The effect of water temperature on aquatic organisms: a review of knowledge and methods for assessing biotic responses to temperature

Report to the
Water Research Commission

by

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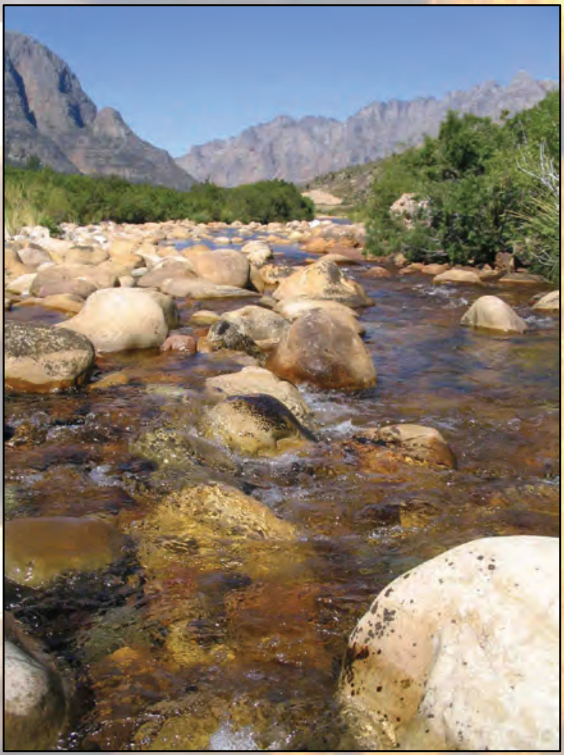

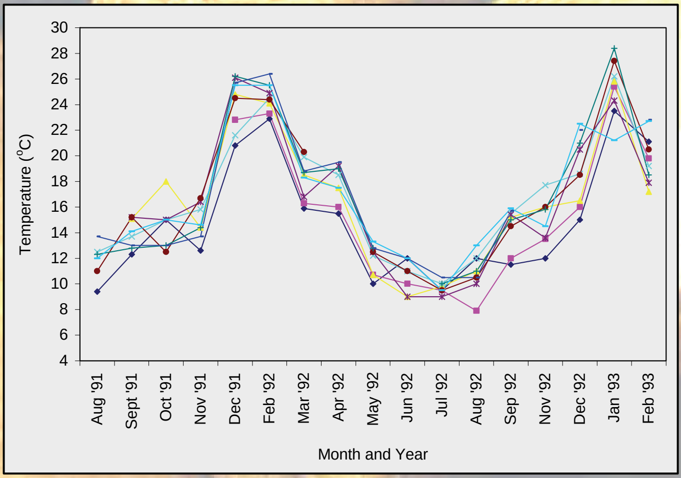

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Preface

This report comprises five deliverables for the one-year consultancy project to the Water Research Commission, entitled **"The effect of water temperature on aquatic organisms – a review of knowledge and methods for assessing biotic responses to temperature"** (K8-690).

Deliverable 1 (Chapter 1) is a literature review aimed at consolidating available information pertaining to water temperature in aquatic ecosystems. The review describes the:

- importance of water temperature in aquatic ecosystems, including spatial and temporal variation in water temperature;
- measurement of water temperature in river systems, including *in situ* measurement and modelling;
- anthropogenic factors that modify water temperature;
- effects of water temperature on the physical and chemical characteristics of water;
- effects of water temperature on aquatic organisms and ecosystems;
- assessment of the effects of temperature changes on aquatic organisms, including thermal tolerance, sublethal effects and behavioural preference and avoidance; and
- water temperature guidelines for the protection of aquatic ecosystem.

South African examples are given in instances where they are available, although generally local information on the effect of water temperature on aquatic organisms and ecosystems is relatively scarce.

Deliverable 2 is a scientific paper based on the literature review and submitted to Water SA. This review paper will enhance dissemination of existing knowledge on water temperature and aquatic organisms.

Deliverable 3 (Chapter 2) is a short report on site selection for the installation and testing of temperature loggers, and includes data collected during the consultancy on within-site spatial variation in water temperature.

Deliverable 4 (Chapter 2) is a section on issues to be considered and criteria to be used when selecting sites for temperature monitoring. These criteria will serve as a guide for future temperature related research and application of temperature monitoring at regional and national levels.

Deliverable 5 (Chapter 3) is the Terms of Reference for the long-term temperature programme (jointly written with Dr Rivers-Moore, and contributed to by Dr Harding).

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Thank you to the Water Research Commission for funding this research consultancy and to Steve Mitchell and Stanley Liphadzi for facilitation of this research. Thanks also to Geordie Ractliffe who generously made available unpublished data. This consultancy was undertaken whilst the Helen Dallas was a research associate of the Freshwater Research Unit, University of Cape Town. Thanks to my colleagues Dr Nick Rivers-Moore for a rewarding collaboration to develop the terms of Reference for the future solicited WRC temperature project.

CHAPTER 1: LITERATURE REVIEW

1. Introduction

Natural thermal characteristics of riverine ecosystems are dependent on hydrological, regional, climatological and structural features of the region and catchment area (Figure 1.1). Hydrological factors such as the source of water (surface runoff, lake-outlet, snow melt, etc), the relative contribution of groundwater, rate of flow or discharge, volume of water, and inflow from tributaries, will influence the thermal regime (Ward, 1985). For example, rivers that are spring-fed or receive a large proportion of groundwater exhibit a high degree of thermal constancy (e.g. Hopkins, 1971). Regional factors such as latitude and altitude (upland versus lowland rivers); and climatic factors such as air temperature, solar radiation, cloud cover, wind speed, vapour pressure, precipitation and evaporation, all influence the thermal conditions in rivers. Precipitation events may temporarily elevate or depress water temperatures (Ward, 1985). For example, Chutter (1970) and Appleton (1976) recorded instantaneous depressions of water temperature resulting from summer hailstorms in the Vaal River and Gladdespruit (Mpumalanga) South Africa. Structural characteristics of the river and catchment, including topographic features, aspect and slope, riparian vegetation cover, channel form (morphology), geology/substratum, water depth, turbidity, and the percentage of pool habitat, affect the amount of solar radiation reaching and heating the water, and thus its thermal regime. For example, the nature of the streambed (substratum) may influence the extent to which it acts as a heat sink (during midday) or energy source (night time) (Gu *et al.*, 1998; Evans *et al.,* 1998). The high specific heat of water results in an extremely high capacity for heat absorption and extremely slow release of heat and thus contributes to thermal stability, which in turn has important consequences for aquatic organisms (Reid and Wood, 1976).

The relative importance of the hydrological, regional, climatological and structural features differs amongst rivers and river reaches. For example, water temperature in small, shallow upland streams with low flows may be determined largely by structural features such as channel form and vegetation cover (e.g. Hawkins *et al.,* 1997; Rutherford *et al.,* 2004). Small upland streams that are heavily shaded and fed by thermally stable groundwater, have been shown to remain relatively cool with little diurnal variation in water temperature (e.g. Buffalo River, South Africa, Palmer & O'Keeffe, 1989). In contrast, water temperature in wide, shallow lowland rivers might be largely determined by solar radiation because of their high surface area to volume ratio (Sinokrot & Gulliver, 2000). The complexity of a river channel also influences water temperature variations within the channel. Complex channels with backwaters, shallow margins, deep pools, side channels, etc. have more diverse temperature regimes, whereas simple uniform channels have simplified temperature regimes (Poole *et al.,* 2001). The term “temperature regime” is used to describe the concepts of magnitude, frequency, duration, timing, and rate of change with respect to water temperature (Poole and Berman, 2001; Poole *et al.,* 2001).

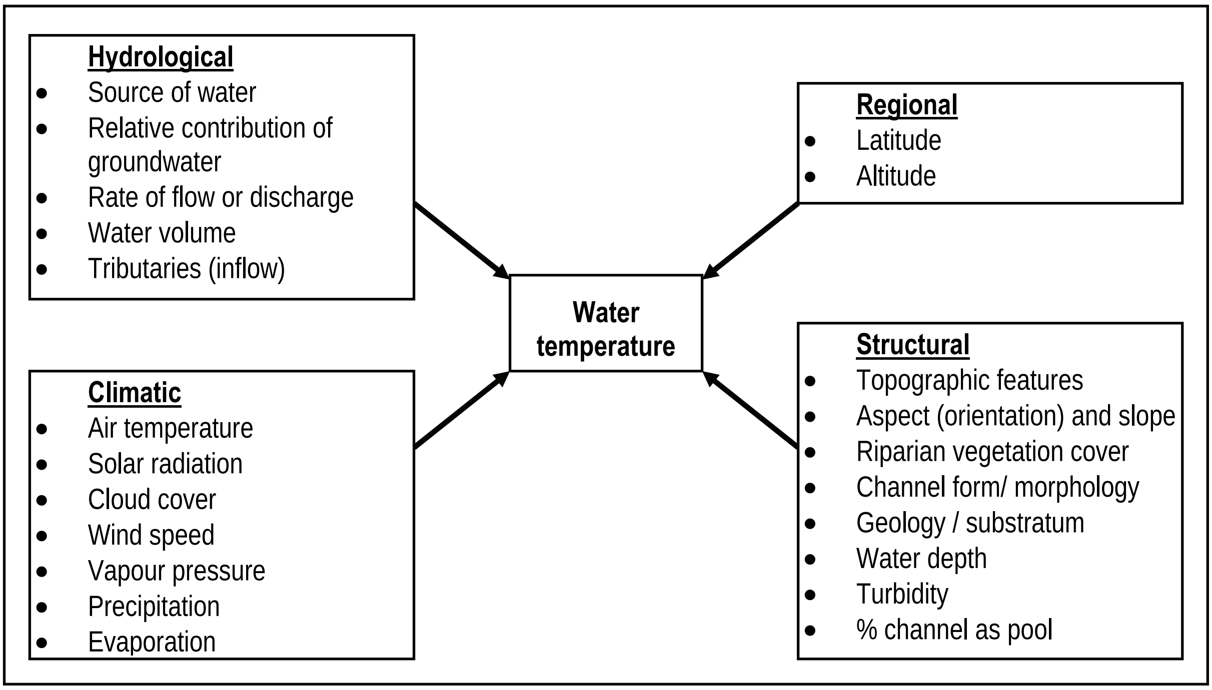

Figure 1.1 Hydrological, regional, climatic and structural factors that influence water temperature

1.1. Spatial variation in water temperature

Water temperature may vary regionally at the catchment scale; longitudinally down a river system; and at a finer scale determined by geomorphic variation, i.e. that of habitat (riffles, pools, backwaters, etc). Differences between river catchments are driven by differences in climate, geography, topography and vegetation between catchments (Poole *et al.,* 2001). The climate of Southern Africa varies from warm water tropical in the north-east to a temperate Mediterranean-type in the south-western Cape. Coastal areas are influenced by the Mozambique-Agulhas ocean current, while highveld regions are moderated by altitude (Skelton, 1993). Summer rainfall is normal for most of Southern Africa except the southern and south-west Cape, where all-year and winter rainfall respectively occurs.

Longitudinal variation often occurs down a river system, with headwaters typically cooler than lowland areas, with maximum temperatures increasing downstream (Ward, 1985); while the maximum range is often found in the middle reaches (Vannote and Sweeney, 1980). In the northern hemisphere a rate of 0.6^{o}Ckm^{-1} has been reported for small streams (Zwieniecki and Newton, 1999) and 0.09^{o}Ckm^{-1} for larger rivers (Torgersen *et al.,* 2001). Two longitudinal zones are often defined, namely the rhithron (cold, highly oxygenated, fast flowing water) and potamon (warmer, slow flowing water), with different aquatic organisms occurring in each zone. Harrison (1965) suggested that using temperature as a major factor for the primary division of rivers into rhithron and potamon zones is generally applicable to lotic systems in southern Africa, although he recommended that summer maxima, and in some cases winter maxima, would be more useful in delineating zones than the range of monthly mean temperature. The temperature difference between headwater sites and lowland sites within a river is often greatest in summer (e.g. King, 1981). The length of the river also influence the diel ranges of water temperature with short rivers exhibiting increases in diel thermal amplitudes for their entire length, whereas long river systems have declining diel ranges in the lower reaches (Ward, 1985).

Water temperature may also vary at the level of reach or site, with variation occurring laterally across the channel and in relation to side-channels and different habitats (e.g. wood snags, off-channel habitats) (Poole *et al.,* 2001). Mosley (1983) noted a 17.7^{o}C range, from 17.2 to 34.9^{o}C, in temperature in a single reach of the Ashley River in New Zealand. This was the result of temperature differences in small side channels, which received seepage of cool underflow from the streambed. Ebersole *et al.* (2003) examined reach scale heterogeneity in water temperature and found that cold water patches were associated with side-channels, alcoves, lateral seeps and floodplain spring brooks. These patches were at least 3^{o}C cooler than ambient water temperature and offered thermal refugia for cold water fishes during periods of thermal stress. Habitats such as riffles may have a different temperature profile from pools (e.g. Nordlie and Arthur, 1981), which may exhibit vertical stratification in relation to water depth (e.g. Elliot, 2000). Variation within a riffle has been reported by Evans and Petts (1997) and linked to downwelling of surface water at the heads of riffles versus upwelling of groundwater at the tail of riffles. Harrison and Elsworth (1958) reported a 10^{o}C gradient in a 2 m deep pool on the Berg River, Western Cape, South Africa. Appleton (1976) observed a 1.9^{o}C difference in temperature of a 1.4 m pool in the Gladdespruit, Mpumalanga, South Africa, and a 0.9^{o}C difference in a 0.70 m pool. Backwaters may attain higher summer maxima than water of the main channel (e.g. Appleton, 1976; Harrison and Elsworth, 1958; Allanson, 1961) and marginal/lateral areas have been reported to have higher temperatures than mid-channel ones (Clark *et al.,* 1999). Studies examining temperature variation at the habitat scale are however relatively scarce. In relation to temporal variation in water temperature, Clark *et al.* (1999) showed that local temperature gradients were smaller than seasonal temperature differences.

1.2. Temporal variation in water temperature

Lotic systems in regions of seasonal climates exhibit diel (daily) and annual (seasonal) temperature periodicity patterns (Ward, 1985). Temporal patterns of thermal change may vary both within and among rivers, and at any given time a river may have different temperatures at different locations. Both daily and seasonal temperatures are relatively predictable for a specific location.

In terms of diel cycles, temperatures are generally lowest during the night time or early morning and highest in the mid to late afternoon, although this may shift slightly with season (e.g. Hopkins, 1971) and size of river, with small streams having maximum daily temperatures earlier due to their shallowness (Vugts, 1974). Small, heavily canopied streams and large, deep rivers exhibit the least diel ranges in water temperature, while shallow streams exposed to direct solar radiation and braided rivers exhibit the largest diel ranges in water temperature (Ward, 1985). Conversely, small streams exposed to intense solar radiation but which have a low discharge may have a diel temperature range that exceeds 10^{o} or 15^{o}C, while the temperature range of a large river may vary only 1^{o} to 2^{o} over the same period (Constantz *et al.,* 1994). As mentioned previously, rivers where groundwater inputs occur, may not exhibit much diel fluctuation in water temperature. The annual (seasonal) cycle is a sinusoidal one, with temperatures highest in the summer and lowest in the winter. The amplitude, as revealed by minimum and maximum daily temperatures, may vary on the basis of regional factors such as altitude and latitude. Variation from one year to another, i.e. inter-annual variation, is less predictable with variation in temperature regimes reflected as “hot-dry” and “cool-wet” years (Poole *et al.,* 2001). Average winter temperatures may vary by 6^{o}C from one year to another (Ward, 1985).

If spatial and temporal variation is combined, three broad spatio-temporal scales may be defined (Gunderson *et al.,* 1995 cited by Rivers-Moore *et al.,* 2004), namely:

- Micro-scale: operating at areas < 10 m^2 (site or reach) and over a time period of hours (diel);
- Meso-scale: operating between 10 m^2 to 10 km^2 (longitudinal) and over a time period of days (seasonal);
- Macro-scale: operating at areas > 10 km^2 (regional) and over a time period of years (inter-annual).

Understanding temporal and spatial trends and variation in water temperature is necessary if the ecological responses of aquatic organisms to changes in water temperature are to be determined. Except for birds and mammals, all organisms associated with fresh water are poikilothermic: i.e. they are unable to control their body temperatures, which are therefore the same as that of the ambient water. Aquatic organisms are very susceptible to changes in water temperature since a 10^{o}C increase results in a doubling of the organism's metabolic rate (Hellawell, 1986). Temperature is recognised as a key environmental variable structuring aquatic invertebrate and fish communities (Arscott *et al.,* 2001) and several studies have shown links between the optimum temperature for the performance of many physiological functions such as growth rate, and the preferred temperature (e.g. Magnuson *et al.,* 1979). It is also considered to be a major factor controlling the distribution of aquatic insects, with the degree of thermal fluctuation being the most important aspect of the thermal pattern (Kamler, 1965 cited by Arscott *et al.,* 2001).

1.3. The importance of water temperature in aquatic ecosystems

The importance of water temperature in aquatic ecosystems, particularly river systems, has been recognised for some time (e.g. Whitney, 1939) and several authors have reviewed the subject (e.g. Smith, 1972; Ward, 1985; Cassie, 2006). Studies from the 1960s to 1980s focused on the effects of thermal pollution resulting from power stations and changes in the thermal regime below impoundments, while more recently (1990s and 2000s) the potential impact of climate change on aquatic ecosystems has been driving research. Studies have broadly focused on reporting and understanding the thermal regime including water temperature modelling; documenting anthropogenic causes of thermal changes and the ecological consequences of these changes; and developing methods for estimating thermal tolerance ranges, via both field experimentation and laboratory studies. In the northern hemisphere (Europe, North America and Japan) the thermal characteristics of lotic habitats have been reasonably well documented (Ward, 1985) and are considered important in influencing life histories of aquatic organisms (e.g. Brittain, 1975; Vannote and Sweeney, 1980; Elliot, 1987a, b).

Thermal data for southern hemisphere rivers is however limited, with most information for Africa and Australia derived from ecological and hydrobiological studies (e.g. Appleton, 1976; Harrison and Elsworth, 1958; Oliff, 1960), with few focused studies on water temperature (e.g. Campbell, 1986;Brittain, 1991; Brittain and Campbell, 1991; Rivers-Moore and Jewett, 2004; Rivers-Moore *et al.,* 2004, 2005). There has been debate on the validity of ecological concepts developed in the northern hemisphere to southern hemisphere rivers (Lake *et al.,* 1985), including those related to the life histories of aquatic organisms, and it has been suggested that environmental variability (including extreme variations in flow) overrides life history features such as synchrony (Hynes and Hynes, 1975; Campbell, 1986; McKie *et al.,* 2004). Several papers dealing with lotic temperatures are available for New Zealand (e.g. Boubee *et al.,* 1991; Quinn *et al.,* 1994; Richardson *et al.,* 1994; Huryn, 1996).

1.4. Rivers versus “non-riverine wetlands”

Rivers and non-riverine wetlands are fundamentally different in terms of water movement as encapsulated in the terms lotic (running water) and lentic (standing water). Factors that modify water temperature may be more or less important in one or other system. For example, water temperature is known to vary down the longitudinal length of a river, whilst large, deep standing water bodies may exhibit thermal (vertical) stratification. Many non-riverine wetlands are shallow and have large surface areas and as a consequence the water column is not particularly stable and the water undergoes continuous or intermittent wind-driven mixing. Temperatures at or near the surface of shallow systems have been shown to respond to changes in solar radiation, water circulation and substrate colour (Dale and Gillespie, 1977), while in deeper systems, including artificially deepened wetlands and the small, relatively deep, highly coloured wetlands, thermal stratification may occur. Thermal stratification leads to de-oxygenation of the bottom layer of water, which is often cooler and rich in nutrients. This review focuses on lotic systems because these systems are subject to flow regulation and water abstraction to a much greater extent than lentic systems.

1.5. South African examples

The following examples provide insight into the spatial and temporal variation of water temperatures in South African rivers.

- Water temperature in the Lang River, a shaded mountain stream in the **Western Cape** (King *et al.,* 1988), varied from 7.5 to 15.1°C with a mean of 10.9°C at one site (altitude = 671 m), and from 7.0 to 20.0°C with a mean of 13.1°C at a second site (altitude = 335 m).
- Water temperature in the Molenaars River, an upper foothill river in the **Western Cape** ranged from 7.9 to 28.4°C with a median temperature of 15.6°C, when data from 9 sites were combined for monthly measurements from August 1991 to February 1993. The maximum in the upper sites was 25.8°C. Summer peaks occurred between mid December to end of February although inter-annual variation was apparent (Unpublished data, GR Ractliffe, Freshwater Research Unit, University of Cape Town)
- Water temperatures, given as the winter minimum to summer maximum range per zone, for the Berg River in the **Western Cape,** were measured in the 1950s (Harrison, 1964). Values per zone (excluding Source zone) were: Mountain Torrent zone (8.9-22.8°C), Foothill, stony run zone (9.0-29°C), Lower foothill, stony run zone (9.0-32.5°C), Foothill, soft-bottom zone (10.0-31.7°C) and the Flood plain zone (9.0-25.5°C).
- The Buffalo River in the **Eastern Cape** had average minimum and maximum temperatures ranges of 12 to 20°C in the Mountain Torrent zone, 15 to 30°C in the Upper Foothill zone and 19 to 35°C in the Lower Foothill zone (Palmer and O'Keeffe, 1989). In winter, the cold waters typical of the upper reaches, extended further downstream.
- Water temperatures (minimum and maximum) in the Umzimvubu (4-28°C), Umzintlava (1-27°C), Kinira (9-28°C), Tina (12-25°C) and Tsitsa (11-23°C) rivers in the **Eastern Cape** (Madikizela and Dye, 2003) were measured seasonally.
- Minimum and maximum daily means measured in each season in the Gladdespruit, **Mpumalanga** (Appleton, 1976) showed that minimum and maximum temperatures ranged from 15.2 to 29.3°C in summer, 12.1 to 21.6°C in autumn, 6.5 to 15.4°C in winter, and 12.2 to 21.1°C in spring.
- Mean and maximum water temperatures (summarised from daily water temperature) increased longitudinally down the Sabie River, **Mpumalanga** (Rivers-Moore *et al.,* 2004), as did variability, with lowland reaches having a greater daily range than upper reaches. Variability varied with season, with greatest variability in winter (June to August). Minimum temperatures remained relatively constant. The average daily water temperatures could be divided into two clusters reflecting longitudinal distance: 0 to 57 km and 57 to 160 km, which coincided with foothill and lowland zones.

- Instantaneous water temperature was measured at many sites in the Vaal Dam catchment, **Free State** (Chutter, 1970). Minimum and maximum temperatures for each zone were: Source zone (5.9 to 27.0°C), Eroding zone (7.0 to 28.8°C), Stable Depositing zone (4.2 to 24.4°C), Unstable Depositing zone (4.5 to 28.2°C) and a High-lying Unstable Depositing zone (4.4 to 30.5°C). Temperatures were lower in the Source zone, but mean temperatures in the remaining zones were relatively uniform. Diurnal ranges measured over two periods showed an April range of 15.0 to 21.6°C and September range of 13.5 to 18.2°C.
- Fluctuations in Vaal River surface water temperature followed a seasonal pattern, marked by rapid warming of the water during September, October and November, and rapid cooling during April, May and June (**Free State**, Roos and Pieterse, 1994). The seasonal extremes were small in comparison to the air temperature fluctuations where monthly average was between -1.1 and 33°C, whilst the difference in water temperature (midday) was between 10 and 27°C. There was a lag of days to several weeks between water and air temperature.
- Studies undertaken in the 1960s and 1970s for many rivers in the **Kwazulu-Natal** region (e.g. Brand *et al.,* 1967; Archibold *et al.,* 1969) reported temperatures ranging from 7.5 to 35°C, with some differences between zones.

