, temperature preference, and optimal growth temperature to improve standardization (Box 1). We believe most are straightforward given issues with previous studies identified during our review. However, our recommendations related to acclimation and rearing temperatures warrant additional explanation. Acclimation temperatures can have significant influence on final estimates of temperature tolerance and, to a lesser extent, preference (Beitinger et al. 2000). Out of 21 studies that reported lab acclimation of crayfish, 71 % used acclimation temperatures of 25 ($\pm$1) °C, 48 % used 20 ($\pm$1) °C, and 43 % used 15 ($\pm$1) °C. No study reported an upper thermal tolerance lower than 26.6 °C and only one species (*C. quadricarinatus*) was reported to have a lower tolerance limit above 15 °C. Thus, we suggest using acclimation temperatures of 15, 20, and 25 °C for all temperature tolerance and preference studies. We believe at least one temperature in this range is likely to occur within the thermal

tolerance range for both warm- and cold-adapted species. For optimal growth, 69 % of estimates were within the range of 20–25 °C, prompting us to suggest these two temperatures be included as treatments in all future studies of this metric. Further, to assist in future comparisons, we suggest reporting the growth rate at 20 °C as a percentage of the maximum observed growth rate. We encourage researchers to use additional temperatures to provide context for study-specific hypotheses, but inclusion of standard acclimation and rearing temperatures will enhance data applicability in subsequent ecological investigations.

It was our original intent to recommend specific metrics and methodologies for the study of crayfish thermal ecology; however, evidence is lacking to warrant promoting one metric or methodology over another. Additional research that compares methodology for multiple species will best elucidate what methods produce the most valuable or consistent output. For example, the rate at which water temperature is raised during CTM trials affects the outcome of the experiment as heat transfer to the interior of the body lags behind the heating rate of the water (Becker and Genoway 1979). The suggested heating rate for freshwater fishes is 0.3 °C/min based on testing of various rates ranging from 1 °C/min through 1 °C/h (Becker and Genoway 1979). This rate has not been used for crayfish, but rather rates of 0.5–0.8 °C/min were most common. Given the relatively smaller body masses of crayfish compared to fish, we believe a rate of 0.8 C should suffice for most crayfishes. However, additional investigation of heating rates for CTM studies in freshwater crayfish is warranted.

This research need is complemented by the need to determine what temperature metrics are most useful for trait-based modeling efforts that predict species distributions, response to climate change, and invasion potential (Buckley and Kingslover 2012). For example, climate change studies often predict water temperatures for future time-steps based on mean weekly or monthly temperatures during the warmest part of the year (Eaton and Scheller 1996; Buisson et al. 2008). Perhaps tolerance metrics that best simulate this duration of thermal stress are most useful for parameterizing models. However, temperature effects from climate change may be sub-lethal (Parmesan 2006), which may be best predicted through optimal growth estimates. Further, proxies for temperature tolerance such as those used to populate a species trait

Box 1 Considerations to improve standardization of methodology used to estimate freshwater crayfish temperature tolerance, temperature preference, and optimal growth

Clearly state the origin and status of test organisms

    Location and date of capture

    Temperature of water at time of capture

    Size (carapace length) and gender of crayfish used in tests

    Development stage (e.g., hatchling, juvenile, adult)

    Satiation state

Provide detailed reports of laboratory testing device specifications

    Range of temperatures available in gradient devices

    Rate of water temperature change for dynamic tolerance tests

    Duration of study

    Relevant water quality parameters and laboratory conditions

Clearly state and define which temperature metrics were estimated in the text

    Describe how each metric was calculated and what defined the experimental endpoint

    Pertinent statistics should be included in the text, including sample sizes, means, and measures of variation around estimates

Acclimation at multiple temperatures should occur prior to experimental testing for tolerance and preference studies

    We propose that crayfish acclimate at temperatures of 15, 20, and 25 °C for at least 2 weeks prior to testing. Additional acclimation temperatures can be used, but testing and reporting of values at these standard values will allow more meaningful comparison across species

    At a minimum, all studies should include the 20 °C acclimation for comparison purposes

Establish standardized test temperatures for all optimal growth studies

    We propose that temperature treatments of 20 and 25 °C be included in all optimal growth estimates that occur for crayfishes

    Researchers should report growth at 20 °C as a percentage of maximum optimal growth

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database can be based on minimum or maximum temperature observed at the centroid of a species' range (Frimpong and Angermeier 2009). However, the utility of these measures has not been thoroughly assessed.

The information we reviewed represents selected aspects of crayfish thermal ecology. Many additional aspects were not covered in this review, such as how temperature influences molting and reproductive events (DiStefano et al. 2013), description of temperature conditions at field locations occupied by species of interest (Sargent et al. 2011), and temperatures related to specific physiological processes (Paglianti et al. 2004). Further consideration of these topics was beyond the scope of this contribution, but was explored broadly for aquatic insects (Ward and Stanford 1982) and across taxa in the context of evolution (Angilletta 2009). These characteristics may have additional value for use in efforts that seek to describe crayfish thermal ecology and ultimately how it can inform conservation or management.

Novel approaches to the study of crayfish thermal ecology may complement or replace current

approaches. Aquatic organisms do not normally experience constant water temperatures over long periods of time in wild settings, yet almost no studies of crayfish thermal ecology use fluctuating temperatures to estimate optimal growth or other parameters. Recsetar et al. (2014) studied growth of a salmonid under both static and fluctuating temperatures and showed that the fish could survive exposure to higher temperatures if they fluctuated. In a different approach, Simčič et al. (2014) estimated temperature tolerance for two species of crayfish using respiratory electron transport system activity. This approach used a biochemical measure of metabolic activity based on oxygen consumption by enzymes and represents a rapid and non-lethal alternative to traditional temperature tolerance approaches (Simčič et al. 2014). Another physiologically-based approach that has gained popularity, especially for marine fishes, is the oxygen- and capacity-limited thermal tolerance (OCLTT) methodology (Pörtner 2010; Bozinovic and Pörtner 2015). This approach is based on the hypothesis that fitness is highly correlated to delivery of oxygen to tissues and aerobic performance (Pörtner 2010). Although promising, this

approach has limitations and has not been used on crayfishes (Clark et al. 2013; Ern et al. 2014; Norin et al. 2014). Additionally, heat shock proteins, which are released by organisms in response to thermal stress, hold promise in elucidating thermal ecology of crayfishes at the cellular level (Basu et al. 2002).

Our study highlights the lack of easily accessible information on the thermal ecology of 94 % of freshwater crayfish species worldwide. Further, our results showed that methodological variation limits the inferences we can make for the 6 % of crayfish investigated. Many of the studies we summarized successfully addressed their individual objectives, but we believe greater standardization in methodology will increase our ability to fully use thermal ecology to investigate broad ecological questions. We also believe further investigation of methodological differences will assist researchers in selection of the most informative thermal metrics to inform conservation and management of freshwater crayfishes.

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