2. Measuring water temperature in aquatic ecosystems

2.1. *In situ* measurements

Studies measuring water temperature either record instantaneous measurements at different periods of the day or utilise water temperature loggers which measure temperature on an hourly (or less) frequency. The latter is the more useful from an ecological perspective as it provides detail on the diurnal variation, which is important, and allows for the measurement of extreme temperatures that are likely to be more ecological significant than average temperatures. For example, the presence or absence of a fish species is best predicted by the number of days a site exceeds a critical temperature threshold (Rivers-Moore *et al.,* 2005). Water temperature is routinely measured in many rivers in the United States (e.g. Eaton and Scheller, 1996; Gu *et al.,* 1998; Sullivan *et al.,* 2000), United Kingdom (e.g. Webb and Walling, 1993a; Webb and Walling, 1997; Webb *et al.,* 2003) and Europe. Airborne thermal infrared (TIR) remote sensing has also recently been used in the United States although it is costly and data intensive (Torgensen *et al.,* 2001).

Water temperature has not been routinely measured in South African rivers although spot measurements of water temperature are available for many rivers via the Department of Water Affairs and Forestry. The number of measurements per gauging station varies from one to 2122 readings (A2H027Q01 Pienaars River @ Baviaanspoort), earliest records begin in 1969, frequency of readings varies from weekly to monthly, time of day varies from 07h00 to 17h00 with no consistency at a site, and the duration or length of the record varies from site to site. This allows for some understanding of broad trends in water temperature but does not allow for an understanding of diurnal variation or temperature minimum and maximum values. For example water temperature data from the Molenaars River in the Western Cape (July 1980 to July 1997, weekly measurements), sorted by season and plotted as a function of time of day, provides information on variation of water temperature within and between seasons (Figure 1.2). Mean, minimum and maximum values can be derived for each month (Figure 1.3). Water temperature was not significantly correlated with time of day for any season.

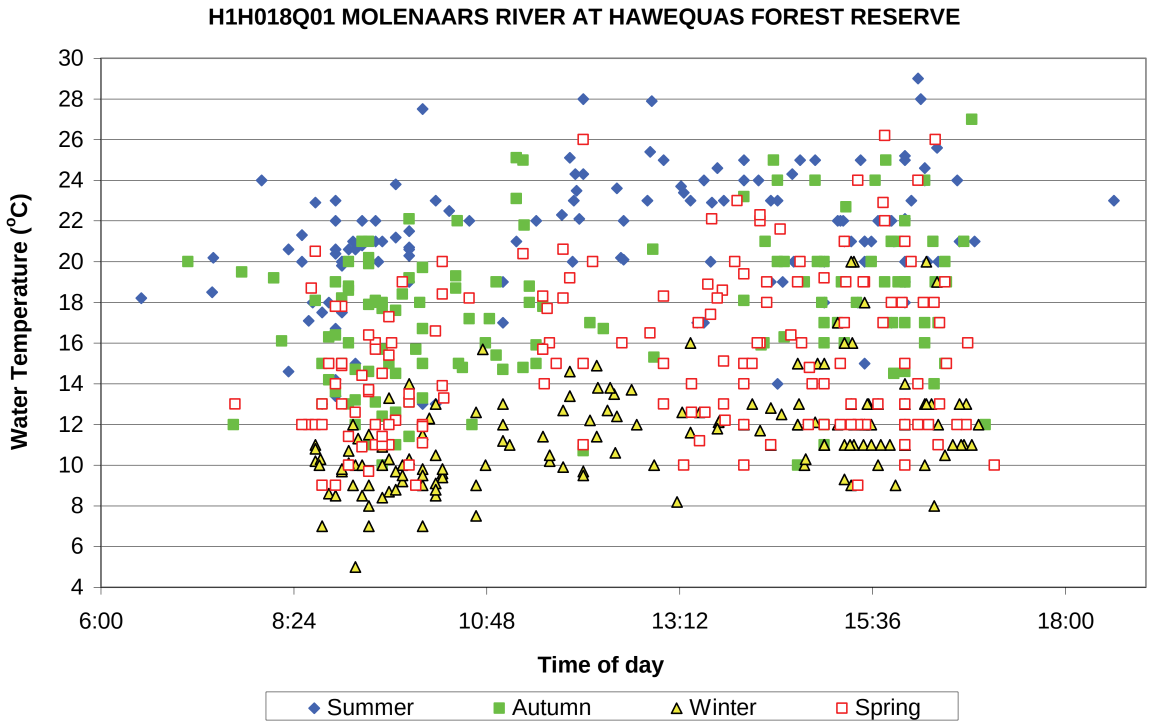

Figure 1.2 **Water temperature recorded in each season plotted as a function of time for a gauging station (H1H018Q01) on the Molenaars River in the Western Cape**

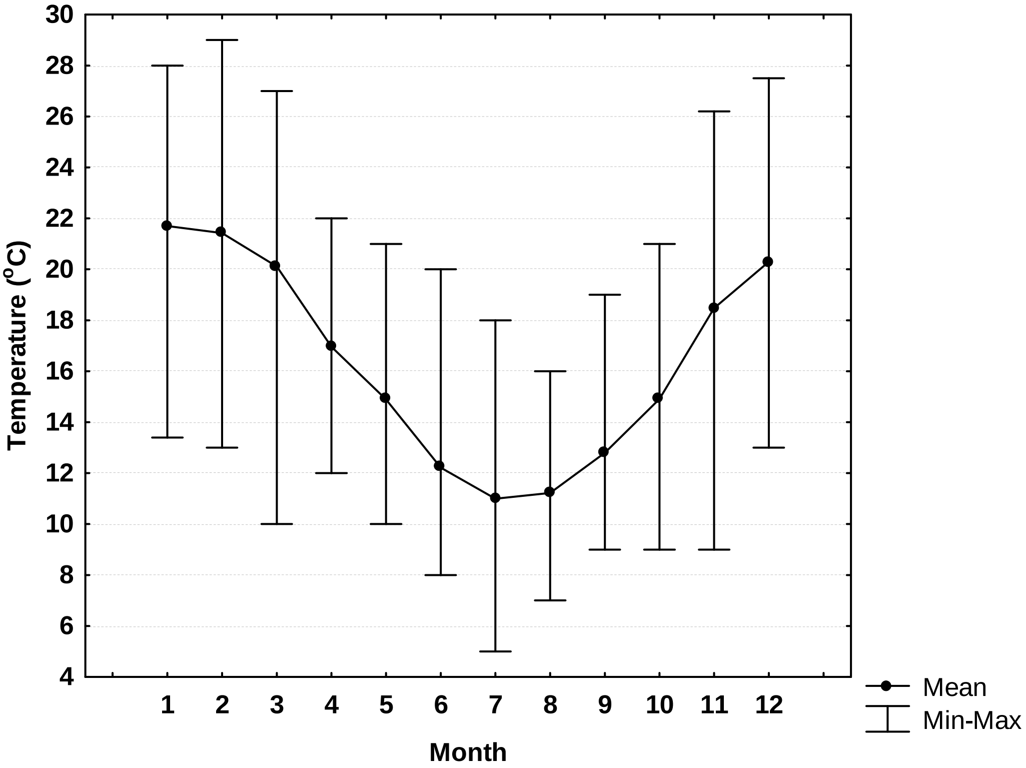

Figure 1.3 **Median, minimum and maximum water temperature recorded in each month and season plotted for a gauging station (H1H018Q01) on the Molenaars River in the Western Cape**

Detailed studies have been undertaken where continuous water temperature was recorded but data are not readily available (e.g. Appleton, 1976). More recently, Rivers-Moore *et al.* (2004) conducted a study to determine the intra-annual thermal patterns in the main rivers of the Sabie catchment in Mpumalanga. Other *ad hoc* studies have generated water temperature data for various upland rivers in the Western Cape (Dallas *et al.,* 1998, and unpublished data), the Salt River in the southern Cape (Rivers-Moore and de Moor, unpublished data), the Great Fish River in the Eastern Cape (Rivers-Moore *et al.,* 2006) and the Mgeni River in Kwazulu Natal (Dickens and Graham, in prep).

2.2. Modelling water temperature

Studies aimed at developing water temperature models are widespread (e.g. Smith, 1981; Mackey and Berrie, 1991) and models are broadly classified into three groups: regression, stochastic and deterministic models (Cassie, 2006). The subject is reviewed extensively by Cassie (2006), and only a brief overview is provided in this review. Further details are also provided in a collaborative project undertaken by Rivers-Moore (in prep.).

Regression models include linear (e.g. Stefan and Preud'homme, 1993; Webb and Nobilis, 1997; Erickson and Stefan, 2000), multiple or logistic (nonlinear, e.g. Mohseni *et al.,* 1998, 1999) models used to describe water temperature. Simple linear models predict water temperature as a function of air temperature (mostly weekly or monthly). Multiple regression models include other factors such as discharge, time lag, etc. Logistic or non-linear models account for groundwater and evaporative cooling and thus the overall water temperature-air temperature relationship often resembles an S-shaped function (Mohseni and Stefan, 1999; Webb *et al.,* 2003). Gardner *et al.* (2003) tested several models to predict instream water temperature from air temperature within the catchment in New York State (USA) and concluded that the strongest model was that based on in-water distances (i.e. along the course of the river).

The use of air temperatures measured at meteorological stations have been successfully used to predict average water temperatures (Palmer and O'Keeffe, 1989) but air temperatures, especially weekly or monthly means, do not provide information on the extremes in water temperature, which is likely to be more important in determining the distribution of aquatic organisms. Inaccuracies also arise with this method when the meteorological station is some distance form the river, if the river is predominantly spring fed, or if the river is impounded (Crisp, 1988). More realistic, but data intensive models are the stochastic and deterministic models, which are more often used when water temperature modelling is carried out for daily time steps (Cassie, 2006). Stochastic models are simpler as they require only air temperature as the input, while deterministic models use all relevant meteorological data to calculate energy components, i.e. deterministic models use an energy budget approach (Stefan and Sinokrot, 1993). Deterministic models such as that of Kim and Chapra, 1997) takes into account hydrodynamics (flow depth and velocity) and heat transport (surface and diffusion in the sediment). The selection of a particular water temperature model depends on the modelling objectives as well as data requirements.

Rivers-Moore *et al.* (2005) tested five different regression water temperature models using maximum daily water temperatures for the Sabie River, Mpumalanga, and concluded that multiple linear regression models were the most pragmatic for simulating ecologically important water temperatures. Water temperature models are able to provide data for use in constructing thermographs for rivers (Rivers-Moore *et al.,* 2005). Two common outputs are duration curves (percentage time versus temperature) and degree curves (hours, days), which facilitate the comparison of sites and quantify cumulative warmth at a site within a season (Essig, 1998 cited by Rivers-Moore *et al.,* 2005), respectively. Cumulative degree days are also useful for relating field results to experimental data (Appleton 1976). Rivers-Moore *et al.* (2005) recommend that the use of air temperatures as a surrogate for water temperatures is a useful tool for aquatic scientists who need to consider the links between the distribution of aquatic biota and water temperatures. Maximum and minimum daily air temperatures are available for over 700 stations (Schultz and Maharaj, 2004), which would enable such models to be developed for South African rivers. Rivers-Moore *et al.* (2005) caution, however, that water temperature in rivers is a complex issue, affected by a range of local and catchment scale factors, and that cognizance needs to be taken of these factors when developing water temperature models. The importance of ensuring that predictions are only made for rivers within the same geographic area, reach and river type is widely recognised.

2.3. Predicting historical or natural temperature regimes

Few data exist that can be used to describe the natural temperature regimes of most rivers (Poole *et al.,* 2001). For this reason it is useful to study the temperature regimes in protected areas such as national parks and other areas where humans have not impacted on the river systems. Establishing spatial and temporal trends in water temperature within geographically similar regions or zones or river types may provide a useful way of understanding natural trends in water temperature, as well as deviation from natural. The concept of "thermal regions" or "thermal types" is an avenue worth exploring as a tool for classifying rivers into homogeneous groups with similar thermal regimes.

3. Anthropogenic factors that modify water temperature

Several factors have been shown to modify water temperature thereby causing a shift in the water temperature distribution, with an increase or decrease in temperature extremes; or a change in temperature variation. Elevated water temperature is more common and widely documented in the literature, although examples for South African rivers are relatively scarce, with the exception of the impact of river regulation on water temperature. The effect of a change in water temperature may be direct, including thermal discharges; or indirect including land use changes, agricultural irrigation return-flows, flow modifications (river regulation), interbasin water transfer, modification to riparian vegetation and global warming. The extent to which each of these thermal modifiers affects river systems in South Africa is not known, but it is likely that all modifiers are present within the country. Certainly, agricultural practices, flow modifications (both regulation and interbasin water transfer) and afforestation are widespread within the country, although the extent of each is likely to vary between regions. For example, many lowland rivers in the Western Cape run through extensive agricultural land, which is likely to affect the thermal regime of the river. In assessing the potential impact of modified thermal regimes for such rivers, the problem arises of how to distinguish between thermal impacts and other impacts (e.g. nutrient enrichment, salinisation), which are often also an issue. More broadly, global warming is of significance for southern Africa and is likely to have consequences for lotic ecosystems and the associated biota, although the severity of the effect may vary with geographic region. The identification of the extent of each thermal modifier within South Africa would provide insight into management of thermal changes in river systems.

3.1. Thermal discharges

The introduction of heated discharges, including heated industrial discharge, heated cooling waters from power stations, returning irrigation waters and groundwater, into a natural water body elevates water temperature in the receiving river.

3.1.1. *Heated power station discharges*

The effect of heated effluent discharged from power stations on aquatic ecosystems is variable and, to some extent, dependent on season (Wellborn and Robinson, 1996) and on the degree to which the heated effluent mixes with the receiving water (Mann, 1965). Several studies have reported a deleterious effect on aquatic biotas (e.g. Mann, 1965; Wellborn and Robinson, 1996). Mann (1965) concluded that the critical aspect of heated discharges was related to the pattern of discharge. The most deleterious effect occurred when a surface layer of heated water covered the whole river, as this "concentrated" the temperature increase and prevented aquatic organisms that periodically surface from doing so comfortably. Other potential patterns included a narrow band of hot water on top of a cold layer (a common pattern in fast-flowing narrow streams) and the complete horizontal mixing of the discharge water with the river water, which would normally result in an overall temperature increase of only a few degrees and hence in a lesser impact.

3.1.2. *Heated industrial discharges*

Heated industrial discharges are frequently linked to other forms of pollution (e.g. chemical pollution). No published studies have isolated the effect of the temperature changes per se, although presumably the effects of elevated temperature would be similar to those of power-station discharges. The toxicity of the associated chemicals may be significantly increased when released in association with elevated temperatures (Duffus, 1980; Förstner and Wittmann, 1981).

3.1.3. *Returning irrigation water*

Water temperatures may increase by 10 to 20^{o}C as a result of irrigation practices and the return of agricultural drainage (Eldridge,1960 cited by McKee and Wolf, 1963). No specific published studies on the consequences for aquatic organisms were noted, presumably because returned irrigation water is not a ’point’ source and thus the effects are difficult to isolate. Furthermore, it is difficult to separate the effects of thermal pollution and other pollution, such as nutrient enrichment and salinisation, often associated with agricultural practices.

3.1.4. *Groundwater*

The thermal regime of groundwater is often different to that of surface water although the difference, either positive or negative, is dependent on the specific geological and sub-surface conditions. In instances where groundwater is utilised as a water source via discharging into a river, the water temperature of the receiving water may be elevated or depressed by the discharge of groundwater into the system. In South Africa, groundwater with a water temperature higher than local surface water is temporarily being discharged into the Klip River in the southern Cape region (Pers. comm. Dr C. Hartnady, Umvoti, Dr B. Harding, DHL Consulting). The implications of such activities are not being recorded, but it is likely that the heated water will alter the aquatic communities downstream of the discharge point.

3.2. Flow modifications

Modifications to the natural flow regime may lead to changes in water temperature. In a natural river, water temperature is inversely related to flow, i.e. water temperature increases as discharge decreases (Hockey *et al.,* 1982; Webb *et al.,* 2003) and the magnitude of diurnal variation is typically inversely proportional to flow rate (Constanz *et al.,* 1994). An alteration in the volume of discharge may affect the thermal capacity of a river and may encourage higher water maxima and lower minima (Webb, 1996; Gu *et al.,* 1998). Thus, decreasing flow is likely to increase daily water temperatures, including daily maxima, due to the lower corresponding depth of flow (Sinokrot and Gulliver, 2000). Daily maximum river temperature was shown to be more sensitive to flow rate than daily mean temperature (Gu and Li, 2002). The effects of low flow conditions in promoting unusually high water temperatures was reported in the 1976 drought in the United Kingdom (Walling & Carter, 1980 cited by Webb and Walling, 1993a). The time lag between daily maximum equilibrium (air) temperature and the daily maximum water temperature is also related to depth or discharge (Gu *et al.,* 1998) and flow depth moderates the amplitude of water temperature variation, i.e. the difference between daily minimum and maximum water temperatures (Gu *et al.,* 1998).

3.2.1. River regulation

The extent to which an upstream impoundment modifies downstream thermal conditions depends on operational variables (release depth, discharge pattern), limnological variables (retention times, stratification pattern and thermal gradients), and the position of the impoundment along the longitudinal profile of the river (Ward and Stanford, 1982; Palmer and O’Keeffe, 1989). In general, river regulation exerts a moderating influence on the downstream thermal regime, including diurnal and seasonal thermal constancy (Ward, 1982). Effects may include an increase in mean water temperature and a reduction in the extent of variability between temperature extremes (Webb and Walling, 1993b, 1997), as well as delayed seasonal temperature maximum (Ward, 1982). Deep-release dams typically result in summer-cool and winter-warm downstream conditions (Pitchford and Visser, 1975), although winter-warming, a phenomenon more often reported for northern hemisphere rivers, does not always occur in southern hemisphere rivers, with water below deep-water releases remaining cooler than the impoundment in winter (Palmer and O’Keeffe, 1989). The withdrawal of deep-water may also lower the thermal stratification of the impoundment by depleting the cool, lower stratum of the thermally stratified impoundment (Coutant, 1987). Thermal recovery distance, i.e. the distance for temperatures to return to expected, natural conditions (pre or above-impoundment), varies with discharge, with larger recovery distances associated with larger flows (Palmer and O’Keeffe, 1989). Impoundments have been shown to modify the downstream biota including changes in community structure of aquatic invertebrates (e.g. Petts and Greenwood, 1985; Storey *et al.,* 1991; Ogbeibu and Oribhabor,

2002) and timing and spatial pattern of fish spawning (e.g. Bok and Heard, 1982; Tomasson *et al.,* 1984; Paller and Saul, 1996; Cambray *et al.,* 1997; King *et al.,* 1998).

South African Examples

Palmiet River, **Western Cape** – five impoundments occur within the first 40 km, mostly irrigation storage, but including a pumped hydro-power scheme. Seasonal shifts (decreased summer and increased winter temperatures) and dampening of temperature variation (increase in constancy) were observed below both the upper-reach Nuweberg Dam and the middle-reach Arieskraal Dam (Byren and Davies 1989).

Olifants River, **Western Cape** – daily maxima and minima water temperature below the Clanwilliam Dam dropped by 8^{o}C and 5^{o}C respectively following hypolimnetic releases in November (King *et al.* 1998).

Buffalo River, **Eastern Cape** – a surface-release impoundment in the upper catchment increased summer maximum temperatures by as much as 8^{o}C (Palmer and O'Keeffe 1989). Subsequent habitat alteration is reported to be the cause of the loss of the endangered minnow, *Barbus trevelyani* (Bok and Heard 1982).

Buffalo River, **Eastern Cape** – bottom-release impoundment in the lower reaches caused reductions in maximum temperatures of 16^{o}C (Palmer and O'Keeffe 1989).

Orange River (Gariep Dam), **Northern Cape** – post-dam water temperature below the dam increased during the winter and decreased during spring and summer (Pitchford and Visser 1975); diel variation was reduced in spring and summer; post-dam temperatures were higher in autumn compared to summer.

Recently, engineers and associated developers responsible for the construction of water storage reservoirs are aware of the importance of maintaining the natural temperature regime below an impoundment, and often make provision for this by designing structures and management regimes that facilitate the ecologically sensitive release of water (e.g. multi-level outflows that mimic natural changes in discharge). For example the Berg River Dam in the Western Cape has "a diversion conduit tunnel through the dam wall that will be used to undertake environmental releases. Up to 200 m^{3} per second of water will be released into the river to stimulate the natural floods during periods of high rainfall. Smaller releases, known as freshets, will be made to maintain the natural flow patterns of the river"(http://www.tcta.co.za/). Many small farm dams (< 250 000 m^{3}) constructed on small tributaries do not however have any of the above control measures and potential temperature impacts may be significant, particularly since they are small and thus heat up rapidly and do not stratify (Davies *et al.,* 1993).

3.2.2. Interbasin water transfer (IBT)

An IBT constitutes "the transfer on water from one geographically distinct river catchment to another, or from one river reach to another" (Davies *et al.,* 1992). For example, a "cold" headwater transfer to a "warmer" mid-reach will have a temperature effect on the recipient river. IBTs have been shown to have an impact on the aquatic organisms of the recipient river, with a shift in composition often occurring. An extensive review of IBTs in internationally is given in Snaddon *et al.* (2000).

South African Examples

Riviersonderend River-Berg River-Eerste River, **Western Cape**: The transfer of water from Theewaterskloof Dam in the Riviersonderend catchment into the cooler upper Berg River altered the biotic communities of the receiving stream (Snaddon and Davies 1998).

Orange River-Teebus tributary-Great Fish River-Sundays River, **Eastern Cape**: The transfer of water from the perennial Orange River to the seasonal Fish River.

Tugela River-Nuwejaarspruit (Vaal) River, **Free State-Kwazulu Natal**: The difference in water temperature between the two systems has prevented the transfer of freshwater host snails for schistosomiasis, *Biomphalaria* sp and *Bulinus* sp.

3.3. Modification to riparian vegetation

Removal of riparian vegetation, which provides shading to a river (riparian vegetation can shade the river by 80%, Beschta and Taylor, 1988) exposes water to increased direct solar radiation. This leads to higher temperatures, particularly during summer low flows, and greater temperature ranges and fluctuations. Canopy-like riparian vegetation is generally more abundant in the upper and more sensitive reaches, where streams are smaller (shallow depths, smaller volumes and flows) and more likely to experience significant temperature changes if the vegetation is removed (e.g. Brown and Krygier, 1967). Open-canopied streams have water temperature regimes where spring and summer temperatures are generally higher (between 0.6 and 6.5^{o}C) than forested streams (natural forest or plantations) (e.g. Graynoth, 1979; Weatherley and Ormerod, 1990; Quinn *et al.,* 1992' Quinn *et al.,* 1997; Rutherford *et al.,* 2004). Conversely, winter temperatures are cooler in open-canopied compared to forested streams and open-canopied streams exhibit greater temperature fluctuations (Graynoth, 1979). Reduction in riparian shading in larger rivers seemed to have less of an effect on water temperature (Quinn *et al.,* 1992). Stefan and Sinokrot (1993), using a deterministic heat transport model, reported a predicted increase of 6^{o}C in water temperature if shade tree vegetation in the riparian zone was removed. Buffers of 5 m have been shown to moderate fluctuations in air temperature (Meleason and Quinn, 2004) and to reduce daily maxima by 3.2^{o}C when compared to open/clearcut sites, while buffers between 9 to 31 m wide have been shown to shade the water in harvested forest streams, thereby preventing increases in water temperature above their normal warming trends (Zwieniecki and Newton, 1999). Removal of riparian vegetation from tributaries has also been shown to lead to an increase in temperature in both the tributary and main channel (Torgersen *et al.,* 1999).

Riparian vegetation affects stream temperature in three ways (Rutherford *et al.,* 1997). It adsorbs some of the incoming radiation (mostly on cloudless days), it emits long-wave radiation (mostly on cloudless nights), and it creates a microclimate (e.g. air temperature, humidity and wind speed), which in turn affects evaporation, conduction, ground temperature and water temperature. Rutherford *et al.* (2004) also found that, while daily maximum temperature was significantly affected by shade, daily minimum water temperatures were not. They attributed this to the fact that daily minimum temperatures are largely determined by air temperature, the exchange of long-wave radiation between the atmosphere and stream at night, and heat conduction from the streambed. Using an estimated maximum thermal tolerance temperature based on local studies (Quinn *et al.,* 1994; Quinn and Hickey, 1990; Richardson *et al.,* 1994), Rutherford *et al.* (1997) developed a stream water temperature model (STREAMLINE) for New Zealand headwater streams aimed at predicting the level of shade required to maintain daily maximum water temperature close below the estimated thermal tolerance level. Their study indicated that moderate shade levels of 70% cover may be sufficient to restore the temperature of headwater pasture streams to 20^{o}C, an estimate of the thermal tolerance for sensitive macroinvertebrates.

Riparian vegetation is not only important from the perspective of shading streams and rivers thereby reducing water temperatures for aquatic biota, but is also important in influencing air temperatures, which affect adult insects (Collier and Smith, 2000). Most aquatic insects have a terrestrial adult phase of several days to two to three months, during which the adults mate and lay their eggs. Air temperatures in forested riparian zones were shown to be within the maximum lethal temperature of adult stoneflies and caddisflies (determined experimentally), while air temperatures in open-canopy sites were close to the lethal limit. Riparian air temperatures are therefore likely to influence aquatic invertebrate communities through the effects on the survival and reproductive success of adults, especially for the more sensitive taxa such as stoneflies and caddisflies that spend lengthy periods in riparian areas as adults (Meleason and Quinn, 2004).

3.4. Climate change and global warming

The major anthropogenic contributions to global warming include the combustion of fossil fuels and biomass, nuclear fission, the burning of forests, and human and animal wastes (NWQMS 2000). Researchers in the United States have predicted that this warming will result in a mean annual increase of between 2 and 5^{o}C in water temperature in rivers of the United States (Mohseni *et al.,* 1999). In South Africa, higher air temperatures are predicted for the entire country, with January air temperatures expected to increase most in the central interior and Northern Cape (2.4 to 4.5^{o}C) and least at the coast (0.5 to 1.0^{o}C) (http://www.sanbi.org/climrep). In general summer rainfall is expected to increase by between 5% in the northern regions to 25% in the Eastern and Southern Cape, while winter rainfall in the Western Cape is predicted to decrease by as much as 25%. The combination of rising air temperatures, combined with decreasing rainfall in some regions, is likely to lead to increased water temperatures, although the extent of the increase has not been modelled.

The consequences of global warming for aquatic ecosystems have been examined in the northern hemisphere with studies conducted on the potential impact of global warming on invertebrates (e.g. Hogg *et al.,* 1995) and fish populations of North America (e.g. Eaton and Scheller, 1996). Experimental results indicate that invertebrate changes in developmental rates, growth rates and emergence times, which are affected by elevated temperatures, may result in changes in community structure and invertebrate density. Hogg *et al.* (1995) concluded that the impact of global warming may depend on the dispersal abilities and population genetics of each species. They suggest that for aerially colonizing species such as the stonefly *Nemoura*, dispersal may offer a potential solution to thermal changes under, for example global warming scenarios, provided an appropriate range of thermal habitats is available for colonization.

Northern hemisphere studies on fish show that higher water temperatures are likely to result in a noticeable reduction in habitat suitable for cold water and cool water species such as salmonids (Eaton and Scheller, 1996; Keleher and Rahel, 1996) and may effectively limit the longitudinal distribution of fish (Meisner, 1990), restrict seasonal migration patterns (Berman and Quinn, 1991) and fragment populations within a catchment by isolating suitable thermal habitats (Keleher and Rahel, 1996; Matthews and Zimmerman, 1990).

Fewer studies have been undertaken on the potential effect of global warming in the southern hemisphere (e.g. Scott and Poynter, 1991). In New Zealand, Scott and Poynter (1991) suggest that winter maxima rather than summer maxima are more likely to affect the distribution of salmonid fish in the future, due to the susceptibility of eggs to elevated water temperatures during the winter incubation period. Further, a 1.5^{o}C increase in water temperature would result in the contraction of fish distribution in northern areas of New Zealand and a 3^{o}C increase would eliminate both brown and rainbow trout from northern areas. The authors, however, recognise that their results are preliminary and recommend that further testing is required before conclusions can be drawn.

No studies have been undertaken in South Africa on the potential impacts of global warming on water temperatures and the distribution of aquatic organisms, although it is likely that similar scenarios may occur as has been shown in the northern hemisphere. The distribution ranges of the more thermally sensitive aquatic organisms, including fish, may be modified, with increasing water temperatures potentially shrinking their distribution. This may have serious consequences for several endemic species of fish, which are already under severe pressure from other factors such as flow modifications, land use changes and the invasion of alien fish species. The Western Cape, which is predicted to have both elevated air temperatures and a 25% reduction in rainfall, also has the highest number of endemic and threatened fish species. This aquatic biota of this region is therefore considered particularly vulnerable to global climate change.

4. Effects of temperature changes on physical and chemical characteristics of water

Temperature exerts a strong influence on many physical and chemical characteristics of water, including the solubility of oxygen and other gases, chemical reaction rates and toxicity, and microbial activity, including the presence or absence of pathogens.

4.1. Solubility of dissolved oxygen and other gases

Higher temperatures reduce the solubility of dissolved oxygen in water, decreasing its concentration and thus its availability to aquatic organisms. Dissolved oxygen minima were negatively correlated with water temperature maxima in summer (Wilcock *et al.,* 1998). If the organic loading is high, oxygen depletion is further accelerated by greater microbial activity at the higher temperature. A recent fish kill in Rietvlei, Western Cape, highlighted the deleterious combination of low dissolved oxygen concentrations (< 3.5 mgl^{-1}) and high water temperatures ($>27^{o}$C) in an organically loaded system (pers. obs, H.Dallas). The effect of low dissolved oxygen concentrations on aquatic organisms has been studied extensively (e.g. Nebeker *et al.,* 1996). At dissolved oxygen concentrations below 4.6 mgl^{-1} egg hatching, larval development, moulting success, pupation, and adult emergence were all delayed (Trichoptera, *Clistoronia magnifica*, Nebeker *et al.,* 1996). Invertebrates differ greatly in their tolerance of low dissolved oxygen conditions and hypoxia (Kolar and Rahel, 1993). Dissolved oxygen concentrations and temperature have also been shown to influence predator-prey relationships (e.g. Cockrell, 1984) and modify prey behaviour in some species (e.g. Kolar and Rahel, 1993).

4.2. Chemical reaction rates and toxicity

Chemical reaction rates and the toxicity of many substances (e.g. cyanide, zinc, phenol, xylene), and the vulnerability of organisms to these toxins, is intensified as temperature increases (Duffus, 1980).

4.3. Microbial activity and reactions

Microbial activity, e.g. growth of sewage fungus, is accelerated at higher temperatures. This reduces the environmental quality of the water as well as affecting its suitability as drinking water and aesthetic values for recreation. Temperature also influences enzyme-dependent microbial processes such as photosynthesis, N_2 fixation, denitrification, respiration and methanogenesis (NWQMS 2000).

5. Biological effects of temperature changes on aquatic organisms and ecosystems

Temperature effects may be evident at the individual level through physiological and behavioural effects; the population level through development of the individuals, fecundity and survival; and the community level by favouring temperature tolerant taxa over temperature intolerant ones leading to a shift in community structure (Mitchell, 1999). All organisms have a range of temperatures at which optimal growth (adult size), reproduction and general fitness occur. This is often termed the “optimum thermal regime” (Vannote and Sweeney, 1980). Temperature outside of the “optimum thermal regime” may effect the geographical distribution and community structure, growth, metabolism, food and feeding habits, reproduction and life histories, movements and migrations, behaviour; and tolerance to parasites, diseases and pollution; of aquatic organisms. There is some debate on the validity of Vannote and Sweeney’s (1980) “Thermal Equilibrium Hypothesis” for southern hemisphere rivers. The Thermal Equilibrium Hypothesis ascribes a dominant role to temperature in maintaining niche differentiation in lotic assemblages and regulating large-scale patterns of species diversity and distribution (McKie *et al.,* 2004). Specifically, it is suggested that this hypothesis in its current form may not be relevant for Australia and other regions of the world where lotic environmental regimes (temperature and flow) are less predictable (McKie *et al.,* 2004). South Africa is one such region.

Langford (1990) broadly categorized aquatic organisms as:

- Cold stenotherms: those organisms with narrow tolerance ranges in cold (arctic) regions
- Warm stenotherms: those organisms with narrow tolerance ranges in warm regions in the tropics
- Eurytherms: those species with wide tolerance ranges, e.g. in temperate or sub-tropical regions. This category may be further sub-divided with respect to distributions within any region, for example, stenotherms restricted to cold mountain stream zones.

In the northern hemisphere different species of fish have been shown to have different thermal niches, with groups of fish species forming three main thermal guilds – warm water, cool water and coldwater (Coutant, 1987; Magnuson *et al.,* 1979). Studies in the southern hemisphere are however limited with some studies (e.g. Richardson *et al.,* 1994, New Zealand) showing that fish species are able to thrive in a wide temperature range. South African freshwater fish are broadly categorized into temperate and tropical fauna, with temperate fauna restricted to areas where the maximum water temperatures are generally below 25 to 28^{o}C during the summer months (Skelton, 1993). Tropical fauna is restricted to areas where the water temperatures do not decline below 15 to 18^{o}C during the cooler winter months (Skelton, 1993).

5.1. Primary production

Temperature regulates ecosystem functioning directly by influencing primary production. Primary producers include phytoplankton (in open water), macrophytes (macroscopic plants, which may be submerged or emergent, rooted or floating) and periphyton (growing on submerged substrates) (Likens, 1973). Studies have shown that primary production generally increases with temperature (e.g. Quinn *et al.,* 1992; Kishi *et al.,* 2005). DeNicola (1996) summarised the response of periphyton to temperature as follows:

- As temperature increases, there is a shift in the dominance of algal classes from diatoms (<20°C) to green algae (15-30°C) to blue-green algae (>30°C).
- Species diversity increases from 0-25°C and decreases at temperatures >30°C.
- The degree to which community composition changes with thermal input depends on the initial ambient temperature. Increases in temperature in environments near 25-30°C usually cause greater changes in community structure than in environments <25°C.
- Community structure usually recovers rapidly (<1 yr) when temperature stress is discontinued.
- Biomass increases with temperature from approximately 0-30°C and decreases at 30-40°C.
- In many natural communities, temperature does not usually limit biomass and primary productivity, but it does set an upper limit for production when other factors are optimal. Maximum areal productivity of lotic periphyton increases exponentially with temperature for temperatures <30°C.
- The degree to which primary productivity is limited by factors such as light, nutrients, and grazing depends on temperature.

In South Africa, a Water Research Commission funded study, which is due to begin during 2007, is going to be addressing various aspects related to primary production in South African rivers (pers. Comm., J. Ewart-Smith, Freshwater Research Unit, University of Cape Town).

5.2. Geographical distribution and community structure

Water temperature strongly influences the geographic distribution of a species (Hart, 1985; Bell, 2006) and changes in water temperature may lead to changes in the abundance, density, biomass, diversity and composition of aquatic communities. In the northern hemisphere, water temperature variability has been positively correlated with species diversity (Vannote *et al.,* 1980) and the maximum temperature reached during the summer is thought to limit the occurrence of certain species (Vannote and Sweeney, 1980). Hawkins *et al.* (1997) also consider summer to be a critical season for many aquatic insect populations in that much of the biological production occurs when temperatures are highest. Various studies have shown a reduction in macroinvertebrate abundance and diversity following an average temperature increase of around 7^{o}C (Coutant, 1962 cited by Mann, 1965; Wellborn and Robinson, 1996; Hogg *et al.,* 1995). Wellborn and Robinson (1996) noted that effects were most pronounced in summer when temperatures of 40-42^{o}C eliminated macroinvertebrates and large blooms of blue-green algae occurred. As stenothermal species (organisms adapted to a very narrow range of temperatures) disappear from heated waters, heat-tolerant species increase in number and replace the original species in the ecosystem (Reid and Wood, 1976). Not all studies have shown a definite change in response to elevated water temperature indicating that effects are not always clear-cut and that local conditions affect the resultant communities (e.g. Langford and Aston, 1972).

5.3. Trophic interactions

Trophic interactions such as predation may be modified by water temperature (e.g. Kishi *et al., 2005*). Kishi *et al.* (2005), in a laboratory experiment, showed that the survival rate of caddisfly larvae was greatly reduced at intermediate water temperatures (9 to 12^{o}C), compared to colder (3 to 6 ^{o}C) or warmer (18 to 21^{o}C) temperatures. The low grazer abundance combined with high periphyton productivity resulted in a large periphyton biomass at 12^{o}C. This highlights the potential for trophic cascading effects resulting from changes in water temperature. The results of Kishi *et al.* (2005) provide evidence that thermal habitat alteration may affect not only thermally sensitive species like fish, but also resistant species like caddisfly larvae and periphyton via indirect effects in food webs. Quinn *et al.* (1992) also showed how changes in algal periphyton abundance and invertebrate community structure were linked to increasing light and water temperature, with certain taxa increasing in response to thicker algal mats, while other taxa, which favoured low periphyton abundance, decreased.

5.4. Metabolic rate

Aquatic organisms are very susceptible to changes in water temperature since a 10^{o}C increase results in a doubling of the organism's metabolic rate (Hellawell, 1986). The increased respiration and oxygen demand combined with reduced supply results in significant stress to aquatic organisms, which are poikilothermic and thus unable to control their body temperatures. Metabolic rate has been shown to increase in spring in the burrowing mayfly, *Ephemera simulans*, with an increase from 0.23 mg.g^{-1}h^{-1} in winter to 0.37 mg.g^{-1}h^{-1} in spring in the northern hemisphere (Eriksen, 1964). It is suggested that this is linked to a surge in growth and gonad development. The metabolic rate of fish has been shown to increase with increasing temperatures (Cech *et al.,* 1990). Increasing temperature within a species range of thermal tolerance accelerated basal metabolism, however the form of the relationship varied between a concave and convex curve (Beamish, 1981). Mortality in fish from acute exposure to elevated temperatures is often the result of metabolic malfunctions (including fluid-electrolyte imbalance, alterations in gaseous exchange and osmoregulation, hypoxia of the central nervous system and inactivation of enzyme systems) (Cherry and Cairns, 1982). Cech *et al.* (1990) concluded that temperature (specifically the effect on metabolic rate) and dissolved oxygen (specifically the metabolic responses to hypoxia – low dissolved oxygen concentration), play a major role in determining the distribution of fish in streams of the Mediterranean region (California) of the United States.

5.5. Growth rate

The growth of aquatic insects has been shown to be strongly correlated with temperature in several species including mayflies, *Ephemerella dorothea* (Markarian, 1980), *Diplectrona modesta* (Markarian, 1980), *Deleatidium* sp. (Huryn, 1996); stoneflies, *Leuctra ferruginea* (Harper, 1973); and isopods, *Asellus* spp. (Thorup, 1973). Ambient water temperature during larval growth has been inversely related to adult body size (*E. dorothea*, Vannote and Sweeney, 1980). Some species exhibit temperature thresholds for growth (e.g. Lavery and Costa, 1976), with zero growth occurring until a particular temperature threshold has been passed. Growth is often correlated with degree-days, which accounts for time and the minimum temperatures necessary for growth, and is a summation of mean daily water temperature above a critical point (e.g. Hart, 1985; Markarian, 1980). Species that have extended emergence patterns such as the stonefly, *Nemoura wui*, and the mayfly, *Paraleptophlebia assimilis*, were not suited to field studies aimed at measuring growth (Markarian, 1980).

Water temperature is considered to be the most important environmental factors affecting fish growth (Wootton, 1998 cited by Nicola and Almodovar, 2004; Marine and Cech, 2004), with growth occurring within a limited thermal range and the temperature regime determining the length of the growth season. Growth rate may vary with age, with ontogenetic shifts in thermal niches occurring as fish age (Coutant, 1987; Richardson *et al.,* 1994). For example, juvenile striped bass grow best and prefer temperatures near 24 to 26^{o}C, while larger fish select progressively cooler temperatures (Coutant, 1980 cited by Coutant, 1987). Temperatures for optimal growth rates in both aquatic insects and fish may however be suboptimal for growth efficiency, emergence success or adult longevity (Heiman and Wright, 1975).

Growth rates in aquatic invertebrates has rarely been studied in South Africa (e.g. Hart, 2001), while studies on fish are mostly on fish living in impoundments or natural lakes (e.g. Bruton and Allanson, 1974; Hecht,1980) and rarely in rivers (e.g. Baird, 1976). King (1981) and King *et al.* (1988) suggest that the aquatic invertebrates in mountain streams of the Western Cape, South Africa, have extremely slow growth rates due to the oligotrophic water.

5.6. Food and feeding habits

Temperature may influence the rate of feeding of invertebrates and fish. Kishi *et al.* (2005), in a laboratory experiment undertaken on a predatory salmonid fish and grazing caddisfly larvae of the family Glossosomatidae, showed that feeding rates varied significantly between temperatures, with highest feeding rates at intermediate temperatures (9 to 12°C). This coincided with the mean summer temperature in forested stream of Hokkaido, Japan, where the experiment was undertaken. There appears to be a temperature threshold for some fish species below which they stopped feeding or only fed sporadically (Keast, 1968 cited by Mohseni *et al.,* 1998).

5.7. Reproduction, development rates and life histories

Terminology around life histories varies considerably and for clarity key terms are defined using definitions given by Lake *et al.* (1985):

- Cohort – used to designate a group of animals hatching from eggs at a single time
- Generation – refers to the growth period from egg to adult
- Voltinism – the number of generations per year for a particular species; bivoltine = two generations per year, univoltine = one generation per year; multivoltine or polyvoltine = several generations per year; and semivoltine = one generation per two years. Univoltine species are characteristic of predictable environments whereas multivoltine species characterise unpredictable environments.
- Synchrony – is determined by the degree of size and developmental variation within a cohort; a highly synchronous life history is one where all members of the cohort are identical in size or developmental state, whereas an asynchronous life history is one in which a complete range of sizes and developmental stages are present in unvarying proportions all of the time.
- Precision – refers to the period of emergence or appearance of adult forms; usually synchronous species have a precise emergence period, while asynchronous species have long emergence periods.
- Rigidity – describes the temporal variability in the emergence period from one year to another with a highly rigid life history being one with low temporal variability between years, i.e. adults of a species emerge at the same time (month) of year each year.
- Flexibility – describes variability in immature growth patterns of cohorts with time (temporal flexibility) and between sites (spatial flexibility).

Clifford (1973 cited by Campbell, 1986) suggested that life history synchrony decreased towards the equator, i.e. with latitude, with univoltine life cycles dominant in the arctic and cold temperate regions, and growth restricted or completed within one part of the year. In moderate temperate regions univoltine life cycles dominate and growth is throughout the year, while in the tropics multivoltine life cycles dominate. In high latitudes of the northern hemisphere, reproduction, development rates and life histories are largely synchronous and strongly seasonal (e.g. Coleman and Hynes, 1970; Brittain, 1975; Sweeney and Vannote, 1980; Macan, 1981). Short emergence periods are common (e.g. Coleman and Hynes, 1970) and the degree of synchrony in the development of nymphs (e.g. Macanm 1981) enables several species in the same genus to co-exist, thereby facilitating resource partitioning. In contrast, in lower latitudes of the northern hemisphere, emergence is longer and life cycles are less seasonal (e.g. Berner, 1950 cited by Campbell, 1986). These differences were attributed to climatic differences, primarily higher water temperatures at the lower latitudes. Flexibility in the number of generations per year has also been noted as a response to thermal differences between habitats at different latitudes or altitudes (Ward and Stanford, 1982). For example, Macan and Maudsley (1966 cited by Ward and Stanford, 1982) observed an extra generation in the mayfly, *Cloeon dipterum,* during especially warm summer. Wrenn *et al.* (1979 cited by Nordlie and Arthur, 1981) found an increased potential for additional generations of *Caenis* mayflies in channels with water temperatures elevated 4-6°C above ambient. The stonefly, *Leuctra nigra*, which prefers cool water of <14°C, changed from semivoltine to univoltine when water temperature increased, although there are costs involved, specifically survival and egg production (Elliot, 1987b).

In the southern hemisphere, Huryn (1996) also reported latitudinal differences in life cycle synchrony for the mayfly, *Deleatidium lillii*, with North Island, New Zealand (36°S) populations exhibiting a seasonal univoltine winter cycle, with mature larvae present from April to September (austral autumn-spring) and synchronous development, while the same species from South Island (45°S) exhibiting a bivoltine cycle, with continuous presence of mature larvae with no pause in development and emergence from October to May (austral spring-autumn). It is suggested that these differences are linked to differences in thermal maxima during summer between the two locations (Huryn, 1996). In the southern hemisphere, Campbell (1986), Hynes and Hynes (1975), McKie *et al.* (2004) and others have suggested that life cycles of aquatic insects are less rigid and more flexible than those found in the northern hemisphere, and are largely asynchronous with continuous growth and long emergence periods, although there is considerable variation in life histories (Lake *et al.,* 1985; Campbell, 1986; Huryn, 1996). In the Australian tropics, all chironomid species studied (Cranston, 2000 cited by McKie *et al.,* 2004) were multivoltine with year-round emergence. The flexible life cycles are considered an adaptation to the unpredictable and highly variable climate in Australia (Hynes and Hynes, 1975).

Studies in South Africa are scarce, with information inferred from more generalist studies such as King (1981), King *et al.* (1988) undertaken in the Western Cape, rather than from specific life history studies. Hart (1985) reviewed the seasonality of aquatic invertebrates in low-latitude and southern hemisphere inland waters. He noted that life histories of southern hemisphere river fauna appear seasonally flexible and opportunistic by contrast with the apparently synchronous cycles exhibited by north temperate representatives. In the Western Cape, King *et al.* (1988) observed that abundance peaked in spring and late summer, while juvenile recruitment peaked in spring (November). The ‘winter’ communities whose life cycles began in winter, appeared almost simultaneously with the winter rains, and predictable seasonal changes occurred at the same time each year (King, 1981). In addition, many species emerged in summer, possibly to avoid high temperatures.

Temperature appears to be a determinant of synchrony of life history (Lake *et al.,* 1985), although further work is needed over a wider latitudinal range to confirm this. Without a basic understanding of synchrony it is impossible to determine the likely effects of a modified temperature regime on reproduction, development rates and life histories, since effects may be moderated by the extent to which life histories are synchronised and seasonal. False temperature cues caused by modified temperature regimes may affect the timing of life history stages such as reproductive periods, rates of development and emergence times – thereby interfering with normal development.

5.7.1. Eggs and fecundity

There is a linear relationship between egg production (fecundity) in aquatic insects and adult female body size, thus any factors affecting fecundity will affect recruitment and the competitive ability of the subpopulation (Vannote and Sweeney, 1980). Temperature may influence breeding, egg incubation period (e.g. Elliot, 1972; 1987a; Harper, 1973; Humpesch, 1980; Weatherley and Ormerod, 1990; Brittain, 1991), hatching success and duration (Elliot, 1972), and the induction and termination of diapause (Ward and Stanford, 1982) and it is often the reproductive stages that are most sensitive to thermal disruption (NWQMS 2000). Egg development times of mayflies (Brittain and Campbell, 1991) and stoneflies (Brittain, 1991) in Australia showed that the distribution of a common upland genus may be influenced by low winter water temperatures, since the eggs fail to develop below 5°C. Elliot (1972) noted a strong negative relationship between water temperature and number of days for eggs of *Baetis rhodani* to hatch, with variation from 17 weeks for hatching at 3^{o}C and 1 week at 22^{o}C. Diapause, as a response to avoid warm periods, is especially common in stream insects (Harper and Hynes, 1970) and preadapts them to survive drought and colonise temporary waters (Ward and Stanford, 1982).

The temperature in the hyporheos may also influence incubation period of, for example, salmonid and invertebrate eggs, with incubation period shortened by 10 to 11 days when eggs were incubated 20cm in the gravel (Crisp, 1990). This occurred since temperatures in the gravel were different from water temperature, with higher temperatures in winter, lower temperatures in summer, and less diel variation throughout (Evans and Petts, 1997).

5.7.2. Emergence

Many organisms are adapted so that seasonal changes in temperature act as cues for the timing of emergence. The timing and duration of emergence in aquatic insects involves responses to temperature, often interacting with photoperiod and dissolved oxygen (Nebeker, 1971a, b, c, 1972); and in the northern hemisphere, emergence is reported to occur earlier at lower latitudes and altitudes (Nebeker, 1971b) and in warmer years (Ward and Stanford, 1982). In the northern hemisphere several aquatic insects complete their development during winter and await spring temperature increases to initiate emergence (Nebeker, 1971c). Experimental studies in which water temperature was artificially elevated documented the early emergence of insects including hydropsychids caddisflies (elevated by 1°C), chironomids and damselflies (elevated by 10°C, Nordlie and Arthur, 1981), and stoneflies, mayflies (Vannote and Sweeney, 1980), stoneflies (Nebeker, 1971a), caddisflies, chironomids and simuliids (Nebeker, 1971c). Accelerated development and early emergence of insects into an environment unsuited to their existence (lack of food, ambient air temperature too low for emerging adults to survive, etc.) may compromise the survival rate of the adult insects (NWQMS 2000, Ward, 1982). Southern hemisphere studies (e.g. Campbell, 1986) suggest that emergence pattern may be les synchronous (see earlier discussion). Information on emergence in South African aquatic invertebrates, in particular the timing of emergence and the cues required to stimulate emergence, is extremely scarce and largely inferred from field observations (e.g. King, 1981).

5.7.3. Spawning

Temperature, photoperiod, water level or flooding, intra-specific interactions and the presence of suitable spawning substrates are important stimuli that trigger gonadal development and spawning (Lake, 1967; Jones *et al.,* 1978 cited by Paller and Saul, 1996). Water currents, salinities and food availability may also influence spawning (Langford, 1990). Fish tend to spawn during the warmest months of year, partly because rates of egg, embryo and larval development are positively correlated with temperature, and partly because it the time of year in temperate systems when food for larvae and juveniles is most abundant (Jobling, 1995 cited by Humphries *et al.,* 1999; Humphries *et al.,* 1999). The developmental biology of fish has been extensively studied in North America (e.g. Jones *et al.,* 1978 cited by Paller and Saul, 1996) and Europe, where data on the temperature ranges for spawning and temperatures for embryonic development of many fishes have been compiled (Alabaster and Lloyd, 1980). In the northern hemisphere several fish species spawn within 3 to 5°C of their critical thermal maximum.

A few studies have examined the reproductive biology, including spawning, of fishes in South Africa and studies have shown that temperature is an important factor triggering spawning. The importance of temperatures between 18 and 19°C for triggering spawning of several of South Africa's native fish species has been widely reported (e.g. Groenewald, 1951 cited by Tomasson *et al.,* 1984; Wright and Coke, 1975 cited by Tomasson *et al.,* 1984; Bok and Heard, 1982; Tomasson *et al.,* 1984; Cambray *et al.,* 1997; King *et al.,* 1998). River regulation has been shown to modify the timing and spatial pattern of spawning (e.g. Tomasson *et al.,* 1984; Paller and Saul, 1996; King *et al.,* 1998). Reduced water temperatures resulting from a hypolimnetic discharge delayed spawning in direct proportion to the proximity to the dam (Paller and Saul; 1996) as shown by the occurrence of fish larvae along a longitudinal temperature gradient. Maximum densities of larvae occurred at 19^{o}C, although actual egg deposition probably occurred at slightly lower temperatures since there is a time lag of 3 to 8 days between egg deposition and the appearance of the early larvae (Paller and Saul, 1996). Epilimnetic releases resulted in early spawning, while unseasonal hypolimnetic releases resulted in poor reproductive success of *Barbus holubi,* an indigenous cyprinid in Southern Africa (Tomasson *et al.,* 1984).

A study currently underway (funded by the Water Research Commission) has focussed on two fish species endemic to the Olifants and Doring Rivers of the Western Cape (B. Paxton, Freshwater Research Unit, University of Cape Town), the Clanwilliam yellowfish, *Labeobarbus capensis*, and the sawfin, *Barbus serra*. These species are at high risk of extinction due to habitat modification by dams and water abstraction. Data on the seasonal distribution patterns, spawning and early life history has been collected for these two species. A follow-on study aims to investigate further aspects related to spawning including the duration and frequency of seasonal spawning, the optimal flow and temperature conditions required, and to test the specific environmental stimuli required to cue spawning events (pers. comm., B. Paxton).

South African examples

Barbus capensis (Clanwilliam yellowfish), **Western Cape**, ascend rivers and spawn in gravel beds in relatively shallow water (Hey 1947 cited by Cambray *et al.* 1997). Upstream migration occur between September and December (Harrison 1950 cited by Cambray *et al.* 1997), while gonad mass increases in August and September, reaches a maximum between October and December, and decreases in January (Van Rensburg 1966 cited by Cambray *et al.* 1997). Dam releases of high-flow freshes from the Clanwilliam Dam on the Olifants River in spring (October to November) corresponded with successful spawning (Cambray *et al.* 1997). This was linked to favourable water temperatures, with a general spring increase in water temperature. Temperature at the spawning beds was between 19.1 and 23.1^{o}C. In contrast, lower temperatures the following year due to late cold weather, resulted in spawning bed temperatures between 16.6 to 17.5 ^{o}C. No spawning occurred during this period (King *et al.* 1998). A thermal spawning threshold of 19 ^{o}C is proposed (King *et al.* 1998). Various aspects related to seasonality, spawning and life history are currently being investigated (B. Paxton, Freshwater Research Unit, University of Cape Town (see previous discussion).

Labeo umbratus migrate upstream and spawn on the floodplain (Jackson and Coetzee 1982); this has been observed in heavy floods in summer in the Gouritz River system, **Western Cape** (Hamman and Thorne 1982 cited by Tomasson *et al.* 1984); larvae hatched after 30 hours at 22^{o}C (Mulder 1971 cited by Tomasson *et al.* 1984).

Oreochromus mossambicus usually spawn in late November when minimum water temperatures exceeded 18 ^{o}C (**Eastern Cape**, James and Bruton 1992).

Barbus trevelyani (Border barb) requires a minimum water temperature of 18^{o}C for successful induced spawning (**Eastern Cape,** Bok and Heard 1982).

South African examples

Tomasson *et al.* (1984) studied the reproductive biology of four indigenous cyprinids, *Barbus holubi* (smallmouth yellowfish), *Barbus kimberleyensis* (largemouth yellowfish), *Labeo capensis* (Orange River labeo) and *Labeo umbratus* (moggel), in the Le Roux Dam on the Orange River, **Northern Cape**. Although they studied the fish populations in the man-made lake, spawning was observed in the natural riverine section of the lake. Large *Barbus* spawn on gravel beds within the river channel in spring or summer, with *B. kimberleyensis* spawning four to six weeks before the more cold-tolerant, *B. holubi*. Spawning in the regulated section of the dam was governed by water temperature and influenced by the effect of the hydrological regime on water temperatures, with spawning earlier when temperatures were warmer due to leases of epilimnetic water from the upstream Gariep Dam. Unseasonal hypolimnetic releases from the Gariep Dam, however, resulted in poor reproductive success. In contrast to *Barbus*, *Labeo* species spawned on newly flooded ground, and spawning was asynchronous with local conditions triggering, possibly localised flooding due to localised rain. *L. capensis* bred throughout the lake and did not exhibit a longitudinal migration, while *L. umbratus* uses larger inflowing tributaries for spawning. Elsewhere on the upper Orange River *B.holubi* migrate upstream during the first spring floods and spawn over gravel beds within the river (Shortt-Smith 1963 cited by Tomasson *et al.* 1984). Breeding behaviour of *B. holubi* was observed when water temperatures exceeded 18^{o}C (Groenewald 1951 cited by Tomasson *et al.* 1984) and fertilized eggs of *B. halubi* incubated for three to eight days at 18 to 21.5^{o}C (le Roux 1968, Mulder and Franke 1973 cited by Tomasson et al. 1984).

Barbus natalensis migrate upstream to spawn and are unable to breed in still water (**Kwazulu Natal,** Crass 1964 cited by Tomasson *et al.* 1984); they spawn in clean well, circulated gravel in fast flowing water when water temperature exceeds 19^{o}C (Wright and Coke 1975 cited by Tomasson *et al.* 1984).

Oreodaimon quathlambae (Maluti minnow) is limited to the extreme upper area of the 2 300 km Orange River system. Adult's spawn in mid-channel amongst boulders (**Lesotho**, Cambray and Meyer 1988). Eggs are laid in mid-channel which is oxygen-rich, and after a swim-up stage fish are carried by the current to backwaters where they feed, and move without being washed away.

5.8. Movements and migrations

Aquatic organisms, particularly fish, are known to utilise thermal refugia and often thermoregulate by migrating to areas of cooler water when surrounding water temperatures are outside of their preferred range or exceed their upper tolerances (e.g. Torgensen *et al.,* 1999; Elliot, 2000; Ebersole *et al.,* 2001; Gardner *et al.,* 2003). Almost all studies on movement and migration are for fish and no studies were found for invertebrates. Fish possess acute temperature discrimination powers and use behaviour to avoid or rapidly escape thermally hostile areas, if thermally favourable environments are available (Beitinger *et al.,* 2000). The habitat occupied by a particular species (or age class) in the field has been shown to change seasonally and even daily in response to the location of preferred temperatures (Coutant, 1987). Thermal refugia protect biotic communities from extreme thermal disturbances and are most numerous in intact riverine systems with riparian vegetation and groundwater (Torgensen *et al.,* 1999). Undercut banks and overhanging vegetation also increase the availability of less thermally stressful habitats (Bell, 2006). Coldwater patches were normally associated with lateral seeps, cold side-channels, floodplain tail seeps, floodplain seeps and stratified pools (Mosley, 1983; Ebersole *et al.,* 2001). These patches may be 3 to 10^{o}C lower than instream temperatures.

Thermal conditions may override other factors such as food availability, water quality (dissolved oxygen concentration) and risk of predation; with fish migrating to cooler water even when other conditions are compromised. For example, extreme summer temperatures that are near an organism's upper tolerance limits may force individuals to seek cooler refuges in headwater areas that exhibit a lower capability for food and shelter when compared to the more productive downstream reaches (Vannote *et al.,* 1980). High water temperatures may thus limit the longitudinal distribution of fish within rivers (Meisner, 1990) and restrict seasonal migration patterns (Berman and Quinn, 1991). Vertical stratification in pools (Matthews and Berg, 1997; Elliot, 2000; Tate *et al.,* 2006) and lakes (Coutant, 1987) may result in pools acting as thermal refugia with fish migrating to cooler bottom water when surface temperatures exceed their incipient lethal limit. Tate *et al.* (2006) recorded bottom temperatures 7.6^{o}c cooler than top temperatures in pools between 1.5 to 2.5 m deep in the hot, arid rangelands of the United States. They also showed that the magnitude of daily thermal stratification was dependent on air temperature, with the greatest differences between top and bottom of pool water temperature occurring on days with the warmest air temperatures. Bottom waters are often lower in dissolved oxygen than the surface water resulting in a trade-off between high temperatures and low DO (Matthews and Berg, 1997; Elliot, 2000). For example, a pool of 4.1 m depth varied from 21.5^{o}C at the bottom to 28.9^{o}C at the surface (Matthews and Berg, 1997), while DO concentration varied from <1 to 5 mg/l at the bottom to 4.1 to 10 mg/l at the surface over a 24 hour period. Lowest DO occurred from 24h00 to 06h00. Pools were also shown to be more important in warm water streams than cold water streams, while riffle habitats were more frequently inhabited by fish (salmon) in cold streams than in warm streams, even when pool habitats were available (Torgersen *et al.* 1999).

Surveys of endemic fish populations on the Doring River suggest that fish populations consistently choose certain pools over others to over-summer in (B. Paxton, Freshwater Research Unit, Department of Zoology, University of Cape Town). While this may be related to water quality, such as the presence of groundwater input, fish may also be selecting pools deep enough to incorporate thermal refugia.

5.9. Tolerance to parasites and diseases

Water temperature plays a vital role in *Schistosome* (Bilharzia) transmission in permitting a suitable snail population to flourish and in controlling the length of the incubation period of the parasite in the snail (Pitchford and Visser, 1975). Most studies on parasites and diseases, however, are largely related to fish. Generally, it has been shown that fish are more susceptible to diseases when water temperature is elevated and fish are thermally stressed. Parasite populations also increase rapidly in response to elevated water temperatures, which has been shown to cause severe impacts to fish including sockeye salmon (Columbia River, United States, Brett, 1956 cited by Brown and Krygier, 1967).

6. Assessing the effects of temperature changes on aquatic organisms

The effect of water temperature changes on aquatic organisms has been assessed and monitored by direct measurement and observation in the field; and by laboratory studies. The two methods are often used in a complimentary way with one validating the other. Given the wide range of potential effects, it is indeed a challenge to measure and monitor likely changes in aquatic organisms in response to modifications in the thermal regime. The effects of temperature changes may be assessed in terms of an organism's lethal limits (minimum and maximum), sublethal effects or behavioural avoidance preferences. A strong correlation between lethal temperature and preferred temperature, as determined by preference test, exists for fish species (Jobling, 1981; Richardson *et al.,* 1994). Lethal temperature is affected by several factors (Langford, 1990) as indicated in Figure 1.4.

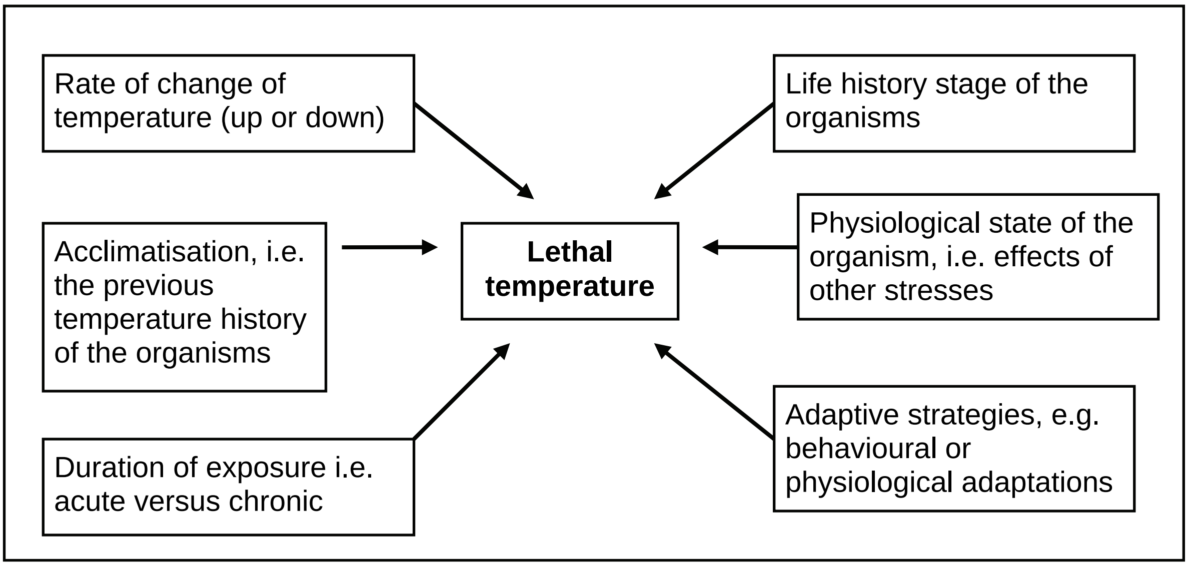

Figure 1.4 Factors affecting the lethal temperature for aquatic organisms (adapted from Langford, 1990)

The rate of change of temperature and the absolute temperature are important in determining the lethal temperature of an organism. For example, slow changes may result in acclimatisation, i.e. the previous temperature history of the organism; or acclimation, i.e. laboratory adjustment to experimental temperatures prior to testing, while rapid changes can lead to thermal shock. Temperature tolerance of the same species may differ over its geographical range, habitat or season as a result of local and temporal acclimatisation. For example, Whitney (1939) showed that mayfly nymphs from slow-running or still waters had a greater resistance to high temperatures than animals from fast-flowing waters and this was correlated with the more extreme temperatures in slow and still waters. Selvakumar and Geraldine (2005) showed that a sudden increase in temperature can induce the synthesis of a specific set of proteins, the heat shock or stress proteins. The duration of exposure, i.e. acute versus chronic, may also affect the aquatic organism’s response to elevated temperature, with increasing duration decreasing the lethal temperature. The life history stage is a factor in that earlier life stages (e.g. eggs, larvae) are often more susceptible to changes in water temperature than adult stages. Multiple stresses whereby the organism is exposed to stress such as water quality impairment, in addition to temperature stress, may increase susceptibility to temperature elevation. Adaptive strategies that allow for behavioural thermoregulation or physiological adaptations may modify the lethal temperature of an organism.

6.1. Field methods – *in situ* measurements

Empirical data derived from field observation can provide useful information on the distribution of aquatic organisms. Field observations involve the measurement of minimum and maximum water temperatures within a species natural distribution range. The potential problem with this method however, is that it does not take into account the heterogeneity often occurring in rivers and which offer aquatic organisms such as fish microhabitats, which differ in temperature from the ambient water temperature (Beitinger *et al.,* 2000). Field data is often used to calculate averages such as the 7-d average of daily maximum temperature (from 30 minute interval temperatures, Huff *et al.,* 2005), which may be related to thermal niches. For example, Huff *et al.* (2005) used field data to estimate the thermal niches of 16 species of aquatic vertebrates (fish and amphibians) and compared these values among five geographic regions (199 sites) in Oregon, United States. There results showed that the thermal niches varied among ecoregions and that the niches were generally comparable to the maximum growth temperatures and upper thermal limits established by other field and laboratory techniques.

In South Africa, water temperature data is largely limited to spot measurements taken at the site, with associated biotic data (e.g. Rivers Database, Ewart-Smith *et al.,* 2000), and summarised data where monthly means, maximum and minimums, etc. are given (e.g. Biobase, Dallas *et al.,* 1999). Some water temperature data has been collected at biotope level (Berg River, unpublished data, GR Ractliffe and K Snaddon, The Freshwater

Consulting Group, University of Cape Town). Water temperature data also exists for fish distribution records but these have not been captured into the distribution database (pers. Comm. R. Bills, South African Institute of Aquatic Biodiversity, Grahamstown). The utility of the two aquatic invertebrate databases in identifying thermally-sensitive taxa, via calculation of the temperature ranges for different invertebrate families (Rivers Database) and selected genera or species (Biobase), was examined as part of this consultancy. Analyses were undertaken for the whole of South Africa and therefore natural distribution ranges are not taken into account.

6.1.1. Tolerance ranges derived from the Rivers Database

Data extracted from the Rivers Database where invertebrates sampling was conducted simultaneously with a spot water temperature measurements, were used to generate frequency histograms of recorded water temperatures for each taxon. Data from 1358 sites and 2950 records (>1 sampling occasion at some sites), providing a total of 46643 matched taxon-temperature records, was used (Figure 1.5). Water temperature was normally distributed and ranged from 3.4^{o}C recorded at RHP site A3DRAAI-DRAAI (Draaifontein River, a tributary of the Groot-Marico in the North-West Province) in September 2005 to 32.8^{o}C recorded at RHP site E4KOEB-DEHOO (Koebee River, a tributary of the Doring River in the Western Cape) in December 2003. Frequency histograms for each taxon were also generated (Appendix 1A to 1P).

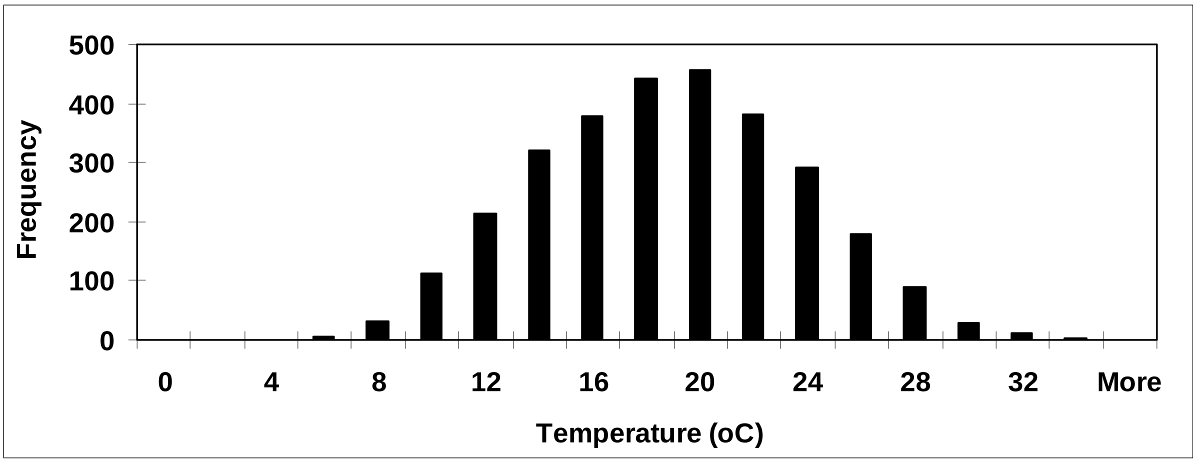

Figure 1.5 Frequency histogram of water temperatures recorded at sites in South Africa based on data in the Rivers Database

The temperature frequency distribution of each taxon was compared statistically to the water temperatures using the non-parametric analysis of variance test, the Kolmogorov-Smirnov test. The non-parametric test was used because data were not always normally distributed. This test assesses for differences in two samples (differences in means) and is sensitive to differences in the general shapes of the distributions in the two samples (i.e., to differences in dispersion, skewness, etc.). It allows one to determine if the recorded temperature range of a particular taxon is lower or higher than temperatures measured at all the sites. Data are presented in Appendix 2. Of the 93 taxa assessed, 29 had temperatures significantly lower than water temperature, 16 of which were significant at $p<0.001$. These included Amphipoda, Notonemouridae, Heptageniidae, Leptophlebiidae, Teloganodidae, Tricorythidae, Chlorocyphidae, Barbarochthonidae, Philopotamidae, Psychomyiidae/ Xiphocentronidae, Helodidae, Psephenidae, Athericidae, Blephariceridae, Dixidae and Tipulidae. 28 taxa had temperatures significantly greater than water temperature, of which 11 were significant at $p<0.001$. These included Hirudinea, Atyidae, Belastomatidae, Gerridae, Naucoridae, Nepidae, Notonectidae, Veliidae/Mesoveliidae, Muscidae, Lymnaeidae and Physidae, some of which may merely reflect the increased likelihood of these taxa occurring in lowland rivers that are generally warmer than upland ones. 36 taxa showed no significant difference from water temperature.

Mean, median, minimum, maximum, range of water temperatures extracted for each taxon (extracted from the Rivers database) is given in Appendix 3. When considering records with > 20 records, Blephariceridae had the lowest average temperature (14.3^{o}C), the lowest maximum temperature (20.5^{o}C) and the smallest temperature range (11.8^{o}C). Belastomatidae had the highest average temperature (20.4^{o}C), while Lymnaeidae had the widest temperature range (29.4^{o}C). Many taxa were recorded at maximum temperatures >32.0^{o}C, including Hirudinea, Oligochaeta, Potamonautidae, Hydracarina, Baetidae, Caenidae, Aeshnidae, Corduliidae, Libellulidae, Gomphidae, Coenagrionidae, Corixidae, Gerridae, Hydrometridae, Naucoridae, Notonectidae, Nepidae, Pleidae, Veliidae/Mesoveliidae, Leptoceridae, Dytiscidae, Hydrophilidae, Chironomidae, Culicidae, Tabanidae and Lymnaeidae. Most of these correspond to those taxa shown to have temperature frequency distributions not significantly different from water temperatures (Appendix 2).

Graphs of mean temperatures (standard deviation, min-max) at which each taxon were recorded are given in Appendix 4 and Figure 1.6. In each case water is given for comparison. Figure 1.6 shows the mean temperatures at which South African stonefly and mayfly families were recorded. Notonemouridae appeared to favour cooler temperatures, while Oligoneuridae favoured warmer temperatures. This no doubt reflects their biogeographic and longitudinal distribution patterns, with notonemourids located cooler upland systems in the Western Cape, and oligoneurids located in more tropical rivers. Families such as Baetidae and Caenidae had a temperature frequency range that was most similar to water temperature suggesting that taxa within these families are able to live in a broad temperature range, i.e. euthythermal. Similar observations may be made with several taxa (Appendix 4).

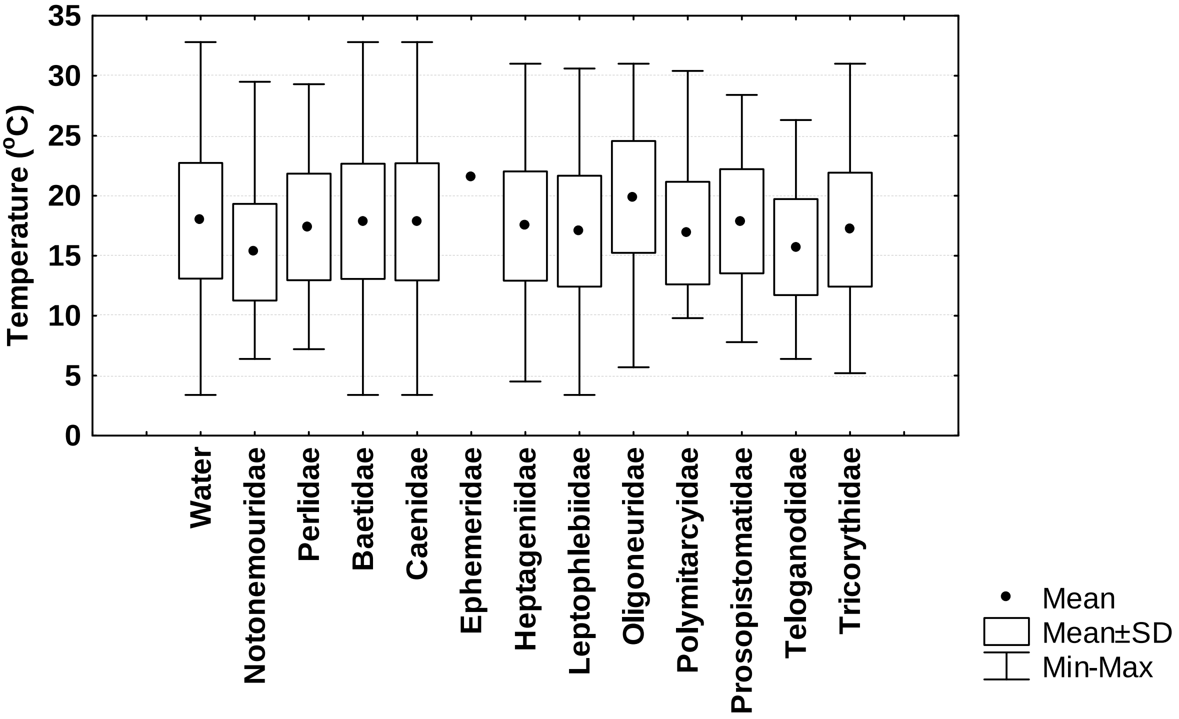

Figure 1.6 **Mean (standard deviation, minimum and maximum) temperatures for each invertebrate taxon (based on data extracted from the Rivers Database)**

These data provide insight for selection of temperature-sensitive taxa for future experimental studies. In selecting taxa for tolerance testing it is important note that the Western Cape is fundamentally different to the remainder of South Africa with respect to climate, specifically rainfall, and that there are several taxa endemic to the region. Further, upland areas, namely mountain streams and upper foothills, of the Western Cape have been shown to be spatially distinct from other parts of South Africa, while lowland areas were not (Dallas, 2004). In addition, one needs to consider the suitability of individuals within the taxon as laboratory organisms. Wild-caught specimens that have successfully been used at the Unilever Centre for Environmental Water Quality include shrimps (Atyidae), flatworms (Planariidae), mayflies (Baetidae, Heptageniidae, Leptophlebiidae, Oligoneuridae and Tricorythidae), damselflies (Coenagrionidae), caddisflies (Leptoceridae), bugs (Pleidae, Naucoridae) and limpets (Ancylidae) (pers. comm. Dr WJ Muller, Institute for Water Research, Rhodes University). Based on all of these factors and results of the analyses undertake, preliminary recommendations for invertebrate families to consider for temperature tolerance testing are:

- Western Cape (upland areas): Amphipoda, Notonemouridae, Heptageniidae, Leptophlebiidae, Telagonodidae, Corydalidae, Barbarochthonidae, Helodidae and Blephariceridae;
- Other regions in South Africa and lowland areas of the Western Cape (*=not Western Cape): Perlidae*, Heptageniidae, Leptophlebiidae, Polymitarcyidae*, Tricorythidae,

Aeschnidae, Chlorocyphidae, Ecnomidae, Philopotamidae, Elmidae/Dryopidae, Helodidae, Psephenidae*, Athericidae, Dixidae and Tipulidae.

There may be additional genera within other invertebrate families that would also be suitable test organisms. This is explored further using the Biobase (section 6.1.2).

6.1.2. Tolerance ranges derived from the Biobase

Temperature ranges for the families selected in 6.1.1 were extracted from the Biobase (Appendix 5, Dallas *et al.,* 1999). For many studies included in the biobase, certain taxa were however not identified beyond family, for example Helodidae, although specimens were often typed to morpho-species (e.g. Helodidae sp. A). Generally the data verifies the data extracted from the Rivers Database, with most family-level data showing similar ranges for water temperature. When genus and/or species level data is examined, different taxa have different ranges. For example, within Leptophlebiidae, *Adenophlebia* spp. and *Aprionyx* spp. have lower temperature ranges than *Chloroterpes* spp. and *Euthraulus* spp. This data provides a useful initial indication of the potentially temperature-sensitive genera and species.

6.2. Laboratory methods – estimation of thermal tolerance of aquatic organisms

Laboratory studies on the thermal tolerance of aquatic organisms are numerous, particularly in the northern hemisphere. Laboratory studies include two approaches: lethal effects and critical thermal methodology. The acute effects of temperature are frequently expressed as effects on survival that result from exposure to elevated temperatures for specified time periods. Lethal effects are determined by acute (short-term) experimental exposure to a range of temperatures in order to measure LT_{50} or LC_{50}'s (e.g. Nebeker and Lemke, 1968; de Kozlowski and Bunting, 1981). The LT_{50} is the median lethal time, which is the duration eliciting 50% mortality at a specific temperature. The upper incipient lethal limit (UILL) is the temperature at which acute mortality does not increase with any further increase in the temperature. The temperature lethal to 50% of the test organisms is determined by plunging them from an acclimated temperature into a series of constant test temperatures near the estimated upper and lower limits of the species (Fry, 1947 cited by Beitinger *et al.,* 2000).

The second laboratory method is the critical thermal methodology (CTM) whereby the organism, usually acclimated to a specific temperature is subjected to a constant linear increase or decrease in temperature until a predefined sublethal but near lethal endpoint is reached. CTM is defined as: *"The arithmetic mean of the collective thermal points at which locomotory activity becomes disorganised and the animal loses its ability to escape from conditions that will probably lead to its death when heated from a previous acclimation temperature at a constant rate (fast enough to allow deep body temperatures to follow environmental temperatures without a significant time lag)"* (Cox, 1974 cited by Ernst *et al.,* 1984). The CTM endpoint is the critical thermal maximum or minima, CTmaximum or

CTminimum (Beitinger *et al.,* 2000) and may include loss of equilibrium and onset of muscle spasms (Beitinger *et al.,* 2000). Survival occurs if the organism is returned to their pre-test acclimation temperature.

The CTM method offers several advantages over the lethal methods, in that temperature tolerances are determined without lethality, which enables tests to be performed on indigenous and possible endangered fish, and the statistical analysis is relatively simple with data compared by t-tests or ANOVA. Consideration however needs to be given to the rate of change of temperature, which needs to be fast enough to avoid acclimation, but slow enough to allow fish internal temperature to equal water temperature. The rate of 0.3^{o}C per minute has been recommended (Beitinger *et al.,* 2000).

Information on temperature tolerances of North American fish is widespread and numerous and approximately 80 studies provide tolerance data (see Beitinger *et al.,* 2000 for a review). There is also evidence that thermal tolerance is a genetically determined trait in fish and that selection pressures in the local environment influence the thermal tolerance range of geographically distinct fish populations within a species (Bell, 2006). Information on the tolerance ranges of southern hemisphere fish is less plentiful (e.g. Richardson *et al.,* 1994), while South African studies on the temperature tolerance of freshwater fish is scarce. There is significant information on the distribution of fish in southern Africa (e.g. Skelton, 1993) but no specific studies have related distribution to water temperature although the data do exist (pers comm. Roger Bills, SAIAB, Grahamstown, South Africa). Tolerances levels of indigenous New Zealand fish suggest that they have slightly higher thermal tolerances than the macroinvertebrates (Richardson *et al.,* 1994).

Several studies in the northern and southern hemisphere have documented lethal and CTmaxima (or CTminima) for aquatic invertebrates. Many of these, together with sub-lethal effects, have been tabulated in Appendix 6, although northern hemisphere studies are exhaustive and only selected studies are included. Lethal limits varied from 16^{o}C for a North American family of Perlidae to 38.4^{o}C for a freshwater prawn acclimated to 32^{o}C in Mexico. In the southern hemisphere lethal limits varied from 21.9^{o}C for a leptophlebiid mayfly to 32.4^{o}C for a hydrobid snail (New Zealand studies). Mean CTM varied from 31.5^{o}C for a North America perlid to 40.7^{o}C for freshwater prawns. No southern hemisphere studies using traditional CTM were found. Sublethal effects ranged from minimum temperature for growth of the aeschnid dragonfly of 8^{o}C, to 6.6 to 9.7 for optimum hatching of stoneflies in the United Kingdom, to 18-19^{o}C for optimal growth rate of adult stoneflies in North America, to 29.4^{o}C as the preferred temperature for freshwater prawns in Mexico. These studies highlight the variability in both lethal and sublethal effects of aquatic invertebrates.

Thermal tolerances of New Zealand aquatic fauna suggest that some Coleoptera and Diptera can tolerate temperatures of 40-50^{o}C, while other Diptera, Hemiptera, Odonata, Ostracoda and Pulmonata tolerate temperatures around 35^{o}C (Winterbourn, 1969; Stark *et al.,* 1976 cited by Quinn *et al.,* 1994; James 1985). Plecoptera and Ephemeroptera seem to be the most sensitive to changes in water temperature, with Plecoptera largely restricted to temperatures typically below 19°C (Quinn *et al.,* 1994). Quinn *et al.* (1994) found that lethal temperatures varied from 22.6 ± 0.9°C for *Deleatidium* spp. (Leptophlebiidae) to 32.5±2.5°C for the least sensitive species tested. They allowed a 3°C safety margin, indicating that the upper thermal tolerance for *Deleatidium* is 19.6°C. This corresponded well with the marked decline in abundance of this species once summer temperatures reached 21°C. When diurnally varying temperatures were used instead of constant temperatures, lethal temperature was 10% lower (Cox and Rutherford, 2000a, b). They recommended that in order to ensure 50% survival, the constant LT_{50} limit should be applied to a temperature midway between the daily mean and the daily maximum temperatures. Lethal temperatures ($_{96}LT_{50}$) were measured for 12 species of aquatic insects in the United States – they varied from 21°C to 33°C, for stoneflies (*Taeniopteryx maura*) and dragonflies (*Ophiogomphus rupinsulensis*) respectively (Nebeker and Lemke, 1968).

6.3. Sublethal effects

Sublethal (chronic) effects of changes in water temperature include those on reproduction, spawning, egg incubation and hatchability, development and growth, survival of fry and emergence success, as well as sublethal physiological effects. In particular, the duration of exposure to elevated temperatures is important is assessing sublethal (chronic) effects on aquatic organisms. Two common measures of chronic exposure are the maximum weekly average temperature (MWAT) and the maximum weekly maximum temperature (MWMT). The MWAT is the maximum seasonal or yearly value of the mathematical mean of daily temperatures over a seven-day consecutive period (Brungs and Jones, 1977 cited by Carter, 2005). The MWMT is the maximum seasonal or yearly value of the daily maximum temperatures over a seven-day consecutive period.

Many studies have examined egg incubation and hatchability rates for aquatic insects (Elliot, 1972; Harper, 1973; Humpesch, 1980; Weatherley and Ormerod, 1990; Brittain, 1991) and fish (e.g. Brungs,1971; Crisp, 1990; Evans and Petts, 1997), while others have examined growth rates (e.g. Thorup, 1973; Markarian, 1980; Vannote and Sweeney, 1980; Coutant, 1987; Richardson *et al.,* 1994) and emergence success (e.g. Nebeker, 1971a, c, 1972; Nordlie and Arthur, 1981). Studies on the physiological effects of modifications to water temperature are often linked to metabolic rates (e.g. Eriksen, 1964; Beamish, 1981; Cech *et al.,* 1990) and oxygen consumption (e.g. Nebeker *et al.,* 1996). The effect of the toxicity of toxic substances such as cyanide, zinc, phenol, xylene to aquatic organisms subjected to elevated water temperatures has also been examined (e.g. Duffus, 1980).

6.4. Behavioural preferences and avoidance

Studies on the behavioural effects of temperature have primarily been undertaken on fish (e.g. Cincotta and Stauffer, 1984) with fewer studies conducted on aquatic invertebrates (e.g. Gerald and Spezzano, 2005). Thermal gradient tanks have been used to determine temperature preferences of aquatic organisms (Cherry and Cairns, 1982; Boubee *et al.,* 1991; Richardson *et al.,* 1994). Essentially, this technique involves the establishment of a temperature gradient that is then used to evaluate the temperatures preferred or avoided by various organisms. The method facilitates the determination of the effects of gradual temperature changes on aquatic organisms, and allows ontogenetic shifts in temperature preferences to be calculated. For example, for spawning and hatching of fish eggs, much lower temperatures are required. Boubee *et al.* (1991) showed experimentally that the final preferred temperature of *Galaxias maculates* resident in New Zealand is about 20°C and temperatures above 29.5°C were totally avoided.

7. Water temperature guidelines for the protection of aquatic ecosystems

A review of literature on the guidelines for water temperature in aquatic ecosystems highlighted the importance of understanding natural spatial and temporal (diel, intra-annual and inter-annual) variability in water temperature. Identification of appropriate temperature criteria to protect aquatic organisms is complicated by the highly variable nature of water temperature in rivers, coupled with the differing temperature requirements of aquatic organisms. Guidelines stress that no single temperature or thermal regime would be suitable for all seasons, all parts of a country, all river zones or all species. The characteristics of temperature regimes relevant to temperature criteria include (Sullivan *et al.,* 2000):

- temperature thresholds that reflects biological effects (acute, sub-lethal)
- temperature fluctuation characteristic (maximum, mean, minimum fluctuation)
- averaging period (instantaneous maximum, 7-day average monthly, seasonal average)

Temperature criteria typically have two key elements – a threshold temperature that signals when adverse biological response is likely to occur, and an averaging period that indexes the duration of exposure likely to trigger that response (Sullivan *et al.,* 2000). The combination of the threshold temperature and the duration of exposure to that temperature are an expression of the risk imposed by the environmental temperature to the targeted species. The following section provides an overview of the current guidelines developed in South Africa and elsewhere, including Australia and New Zealand, the United States and Canada. No appropriate references were located for the European Union.

7.1. South Africa – water temperature in the Reserve

Water temperatures in South African aquatic ecosystems are often higher and more varied than those in northern hemisphere ecosystems. The existing norms for assessing the effects of water temperature on aquatic ecosystems include the measurement of the acute and chronic physiological effects on aquatic organisms, and the effects of changes from "natural" site-specific temperature regimes (= reference) which result in changes to ecosystem structure and functioning (DWAF 1996). Water quality guidelines for aquatic ecosystems in

South Africa, therefore, specify a target water quality range (TWQR) whereby water temperature should not be allowed to vary from the background daily average water temperature considered to be normal for that specific site and time of day, by > 2°C, or by > 10%, whichever estimate is the more conservative (DWAF 1996; Dallas *et al.,* 1998). The current approach used to specify the benchmarks for temperature is to estimate the natural distribution of temperature in the water quality resource unit (Jooste and Rossouw, 2000). This is done by specifying a monthly temperature range, characterised by the 10th and 90th percentile temperatures for each month. Temperature is evaluated as a site-specific deviation from the natural temperature range. Temperatures outside the natural range are regarded as indicative of impacts and the larger the deviation from the natural range, the "poorer" the state of the river. The "no-effect" and "critical effect" levels for temperature would not have a fixed value throughout the year, but would vary in response to natural seasonal variation. Temperature is currently considered an optional variable in ecological water quality Reserve determinations (Jooste and Rossouw, 2000) and is only considered if there is evidence of thermal impacts, for example, below dams with bottom-release valves, inter-basin transfers or downstream of thermal effluents. Jooste and Rossouw (2000) recommend an approach that uses the actual or modelled temperature data for an unimpacted site (= reference site) as close to the resource unit of interest as possible to derive the no-effect range. The following protocol has been developed for setting guidelines for water temperature in the ecological Reserve (Jooste and Rossouw, 2000).

7.1.1. Setting the benchmarks if observed data is available

- Sort the temperature database by month
- Calculate the 10th and 90th percentiles for each month. This represents the natural temperature range for each month.
- Calculate the upper and lower boundaries of the good and fair classes using the approach described in Table 1.1, which gives the three categories from natural, to good to fair.

Table 1.1 Categories for calculating the upper and lower boundaries for water temperature

Category	**Temperature**
Natural range	Monthly 10th and 90th percentiles of observed or simulated temperature data
Good range	Upper boundary = 90th percentile + minimum (0.1*90th percentile, 2°C) Lower boundary = 10th percentile – minimum (0.1*10th percentile, 2°C)
Fair range	Upper boundary = 90th percentile + minimum (0.2*90th percentile, 4°C) Lower boundary = 10th percentile – minimum (0.2*10th percentile, 4°C)

7.1.2. Rapid Reserve – low confidence assessment (no observed data available)

- Calculate the mean monthly water temperatures using a simple model (e.g. Van Schalkwyk and Walmsley, 1984).
- Set the 10th and 90th percentiles for each month by adding or subtracting 2 °C from the monthly mean value.
- Calculate the upper and lower boundaries of the good and fair classes using the approach described in Table 1.1.

7.1.3. Intermediate Reserve – medium confidence assessment

- Calculate daily water temperatures using an empirical relationship between air temperature and water temperature (e.g. Stefan and Preud'homme, 1993; Pilgrim *et al*., 1998 cited by Jooste and Rossouw, 2000).
- Sort the estimated daily water temperatures by month and calculate the 10th and 90th percentiles for each month.
- Calculate the upper and lower boundaries of the good and fair classes using the approach described in Table 1.1.

7.1.4. Comprehensive Reserve – high confidence assessment

- Calculate daily water temperatures (Palmer *et al.,* 2005) using a locally calibrated empirical relationship between air temperature and water temperature (e.g. Stefan and Preud'homme, 1993; Pilgrim *et al.,* 1998 cited by Jooste and Rossouw, 2000) or if resources are available, a deterministic stream temperature model (e.g. Bartholow, 2002 cited by Jooste and Rossouw, 2000).
- Sort the estimated water temperatures by month and calculate the 10th and 90th percentiles for each month.
- Calculate the upper and lower boundaries of the good and fair classes using the approach described in Table 1.1.

7.1.5. Present state classification

- The present state can only be classified if observed temperature data is available.
- Sort the temperature database by month.
- Calculate the 10th and 90th percentiles for each month. This represents the present state temperature range for each month.
- Compare the 10th and 90th percentiles to the natural, good and fair boundaries for the reference site and assign a class to each value.

- The class for the month is the poorest class obtained when comparing the 10th and 90th percentile to the reference site for a specific month.

The lack of baseline data for rivers in South Africa significantly impedes the ability to set site-specific guidelines for water temperature.

7.2. Australia and New Zealand

In the Australian and New Zealand guidelines (NWQMS 2000) temperature is classified as a toxic direct-effect stressor that is naturally highly variable among and within ecosystem types and seasonally. Natural biological communities are considered to be adapted to the site-specific conditions, which suggest that trigger values for this stressor may need to be based on site-specific biological effects data. Generally, guidelines recognise three levels of ecosystem condition:

- high conservation/ecological value (condition 1 ecosystems);
- slightly or moderately disturbed (condition 2 ecosystems); and
- highly disturbed (condition 3 ecosystems), each with an associated level of protection.

Four sources of information are available for use when deriving low-risk trigger values: biological and ecological effects data, reference system data, predictive modelling, or professional judgment. Of these the most relevant with respect to water temperature is using reference data.

7.2.1. Biological and ecological effects data

This is obtained either from biological effects testing using local biota and local waters or from the scientific literature. This method is most appropriate for stressors directly toxic to biota (e.g. salinity, pH, DO, ammonia), but can also be applied to naturally-occurring stressors such as nutrients (e.g. nutrient addition bioassays). Ecological effects data are obtained through site- or ecosystem-specific laboratory and field experiments.

7.2.2. Reference system data

This is obtained either from the same (undisturbed) ecosystem (i.e. from upstream of possible environmental impacts) or from a local but different system, or from regional reference ecosystems. The reference condition must be chosen using information about the physical and biological characteristics of both catchment and aquatic environment to ensure the sites are relevant and represent suitable target conditions. Some of the important factors that should be considered are these:

- data collected prior to the disturbance need to be of sufficient quality and time-span to provide valid comparisons with post-disturbance data;
- where possible, pre-disturbance data should be collected from appropriate control or reference sites as well as from the site(s) subjected to the disturbance;
- the definition of a reference condition must be consistent with the level of protection proposed for the ecosystem in question (unimpacted, or slightly modified or relatively degraded);
- sites should be from the same biogeographic and climatic region;
- reference site catchments should have similar geology, soil types and topography;
- reference sites should contain a range of habitats similar to those at the test sites;
- reference and test sites should not be so close to each other that changes in the test site due to the disturbance also result in changes in the reference sites, nor, conversely, should changes in the reference sites mask changes that might be occurring in the test site.

7.2.3. Predictive modelling

This is particularly useful for certain physical and chemical stressors whose disturbance occurs through transformations in the environment (e.g. nutrients, biodegradable organic matter).

7.2.4. Professional judgement

This may be used in cases where it will not be possible to obtain appropriate data for a reference ecosystem because insufficient study has been undertaken to provide an adequate data base.

7.2.5. Determination of trigger values

Trigger values (20th and 80th percentile) are calculated from data at the reference site. Generally, data collected after two years of monthly sampling are regarded as sufficient to indicate ecosystem variability and can be used to derive trigger values. It is recommended that trigger values be develop for each month (for ecosystems not characterised by large seasonal or event-scale effects) or for each wet-dry season, where reference data is partitioned according to specific flow regimes and/or seasons. The median (maximum or minimum – depending upon whether increase or decrease in temperature) daily temperature should be used for comparison. Trigger values may be modified depending on the management objective, i.e. levels of ecosystem condition. The proposed trigger rule does not claim to define or represent an ecologically important change; it is merely an early warning mechanism to alert the resource manager of a potential or emerging change that should be followed up. Whether or not the actual change in condition at the test site has biological and/or ecological ramifications can only be ascertained by a much more comprehensive investigation and analysis.

7.3. Canadian Water Quality Guidelines

In general terms, Canadian water quality guidelines (CCRME 1999) are derived for all components of the aquatic ecosystem (e.g., algae, macrophytes, invertebrates, fish), where data are available. Where data are available but limited, interim guidelines are deemed preferable to no guidelines. The approach states that guidelines "are set at such values as to protect all forms of aquatic life and all aspects of the aquatic life cycles". The goal is to protect all life stages during an indefinite exposure to water. Whether this goal can be realized is a water management issue and does not affect the guideline derivation procedure. In terms of water temperature, Canadian guidelines are largely based on the protection of important fish species. Generally thermal additions to receiving waters should be such that thermal stratification and subsequent turnover dates are not altered from those existing prior to the addition of heat from artificial origins (largely applies to standing water bodies). Criteria are based on Maximum Weekly Average Temperatures (MWAT), with details as follows:

- In the warmer months, the MWAT is determined by adding to the physiological optimum temperature (usually for growth) a factor calculated as one-third of the difference between the ultimate upper incipient lethal temperature and the optimum temperature for the most appropriate life stage of the sensitive important species that normally is found at that location and time.
- In the colder months, the MWAT is an elevated temperature that would still ensure that important species would survive if the temperature suddenly dropped to the normal ambient temperature. The limit is the acclimation temperature minus 2°C when the lower lethal threshold temperature equals the ambient water temperature.
- During reproductive seasons, the MWAT meets specific site requirements for successful migration, egg incubation, fry rearing, and other reproductive functions of important species.
- At a specific site, the MWAT preserves normal species diversity or prevents undesirable growths of nuisance organisms.

For growth, the short-term maximum temperature is the 24-h median tolerance limit, minus 2°C at an acclimation temperature approximating the MWAT for that month. The short-term maximum temperature for the season of reproduction should not exceed the maximum incubation temperature for successful embryo survival, or the maximum temperature for spawning.

7.4. United States

Guidelines are numerous and often regionally focused with more emphasis placed on fish populations (e.g. McCullough *et al.,* 2001, Poole *et al.,* 2001, http://www.epa.gov/wqsdatabase/reports_inter.html). Temperature criteria generally specify a temperature threshold calculated over an averaging period. Various temperature indices are used including:

- annual maximum – the maximum hourly temperature that occurs each year;
- the 7-day maximum – the average of the daily maximum temperature of the 7 warmest consecutive days; and
- the 7-day mean (MWAT) – the average of the daily mean temperature of the 7 warmest consecutive days.

These are closely related to one another and can be compared or used interchangeably with the appropriate correlation relationships (Sullivan *et al.,* 2000). The 7-day mean temperature (MWAT) is best correlated with the season median, probably because each is respectively characterising the central tendency of the temperature within the daily and seasonal period.

8. Conclusions

This review has highlighted the complexity of water temperature in the aquatic environment. It has also highlighted the importance of understanding the spatial and temporal variability in water temperature and the variable responses of aquatic organisms to thermal stress. Anthropogenic modifiers of the thermal regime, including heated discharges, flow modifications, riparian vegetation removal and global climate change, present ongoing threats to aquatic ecosystems. South Africa is already a country stressed by scarcity of water. The risk of increasingly harsh conditions caused by greater water demands and climate change, reflected as higher air temperatures and lower rainfall, accentuates the need for a greater understanding of the thermal conditions in aquatic ecosystems in South Africa, and the requirements and triggers of the associated aquatic biota. Whilst northern hemisphere information on temperature is plentiful, this review has identified the huge gap that exists in temperature related data in South Africa. Without baseline data on water temperature and the thermal requirements of aquatic organisms, it is extremely difficult to adequately manage aquatic ecosystems. It is thus critical that this knowledge gap be filled through a comprehensive and integrated applied research programme.

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CHAPTER 2: SITE SELECTION CRITERIA FOR SELECTING SITES FOR WATER TEMPERATURE MONITORING

1. Introduction

This chapter addresses two of the deliverables for the consultancy, namely deliverables 3 and 4. The identification and selection of a test site for the installation and testing of temperature loggers is described, pilot data on within-site spatial and temporal variation in water temperature is given, and issues to be considered and criteria to be used when selecting sites for water temperature monitoring are provided.

2. Site selection

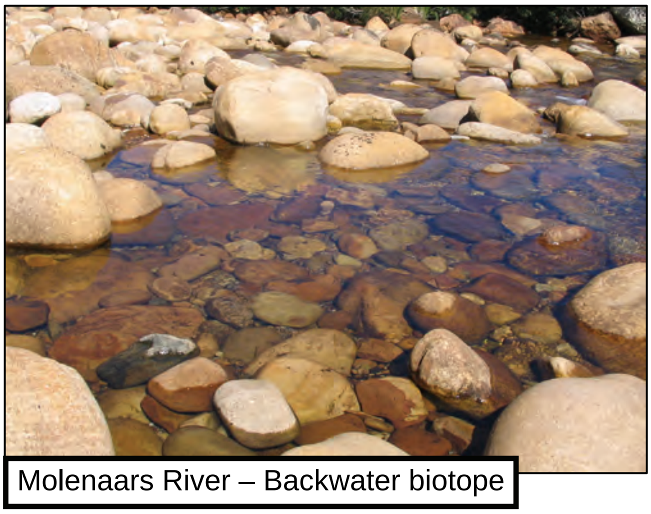
The site selected was on the Molenaars River in the Western Cape, immediately downstream of the N1 Huguenot tunnel between Paarl and Worcester. The site visit was undertaken on the 26 April 2006, together with Dr Bill Harding (project leader, collaborative temperature project) and Geordie Ractliffe (aquatic ecologist, The Freshwater Consulting Group, University of Cape Town). The Molenaars River site has been the focus of several studies since 1991, including monthly monitoring of abiotic and biotic characteristics in response to upgrading of the N1 (unpublished data, GR Ractliffe, Freshwater Research Unit, University of Cape Town), testing of the SASS (South African Scoring System) methodology (Dallas *et al.*, 1995), and more recently, an intensive study examining bed movement in response to hydrological and hydraulic changes (Ractliffe *et al.*, In Press). Ractliffe *et al.* (In press) marked approximately 400 boulders in the channel bed and mapped the boulders after flood events. The site has been mapped using aerial DTM and the positions of the marked boulders tracked accordingly. For approximately 200 of these boulders associated biotope, flow and biotic data (aquatic invertebrates) data are available. The extensive abiotic and biotic data available for this site and river made it ideal for testing of temperature logging.

2.1. Site description – The Molenaars River

The site selected is in the Upper Foothill zone of the Western Cape. It is considered a reference site (Dallas, 2002) and represents a site of high biodiversity. The river is perennial and has a substratum dominated by boulders and cobbles, with smaller pebbles and gravel interspersed between the boulders. Aquatic biotopes present include riffles runs, backwaters, slackwaters and pools. A range of depths and flow velocities are present. The river is strongly seasonal in terms of its abiotic characteristics including discharge and water temperature.

Molenaars River – Upstream view

Molenaars River – Downstream view



Molenaars River – Backwater biotope

Molenaars River – Rifle biotope

3. Preliminary results – temporal and spatial variability

Trends in water temperature were examined to provide preliminary information on temporal (inter-annual and seasonal) and spatial variation (within-site) in water temperature. DWAF data for the gauging station (H1H018Q01) on the Molenaars River, which is approximately 500 m downstream of the study site, comprising spot measurements collected weekly between 1980 and 1997, were examined and plotted with water temperature as a function of sampling date (Figure 2.1). Water temperature recorded in each season was plotted as a function of time (hourly) of sampling (Figure 2.2). Monthly mean, minimum and maximum temperatures are given in Figure 2.3. Both inter-annual (between years) and intra-annual (within years) patterns were evident. Summer temperatures were warmer, with maximum temperatures in January and February (mean water temperature approximately 21.5°C), while winter temperatures were cooler, with lowest temperatures in July and August (mean water temperature approximately 11.5°C). Spring and autumn had intermediate temperatures. Based on this data the seasonal maximum was 29°C (February) and the seasonal minimum was 5°C (July).

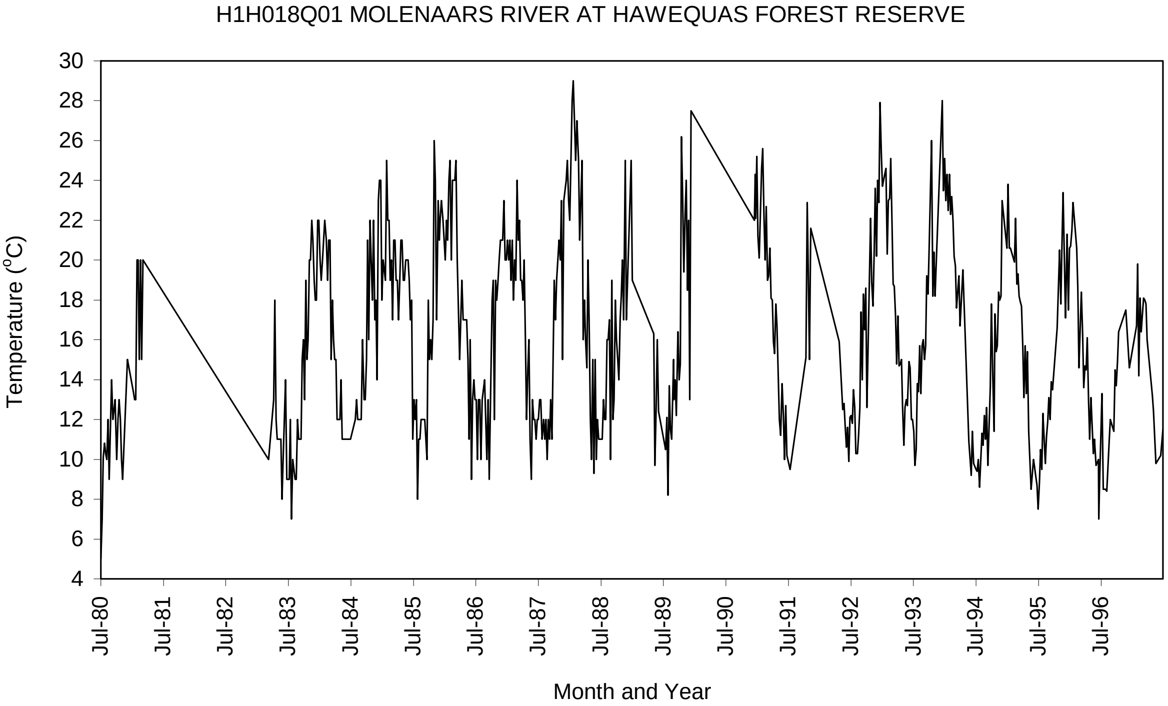


Figure 2.1 **Weekly water temperatures from 1989 to 1997 for gauging station H1H018Q01 on the Molenaars River**

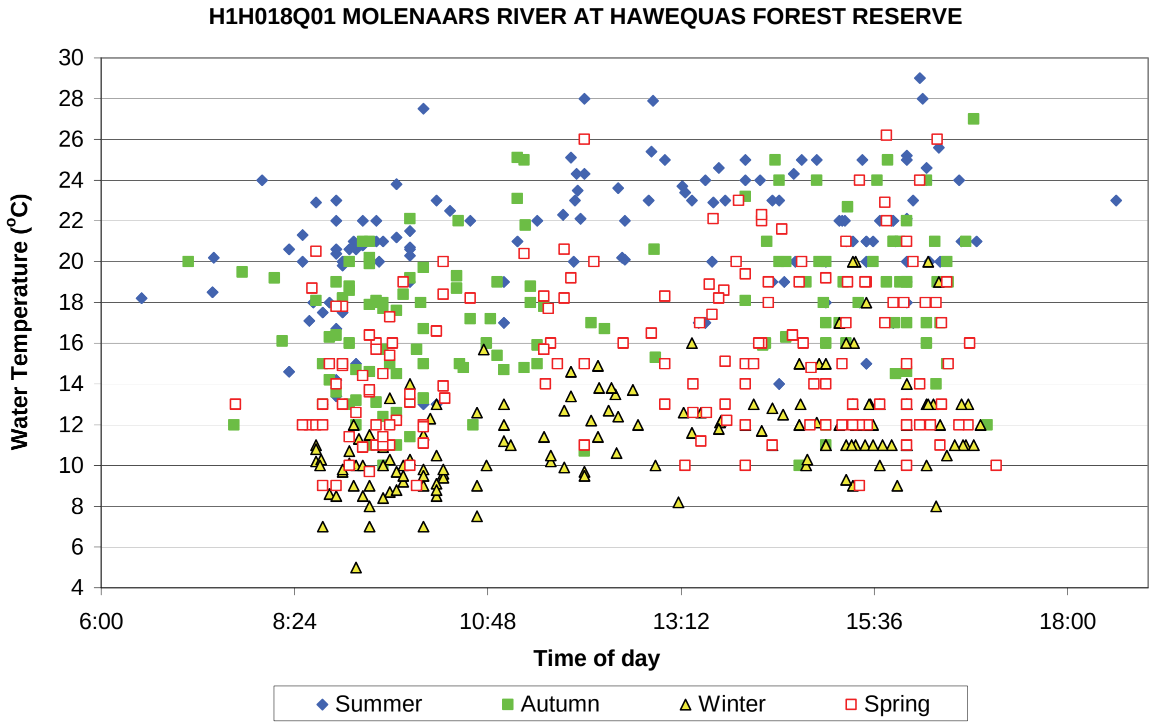


Figure 2.2 Water temperature recorded in each season plotted as a function of time for gauging station (H1H018Q01) on the Molenaars River

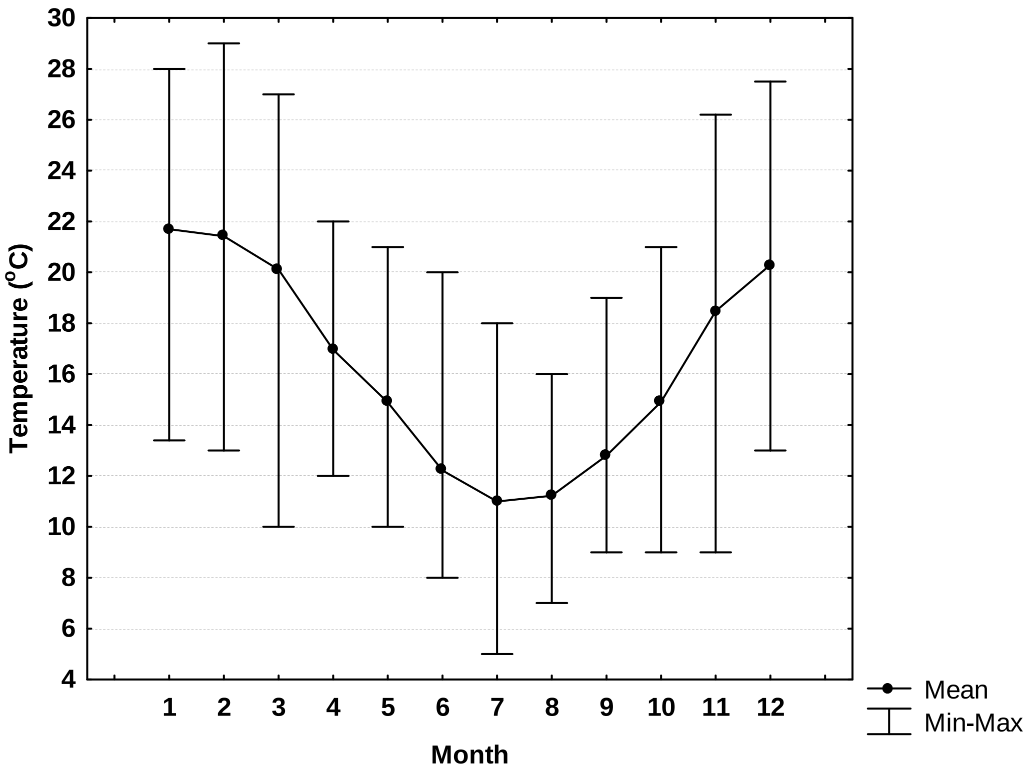


Figure 2.3 Monthly mean, minimum and maximum water temperatures for gauging station (H1H018Q01) on the Molenaars River

Monthly measurements at nine sites within the same river zone (Figure 2.4) are presented to indicate general variation longitudinally down the river (G.R. Ractliffe, unpublished data, Freshwater Research Unit, University of Cape Town). Seasonal trends supported the DWAF data and inter-annual variability is highlighted by highly variable temperatures recorded in February 1992 versus February 1993, which varied from 22.9 to 26.4°C in 1992 and from 17.2 to 22.8°C in 1993. In terms of longitudinal variability down the length of the river, there is a slight increase in water temperatures as one moved downstream until sites 7 and 8, when water temperatures decreases again. The influence of mild anthropogenic activities in the mid-sites may be responsible for this trend.

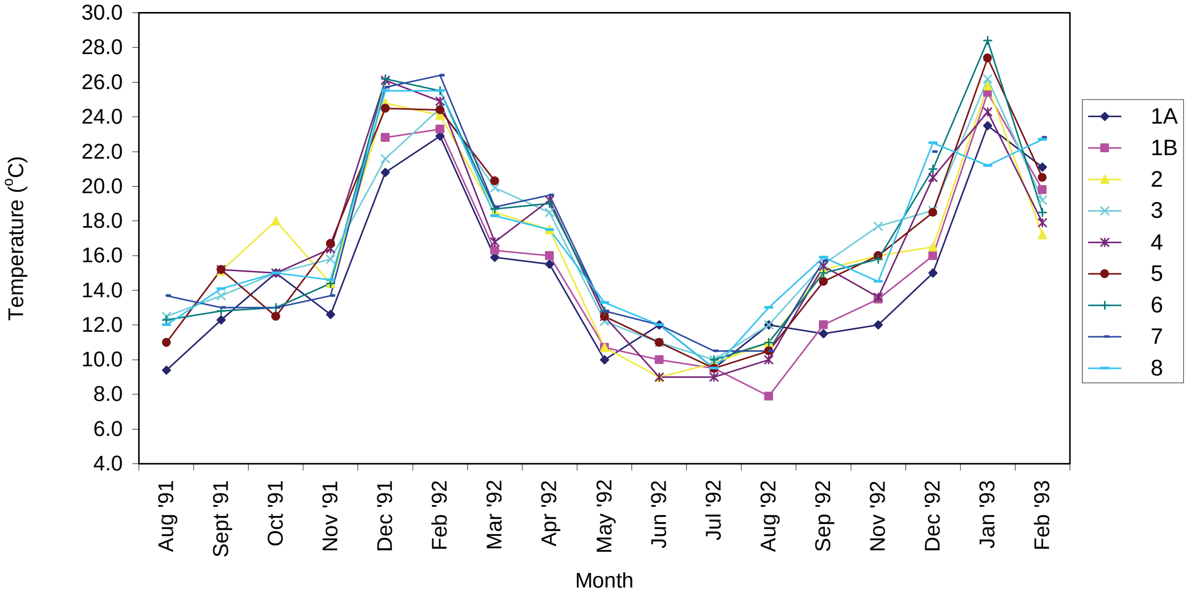


Figure 2.4 **Monthly water temperatures for eight sites on the Molenaars River collected between August 1991 and February 1993 (Unpublished data, GR Ractliffe, Freshwater Research Unit, University of Cape Town)**

Variability of water temperatures at the micro-scale level, i.e. within a site and amongst biotopes, was examined by determining the lateral temperature profile along 5 transects (Figure 2.5) and comparing temperatures in different biotopes and at different depths (Figure 2.6). Measurements were recorded between 12h00 and 16h00 in mid-February, the period when water temperatures were expected to be highest. For transect data (Figure 2.5), there was no general correlation between temperature and depth, although water temperature increased in the lateral margins by as much as 2°C, particularly in backwater (BW) and slackwater (SW) biotopes. Substratum types for figure 2.5 are: G-gravel, P-pebble, C-cobble, B-boulder, or combinations thereof.

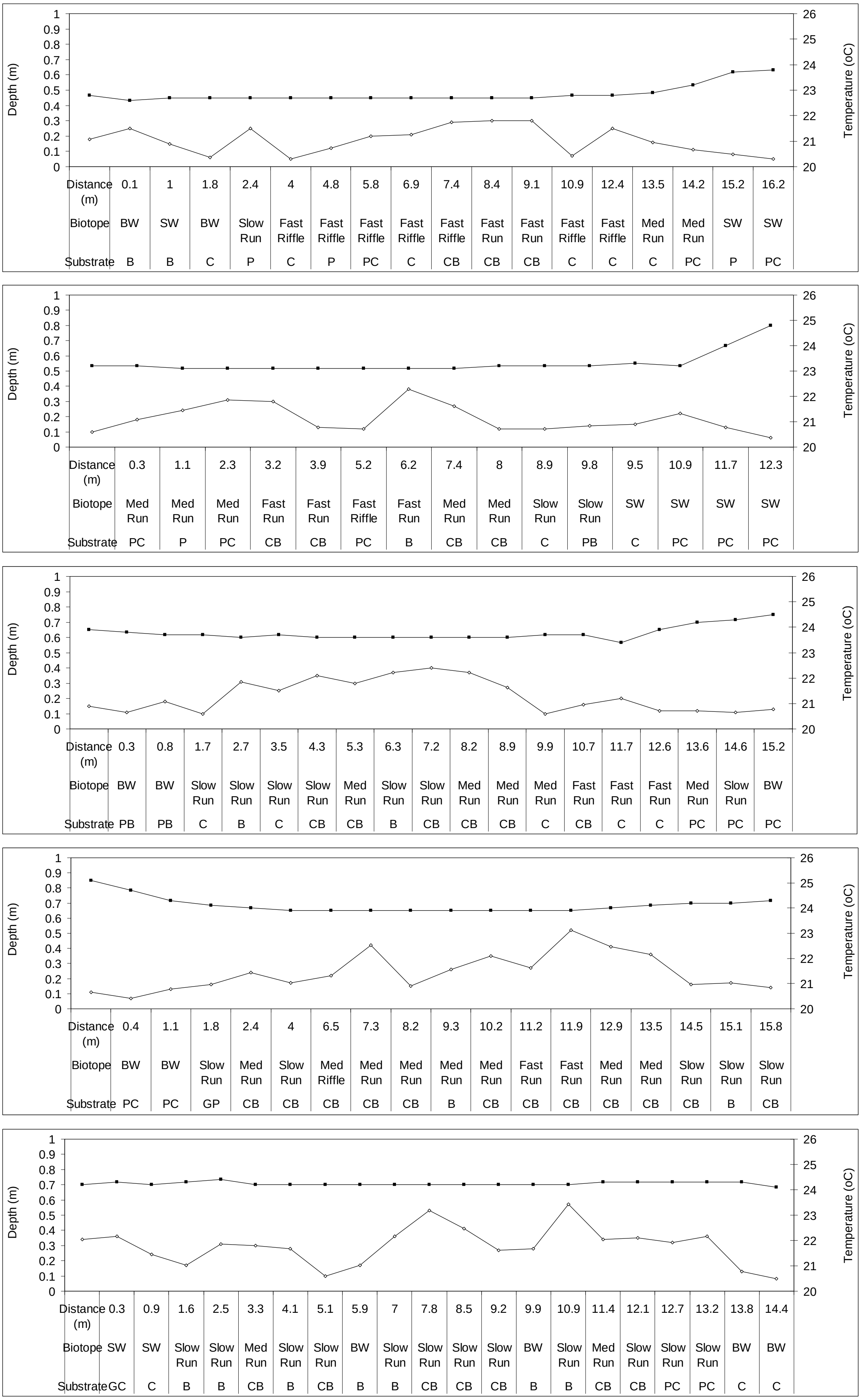


Figure 2.5 **Five water temperature depth transects giving biotope and substrate for the Molenaars River**

Spot measurements were taken of water temperature, depth, in specific biotopes within a 1.5 hours period at the hottest time of the day. Depth ranged from 0.01 m to 0.75 m, and temperatures ranged from 24.7 to 27.9^{o}C (Figure 2.6). Stones-out-of-current biotopes, including backwaters and slackwaters, were much more variable and had a higher maximum temperature than stones in current biotopes (riffles and runs). Temperature variation within riffles and run was < 0.5^{o}C. A wide range of depths was recorded in most biotopes. Differences in water temperatures amongst biotopes were tested using the non-parametric analysis of variance (Kruskal Wallis). Results were significant at $p<0.001$, showing that temperatures did differ amongst biotopes.

A second site in the mountain stream zone of the upper Eerste River was also sampled using both transect and spot measurement methods. Transect data showed very little variation of water temperature in relation to water depth. The spot measurements suggest that biotope and flow velocity (grouped into slow, medium and fast) contributed to statistically significant differences in water temperature amongst groups (Figure 2.6). Backwaters and slackwater had the greatest range in temperature, pools were the least variable, and all three had higher temperatures than run or riffle biotopes. Runs were generally warmer than riffles, which were also the least variable.

Although this data is preliminary, it does suggest that there is a certain degree of variation in water temperature at the micro-scale level. Of the factors considered, flow velocity and biotope type seem be of greater importance than water depth. Further sites and more data, however are needed to validate these findings.

4. Preliminary conclusions

Macro-scale (inter-annual), meso-scale (intra-annual) and micro-scale (within site) variation in water temperature was evident based on the preliminary data. Winter minima and summer maxima were recorded, with inter-annual variation in summer temperatures. Variation within a site indicated that slower flowing biotopes, normally present in lateral margins, were most variable and had the highest water temperatures. No relationship was observed between water temperature and water depth, and pools (<1.0 m) did not exhibit thermal stratification. Factors such as riparian shading and the contribution of groundwater were not considered but may also have influenced water temperatures at the two study sites. The value of measuring water temperature, encompassing both a temporal and spatial scale, is highlighted through these preliminary findings. More detailed and longer term measurement of water and air temperature would further promote our understanding of water temperatures. This, linked to biotic information, will enable the influence of temperature on biota to be examined.

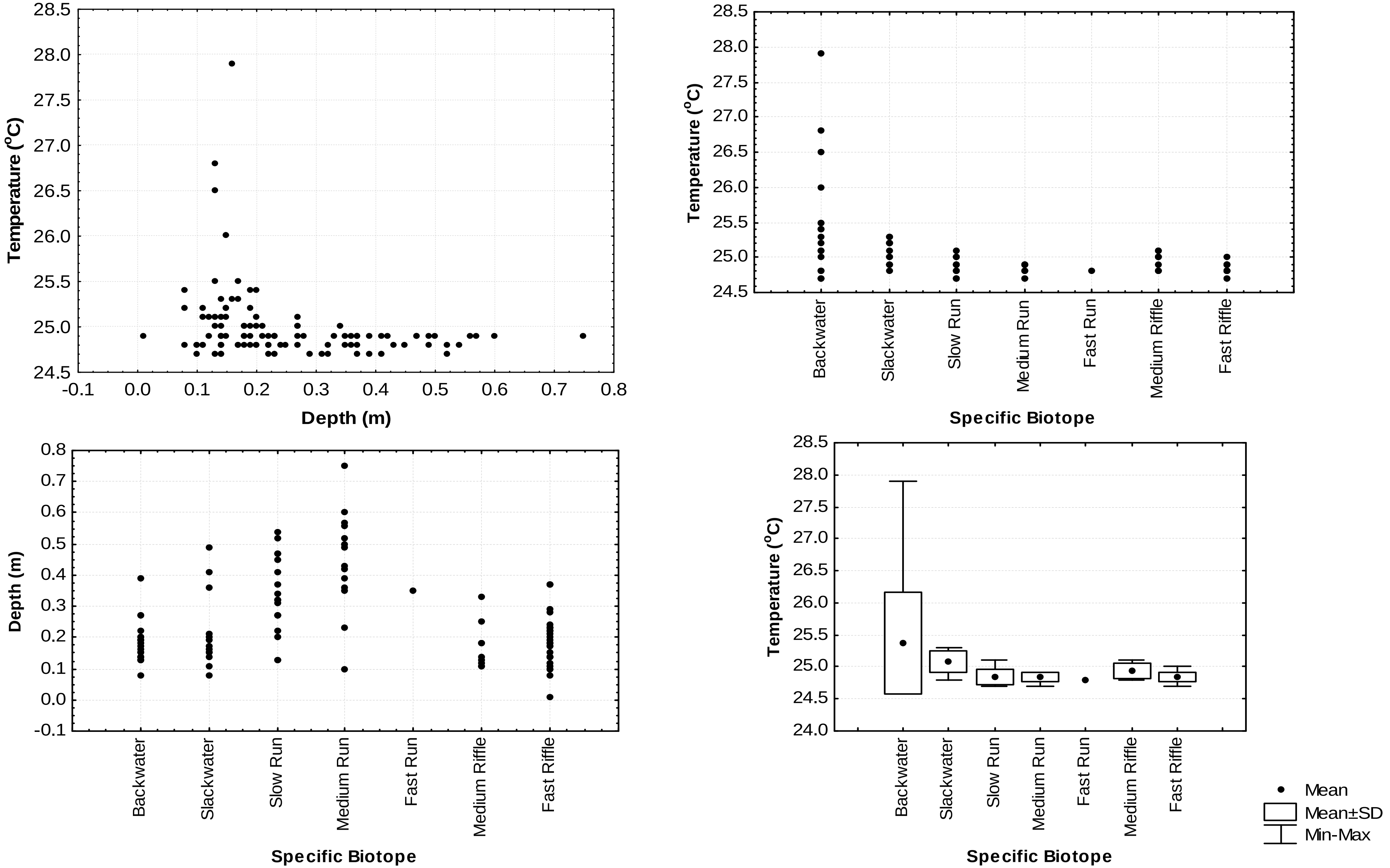


Figure 2.6 Water temperature plotted against water depth; temperature and depth recorded in each biotope; and mean (SD and min-max) values per biotope for the Molenaars River

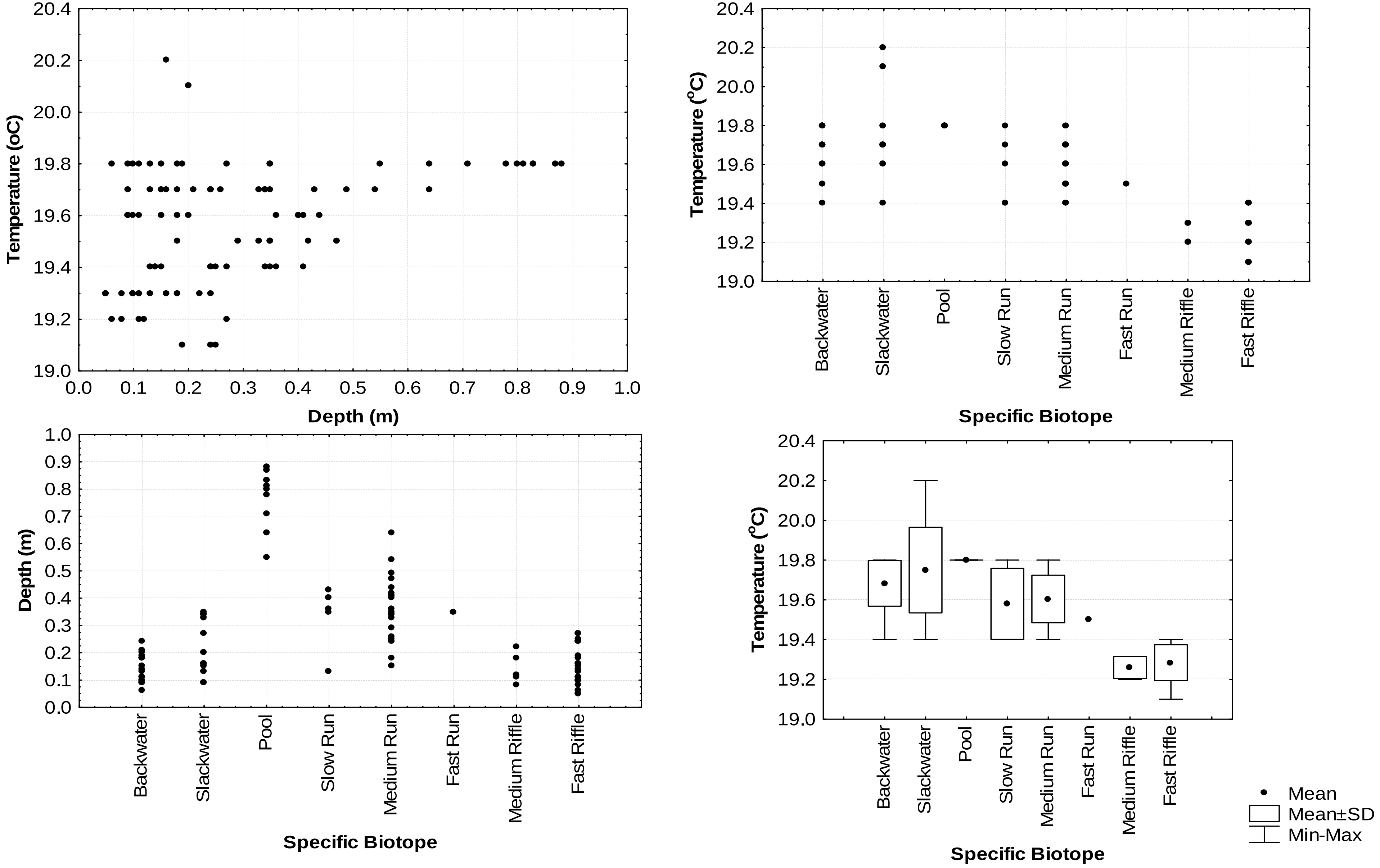


Figure 2.7 Water temperature plotted against water depth; temperature and depth recorded in each biotope; and mean (SD and min-max) values per biotope for the Eerste River

5. Recommendations for selecting sites for water temperature monitoring

Two types of sites are likely to be needed in order to generate data that may be used the management of temperature in aquatic ecosystems, specifically rivers. The first are sites which represent the reference condition or natural condition. These sites are used to provide baseline data with which other data is compared. The second are sites selected to characterise specific anthropogenic impacts that may impact upon water temperature, such as the removal of riparian vegetation, river regulation or the reduction in flow volumes through water abstraction. Reference sites need to be representative of a particular river type, generated within an appropriate spatial framework incorporating, for example ecoregions, longitudinal zones and substrate composition. For example an upper foothill site in the southern coastal ecoregion, with a cobble-boulder substrate and open canopy.

Considerations for selecting sites include (including contributions from Nick Rivers-Moore):

- Accessibility (by vehicle; inter-site distances affect costs)
- Safety (both in terms of leaving data loggers at the site and when sampling site or downloading data)
- Cryptic value (theft risk; private property / reserves offer less risk of loss of loggers)
- Reference sites – absence or limited anthropogenic impacts; lowland rivers may be “best-attainable”
- Reference and monitoring sites – representativeness of the river (i.e. thermal reaches)
- Existing data – water quality (especially temperature), biological data (aquatic invertebrates and fish), hydrological data
- Existing monitoring programmes – water quality monitoring, river health programme
- Hydrological data – presence of a flow gauging station and existing data
- Suitable aquatic biotopes representative of the particular river type
- Heuristic value (considerations = influences of dams, contributions of tributaries and hyporheic flows, effect of shading and aspect, residency times of water)
- Data integrity – may be buried in highly sedimented reaches; fidelity of attachment points!
- Hydrology: accessibility during high flows; likelihood of exposure during low-flows

6. References

Dallas, H. (2002). Spatial and temporal heterogeneity in lotic systems: implications for defining reference conditions for riverine macroinvertebrates, Rep. No. KV 138/03. Water Research Commission, Pretoria, South Africa.

Dallas, H., Day, J., & Reynolds, E. (1995). The effects of water quality variables on riverine biotas, Rep. No. 351/1/94. Water Research Commission, Pretoria, South Africa.

Ractliffe, S., Cullis, J., & Rooseboom, A. (In Press). Determination of Substratum Maintenance Flows in Cobble- and boulder-bed Rivers: Ecological and Hydraulic Considerations. Volume II: Flood disturbance responses of invertebrate assemblages in two cobble-boulder bed rivers of the Western Cape., Rep. No. K5/1411. Water Research Commission, Pretoria, South Africa.

CHAPTER 3: TERMS OF REFERENCE FOR FUTURE SOLICITED WRC WATER TEMPERATURE PROJECT

Deliverable 5 (Chapter 3) presents the Terms of Reference for a future solicited WRC temperature project developed collaboratively with Dr Rivers-Moore[1] and contributed to, from a technical perspective, by Dr Harding[2].

Abbreviations

- **BP**: Bruce Paxton (University of Cape Town)
- **DH**: Denis Hughes (Rhodes University)
- **FdM**: Ferdy de Moor (Rhodes University)
- **HD**: Helen Dallas (University of Cape Town)
- **NM**: Nikite Muller (Rhodes University)
- **NRM**: Nicholas Rivers-Moore (Rhodes University)
- **SM**: Sukhmani Mantel (Rhodes University)

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[1] Institute for Water Research, Rhodes University, PO Box 94, Grahamstown, 6140

[2] DH Environmental Consulting, P.O. Box 5429, Helderberg, 7135

Introduction

Previous deliverables, quoting a large body of scientific literature, have highlighted the importance of water temperature as a primary abiotic driver. The scoping exercise undertaken by the Water Temperature Consortium has highlighted the various crises and pressures faced by freshwater (specifically lotic) systems both globally and within South Africa. We focus on lotic ecosystems specifically, because these systems are subject to flow regulation and water abstraction to a much greater degree than lentic systems.

We further recommend that persistence of these ecosystems is more likely to be achieved through a better understanding of water temperature patterns and processes. This will require true interdisciplinary research, which stems from initial fundamental research, since according to Ashton *et al*. (2005), integrated research can only occur after a foundation of pure fundamental research has been built. We emphasise the necessity of extracting principles on water temperature relevant to South Africa, to inform policy, which in turn must be built on long-term trends and data. Northern hemisphere practices cannot be blindly applied to management issues in southern African rivers.

Significant outcomes of the Water Temperature Consortium have facilitated the drawing up of a Terms of Reference for a larger water temperature research project. It is recognised that only through a foundation of fundamental research linking water temperatures and biotic response will the water temperature requirements for the ecological Reserve be met. Our research has indicated that there are likely to be significant differences between northern hemisphere and southern hemisphere aquatic thermal regimes (Dallas, 2007; Rivers-Moore, 2007). The exact nature of these differences will only truly be understood through a series of carefully constructed *in situ* and *ex situ* projects linking biotic response to thermal triggers. The usefulness of these data will be further enhanced through a more complete spatial understanding of water temperatures, and a series of scenario analyses based on temperature simulations using a suitable water temperature model.

This deliverable was accomplished through regular correspondence between members of the Water Temperature Consortium (Drs. H. Dallas, W. Harding and N. Rivers-Moore). These Terms of Reference form the basis for an extended solicited WRC project aimed at defining guidelines for incorporating water temperatures into the ecological Reserve.

Terms of reference are divided into three themes, with each theme being further broken down into relevant tasks.

Theme A: Monitoring and Modelling

Task 1: Collection of baseline water temperature data (BH, HD and NRM)

Collection of baseline water temperature data is critical to understanding water temperature in rivers in South Africa. During the scoping exercise undertaken by the Water Temperature Consortium, appropriate water temperature loggers and data readers have been manufactured (Harding In prep). This will facilitate the installation of loggers at sites across a broad geographic range, which will generate a substantial amount of data on water temperatures. Sites should represent a range of stream orders and longitudinal zones, and be derived randomly within broad regions. Monitoring sites used for existing programmes such as the DWAF water quality monitoring programme and the River Health Programme (RHP) will be examined and used if appropriate. In addition to these sites, specific temperature-related project sites will be identified. Data generated will be used to contribute to various projects including the identification of thermal modifiers (Theme A, Task 2), temperature and ecology (Theme B) and the spatial framework and characterisation of thermal regions or types (Theme C, Task 1). To achieve this goal, the following will be undertaken:

- Liaison with RHP practitioners and identification of sites for the installation of loggers (approx. 10 per province – 90 sites) (HD)
- Selection of sites linked to proposed temperature projects (HD, NRM)
- Rationalisation and final selection of baseline data sites (HD, NRM, BH)
- Installation of loggers (BH, HD, NRM)
- Collection of hourly water temperature time series (2 years), which will be downloaded at 4-month intervals by suitably trained technicians (still to be identified).

Task 2: Develop a process-based understanding of selected water temperature modifiers (turbidity and flow) in South African rivers (NRM, DH, SM and HD)

The extent to which anthropogenic factors modify the thermal regime of rivers in South Africa is not known. Factors include both direct (thermal discharges) and indirect factors (land use changes, agricultural irrigation return-flows, flow modifications (river regulation), interbasin water transfer, modification to riparian vegetation and global warming). The identification of the magnitude of each thermal modifier within the South Africa context would provide insight into management of thermal changes in river systems. The utility of a proposed water temperature model will be greatly enhanced by the inclusion of flow and turbidity terms. Both these parameters typically reflect changes in catchment land use. If these terms are to be meaningfully used in a water temperature model, it is necessary to understand how water temperatures respond to these variables. Once this has been achieved, it will be possible to simulate water temperature time series under a range of different land use and climate change scenarios. To achieve these goals, the following will be undertaken:

- Collation of information on flow modifications, including river regulation and interbasin water transfers, and calculation of extent of abstraction based on predicted and actual mean annual runoff.
- Evaluation of temperature signals attached to different flow events. This should include, *inter alia*, studies on the following:
  - ⇒ Contribution of tributaries to water temperatures (with possible link to thermal ecotones and associated biotic patterns – see Theme B, Task 5)
  - ⇒ Response of water temperatures to flow modifications – also see Theme B, Task 5
  - ⇒ Relationship between extreme low flows and water temperatures
  - ⇒ Identification of known direct discharges of heated water into river systems;
- Further investigation, based on empirical data, into the relative sensitivity of water temperatures to groundwater versus surface water inputs, and the relative contributions of groundwater and surface water to water temperatures along river longitudinal axes. This would involve collection of primary data (water temperature time series using the logging system identified in Theme A, Task 1, as well as groundwater data using piezometers). These data will be provided with a spatial context by identifying suitable surrogates for hyporheic/groundwater influences on water temperatures at a landscape level. The latter time series would include an evaluation of the use of preliminary groundwater maps available for South Africa, versus the use of simplified geological maps to derive surrogates for hyporheic influences. Biotic species richness patterns relative to groundwater versus surface water driven systems should be tested for correlations, based on data collected as part of Theme B. This could be developed in conjunction with broad river profile types, where different regions of the profile are associated with different hydraulic (and geomorphological) characteristics. Rivers-Moore and Jewitt (2004) have shown a distinct downstream gradient in water temperatures for the Sabie River, which could be related to river profiles.
- Further investigation into the relationship between turbidity and water temperatures. Links between sediment loads/ turbidity, water temperature and catchment condition (which links to primary productivity studies). A more comprehensive understanding of links between land use, changes in runoff and water temperature response is needed to refine the turbidity and flow terms in the water temperature model.
- Examination of available land use maps to identify regions of agricultural and forestry activities, regions of intact riparian vegetation, etc.

Task 3: Development of a working generic water temperature model for South African rivers (NRM, DH and SM)

Development of the water temperature model will rely, in part, on water temperature time series data collected as part of Theme A (Task 1) and Theme B.

- Progression from a conceptual to a working generic water temperature model for South Africa, through development of a simple, process-based water temperature model proposed in this report. This model will be developed to simulate daily minimum, maximum and mean water temperatures, both for within-reach and between-reach water temperature time series.
- An ecoregional approach will be adopted, so that relevant heat exchange coefficients and lookup tables (to include data on river types and geomorphology, and the relative importance of the different hydrograph components per thermal region defined in Theme C, Task 1) can potentially be used to simulate water temperatures for any river system in South Africa.

Task 4: Model evaluation and comparison (NRM, DH and SM)

- Model verification and validation (do turbidity and flow relationships identified in Theme A, Task 2 remain valid?). Explore the potential use of spatially continuous data (forward-looking infrared videography) for model verification.
- Comparison of water temperature simulations using the above-mentioned model and simulations using existing models (SSTEMP).

Theme B: The importance of water temperature in the ecology of aquatic organisms and the identification of biotic responses

Task 1: Identification of thermally sensitive aquatic invertebrates and the determination of threshold, avoidance and preferred temperatures for selected taxa (HD and NM)

Water temperature strongly influences the geographic distribution of a species. An understanding of the distribution of thermally sensitive taxa is essential if potential effects of an alteration in the thermal regime are to be determined. To achieve this goal, the following will be undertaken:

- Laboratory screening for thermal sensitivity of a range of aquatic invertebrates using the critical thermal maxima (CTM) method;
- Focused laboratory studies of selected aquatic invertebrates to determine critical thermal maxima and temperature preferences;
- Links to scenario modelling using degree days and predicted impacts on selected taxa (Theme C, Task 4)

Task 2: Life history studies on selected taxa to determine life history traits of aquatic insects (HD, NRM and FdM)

Temperature is known to influence life history cycles of aquatic insects, which have an immature aquatic phase and an adult terrestrial phase. Life history traits that are influenced by temperature include voltinism (the number of generations per year for a particular species), degree of synchrony, precision and rigidity of emergence, and flexibility. Research suggests that differences exist between the northern and southern hemisphere largely as a response to the unpredictability of lotic environmental regimes (temperature and flow). Latitude also influences life history traits. No studies have been undertaken in South Africa on life history traits. Knowledge on life history traits, in relation to variability and latitude, will provide important baseline data with which associated studies on the effects of changes in temperature on life history traits can be compared (Theme B, Task 2). To achieve this, the following is envisioned, potentially as one or two Master of Science dissertation:

- Selection of sites in rivers which are likely to exhibit different degrees of thermal variability (predictability) and latitude and installation of water temperature loggers at suitable sites.
- Monthly sampling of selected aquatic insects to determine life history traits (selection of suitable taxa will be guided by distribution patterns and thermal sensitivity).

- Water temperature data collected simultaneously with biological data will provide valuable information on thermal cues for different life history traits such as emergence (and possibly growth patterns).
- Relationships between body weight, fecundity and water temperature. This has clear management implications with its links to pest species (for example, predictive models on blackfly outbreaks – Rivers-Moore *et al*. in press) (Potential Honours Project)

Hypothesis to be tested:

- Highly variable river systems will be dominated by multivoltine rather than univoltine species.
- Highly variable river systems will be dominated by species exhibiting an asynchronous life history rather than a synchronous one.
- Ratio of multivoltine to univoltine species provides an index of system variability
- Highly variable river systems will be dominated by species with long emergence periods rather than ones with precise and rigid emergence periods.
- Highly variable river systems will be dominated by species with flexible life histories.

Knowledge generated during this project would expand our understanding of the influence of variability on life history traits and provide critical information on environmental cues for life history traits such as emergence. The data should enable biotic responses to be quantified for selected taxa and selected river types.

Task 3: The influence of water temperature on the emergence of aquatic insects (HD)

Many aquatic insects are adapted so that seasonal changes in temperature act as cues for the timing of emergence. The timing and duration of emergence involves responses to temperature, often interacting with photoperiod and dissolved oxygen. Elevated water temperatures often result in early emergence of insects, although no information is available for South African conditions. An understanding of the emergence of aquatic insects in local rivers, and the potential impact of elevated water temperatures, will provide useful information of temperature cues. To achieve this goal, the following will be undertaken (potential Honours Projects):

- Collection of suitable aquatic insects from the field for laboratory testing of emergence (knowledge of thermally sensitive insects will guide this selection).
- Laboratory manipulation of water temperature to determine the effect on emergence;
- Simultaneous field studies of the same taxa to determine emergence patterns under natural conditions (this may be linked with Theme B, Task 2).

- Identification of temperature cues for emergence for selected taxa and the impact of changes in temperature on emergence timing.

Understanding how temperature influences emergence of aquatic insects is important for setting Ecological Water Requirements. This project may be expanded to include other life history aspects such as growth and fecundity.

Task 4: Water temperature and fish ecology (BP and HD)

Although death resulting from heat stress is uncommon in nature since the upper thermal tolerances of many fish species are well above ambient temperatures, the ability to move, reproduce, feed, or resist disease or predation is impaired by sub-optimal temperatures giving rise to thermal barriers that limit the distribution of many fish species. Regional temperature shifts may therefore increase or decrease the permeability of thermal barriers thereby altering the geographic ranges of fish. This may be of special concern in cases where distributions of indigenous fish are extremely constrained (as is the case for many species in the Western Cape), or where temperature shifts facilitate range extensions by alien fish species. Although the mechanism limiting the distribution of freshwater fish may be difficult to isolate, indices of thermal tolerance such as the critical thermal maxima CTM provide some indication of relative preferences. To achieve this goal, the following will be undertaken:

- The critical thermal maxima CTM of the Clanwilliam sawfin *Barbus serra*, as well as selected redfin *Pseudobarbus* sp. in the Western Cape, will be investigated.
- The option of using in-situ experimental baths will be investigated that will circumvent the need for removing vulnerable fish species from their habitat.
- Where feasible, CTM investigations will be supplemented by an assessment of spawning period in relation to temperature regimes by comparing the relative gonad development stages and population structures of different *Pseudobarbus* groups across the Western Cape over the spawning period.
- Ongoing examination of the role of temperature and flow in the reproduction of *Barbus serra* (WRC Project K5/1483 ‘Fish habitat and movement’).

Task 5: Role of temperature variability in structuring invertebrate communities (NRM, FdM and HD)

Temperature is a key factor affecting the number and kinds of species in a stream (Vannote and Sweeney, 1980). Vannote and Sweeney (1980) proposed that variable seasonal river temperature patterns are the critical factor in maintaining temporal segregation in aquatic invertebrate communities, thus allowing for resource partitioning, and preventing competitive exclusions, while spatial differences in water temperatures allow for zonation of species. Diel temperature change increases the potential number of species which can coexist, as each one will be exposed to an optimum temperature during the day (Vannote and Sweeney, 1980). Within river systems, the role of biotic diversity is less important in maintaining ecosystem stability in highly stable physical systems, such as in headwaters. Conversely, as variability increases with downstream distance, the role of biotic diversity becomes more critical in maintaining ecosystem stability. Within this paradigm, water temperatures contribute to instability (Vannote *et al.,* 1980). Thus biotic diversity mirrors variability in the daily temperature pulse along the longitudinal axis of a river, peaking in the mid-reaches. Within the headwaters, aquatic diversity is low because only invertebrates with narrow temperature tolerances persist (Vannote *et al.,* 1980).

Such predictions have important consequences in terms of testing the applicability of the river continuum concept to South African rivers, and ultimately in developing an ecologically meaningful water temperature classification for the ecological Reserve. An additional implication of establishing links between aquatic community patterns and water temperature variability is that of estimating reset distances in response to thermal and flow discontinuities.

To achieve this, the following is envisioned, primarily as a Master of Science dissertation:

- Selection of two river systems (one variable and one less variable thermally). Quarterly surveys of aquatic macroinvertebrates along the longitudinal axes of both rivers will be undertaken. Hourly water temperature time series will be collected at each survey site (20 loggers and 2 data readers).
- Sites will also be located upstream and downstream of impoundments to study the effects of river discontinuities on aquatic community reset distances, and at the confluence of lower order tributaries with higher order rivers, to determine the effects of thermal ecotones on aquatic macroinvertebrate community patterns.

Hypotheses to test:

- The degree of predictability in a stream’s water temperatures provides an indication of the degree of structure and functional predictability of invertebrate communities (Vannote and Sweeney, 1980).
- Aquatic species typically respond in predictable ways to changing environmental conditions. Biological strategies depend on the reliability of a pattern (Colwell, 1974), or on how often the system fails (Hashimoto et al., 1982). The temporal partitioning of invertebrate species (functional feeding groups, biomass and diversity indices) relates to water temperature variability
- Diversity increases at thermal ecotones

Task 6: Effect of temperature extremes on aquatic invertebrates in the Western Cape (HD)

Effects of temperature extremes on biotic communities (since temperature extremes were shown to be important by Rivers-Moore (2007 – see Deliverable 2). Summer water temperature maxima, which coincide with low flows, have been shown to be important in Western Cape rivers. Climate change is predicted to result in lower rainfall and elevated air temperatures in the Western Cape (Dallas, 2007 – see Deliverable 1). To test the importance of summer maxima is determining the distribution of aquatic invertebrates, field surveys over the summer period will be undertaken in the Western Cape. To achieve this goal, the following will be undertaken:

- Field surveys of approximately 100 sites (primarily upland areas) for water temperature and aquatic invertebrates, identified to family level in the field and verified in the laboratory
- Utilisation of data to predict potential changes in the distribution of aquatic invertebrates

Task 7: Examination of micro-scale heterogeneity in water temperature (HD)

Water temperature may vary at the level of reach or site, with variation occurring laterally across the channel, in relation to side-channels, groundwater seeps and different habitats such as pools, riffles and backwaters. Such heterogeneity is likely to be important to aquatic organisms, particularly fish, which are known to utilise thermal refugia (cold patches) and often thermoregulate by migrating to areas of cooler water when surrounding water temperatures are outside of their preferred range or exceed their upper tolerances. The extent of micro-scale heterogeneity would have implications for the management of water temperature. To achieve this goal, the following will be undertaken:

- Selection of sites for intensive water temperature logging whereby the range of habitats and potential areas of thermal heterogeneity are logged;
- Quantification of thermal heterogeneity at these sites and identification of thermal refugia.

Additional projects undertaken independently but which will be collaborative and provide data relevant to the water temperature project.

- Project 1: Links between thermal pollution and parasite loads in fish (Dr Cecile Reid, Freshwater Research Unit, Department of Zoology, University of Cape Town) Links between flows/temperatures/eutrophication and parasite loads – important for defining the ecological Reserve

- Project 2: Links between water temperatures and primary productivity (Justine Ewart-Smith and Dr Jackie King, Freshwater Research Unit, Department of Zoology, University of Cape Town) – WRC funded project

Theme C: Management issues and the ecological Reserve

Many thermally polluted sites have excellent habitat structure. To avoid this pitfall in defining the ecological Reserve requires that a suitable water temperature classification be developed, to define "reference" conditions, and departure from these with associated suitable confidence intervals. Additional critical water temperature management issues include the effects of thermal ecotones on aquatic macroinvertebrate community structure, often associated with river discontinuities. Effective management can also only occur through an understanding of the effects of scale on water temperatures (stream order), and scenario analyses which consider the impacts of land use change and/ or climate change on water temperatures and aquatic biota.

Task 1: Development of a spatial framework for managing water temperature (NRM and HD)

Water temperature varies spatially (site, zone and region) and temporally (diel, annually and inter-annually). An understanding of hierarchical temporal and spatial dynamics of water temperatures (the extent of this variation in time and space at different scales) is critical for the management of water temperature in river systems. To achieve this it is proposed that a spatial framework be generated whereby "thermal regions" or "thermal types" are identified. These regions or types would classify rivers into homogeneous groups with similar thermal regimes. To achieve this goal, the following will be undertaken:

- Collection of water temperature time series (1 year – see Theme A, Task 1) at selected sites covering a broad geographic range and, where possible, encompassing a range of conditions known to influence water temperature such as extent of riparian cover, groundwater contribution, water volume, etc.
- Linking water temperature metrics to suitable spatial surrogates (which may include, *inter alia*, air temperatures, elevation, rainfall indices, frost duration and groundwater zones) using multiple linear regression modelling in conjunction with a suitable raster-based geographic information system. This will be used to establish broad trends in water temperature and to use this information to identify preliminary thermal regions or types.
- Verification of the preliminary thermal regions or types with water temperature time series (2nd year – see Theme A, Task 1) and finalisation of thermal regions or types.

- Characterisation of each thermal region or type in terms of the natural (reference) thermal regime, including the components considered important from an ecological perspective.
- Generation of a map (if appropriate) and/or key for users to categorise a river into a particular thermal type.
- Map of aquatic thermal variability in South Africa, based on coefficients of variation.

Task 2: Develop an ecologically relevant water temperature classification (NRM, DH, SM, and HD)

- Develop an approach similar to the "range of variability" concept developed by Richter *et al*. (1997) and used in measuring change in flow time series (timing, duration, magnitude and frequency of events) (Richter *et al*., 1996). It should also include defining water temperature states or classes suitable for Colwell's (1974) predictability indices. Understanding of the predictability or cyclical constancy of water temperatures, and how this changes with downstream distance is an important predictive tool in relating biotic response to abiotic change.
- Develop guidelines for the definition of reference conditions, and associated confidence levels/intervals
- Investigate the applicability of the river continuum concept (Vannote *et al*., 1980) to South African rivers, based on a more systematic understanding of northern versus southern hemisphere differences in water temperature regimes, which present both management and simulation challenges.
- Explore the importance of scale in designing management approaches to river systems (see Frissel *et al*., 1986). This should include the relationship between stream order (and flow volumes) and water temperature (diel range, degree days and predictability), with due consideration given to landscape and riverscape approaches.

Task 3: The ecological Reserve and Management issues (NRM, HD and DH)

- Development of indices using aquatic macroinvertebrates (biomass and functional feeding groups) to reflect changes in water temperature based on the water temperature classification (Theme C, Task 2). Explore the response (and response type – linear or non-linear) of invertebrate communities to temperature degradation/ thermal stress.
- Set initial recommended thresholds of variability and seasonality for the ecological Reserve, as defined by geographic region (with due consideration of the applicability of the ecoregion approach (Level I and II) to classifying water temperatures for the ecological Reserve). Define management targets (water temperatures and associated

flows) by linking biotic response to thermal triggers (see Theme B, Tasks 1-4) using agglomerative techniques (duration curves, cumulative degree days) and the water temperature classification (Theme C, Task 2).

- Investigate the relative importance of discontinuities with respect to catchment position and their effect on water temperatures (e.g. effect on diel temperatures). This will involve research on relationships between flow volumes, flow velocity and water temperatures on reset distances (and how this changes seasonally) as reflected in changes in invertebrate communities. Due consideration will also be given to the role of discontinuities in creating thermal ecotones, and how this relates to aquatic biodiversity.

Task 4: Scenario analyses (land use, climate and flow volume changes) (NRM, DH, SM, HD and BP)

- Scenario analyses using temperature triggers for selected economically important species, for example outbreaks of the pest blackfly *Simulium chutteri*.
- Potential impacts of temperature changes (due to land use change, climate change, flow change) on selected invasive aquatic organisms (fish and invertebrate species)
- Potential impacts of temperature changes (due to land use change, climate change, flow change) on cold water stenothermic endemics (selected fish and invertebrate species)

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Summary diagram showing the themes and associated tasks for the proposed WRC Water Temperature project

A1: *Collection of baseline water temperature data*

A2: *Develop a process-based understanding of selected water temperature modifiers (turbidity and flow) in South African rivers*

A3: *Development of a working generic water temperature model for South African rivers*

A4: *Model evaluation and comparison*

Theme A

Monitoring and Modelling

B1: *Identification of thermally sensitive aquatic organisms and the determination of threshold, avoidance and preferred temperatures for selected taxa*

B2: *Life history studies on selected taxa to determine life history traits of aquatic insects*

B3: *The influence of water temperature on the emergence of aquatic insects*

B4: *Water temperature and fish ecology*

B5: *Role of temperature variability in structuring invertebrate communities*

B6: *Effect of temperature extremes on aquatic invertebrates in the Western Cape*

B7: *Examination of micro-scale heterogeneity in water temperature*

Theme B

The importance of water temperature in the ecology of aquatic organisms and the identification of biotic responses

C1: *Development of a spatial framework for managing water temperature*

C2: *Develop an ecologically relevant water temperature classification*

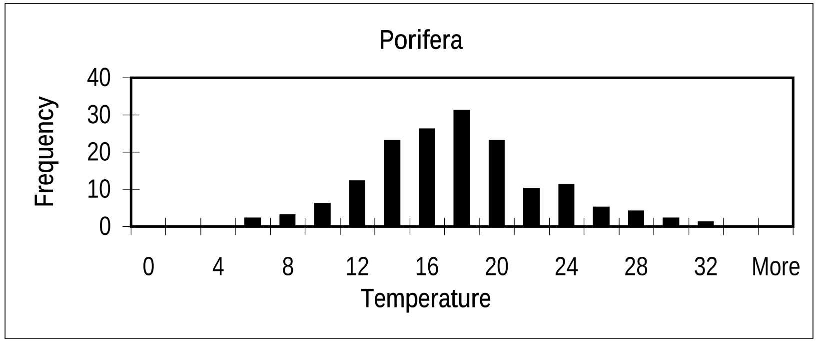
C3: *The ecological Reserve and Management issues*

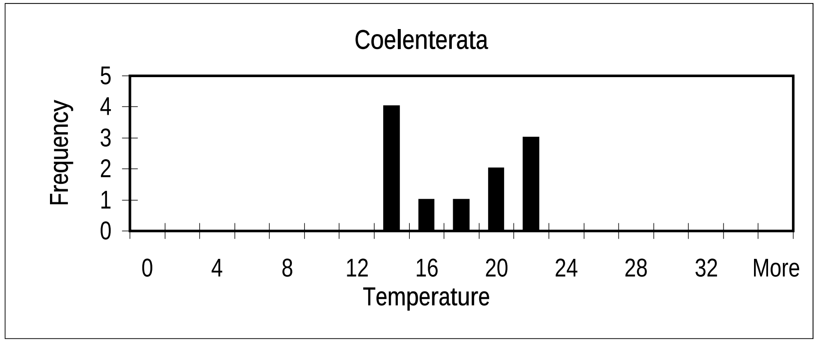
C4: *Scenario analyses (land use, climate and flow volume changes)*

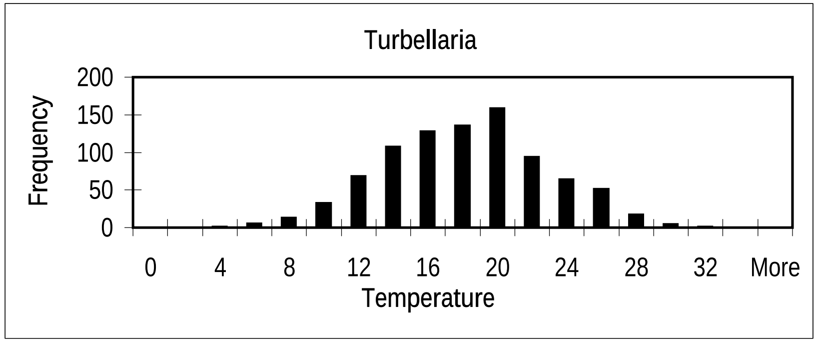
Theme C

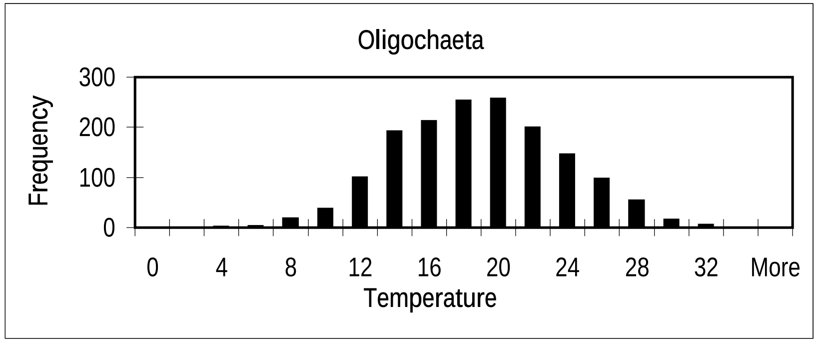
Management issues and the ecological Reserve

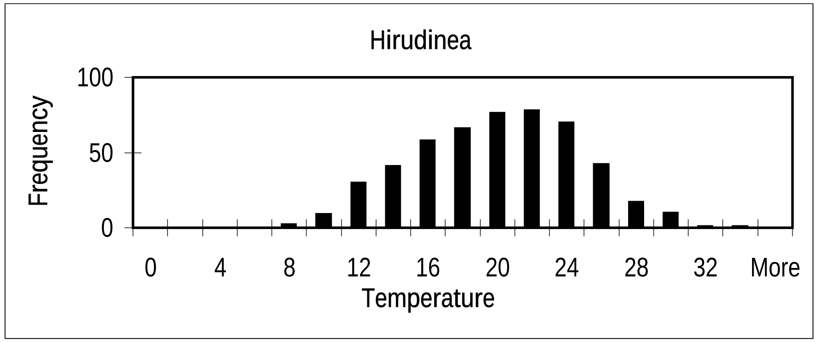
Appendix 1A. Temperature tolerance ranges based on recorded field temperatures in the Rivers Database (January 2007) Porifera, Coelenterata, Turbellaria, Annelida: Oligochaeta and Hirudinea, and Hydracarina

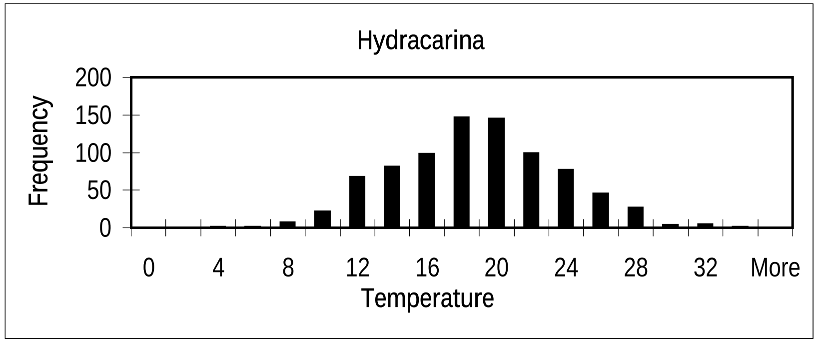




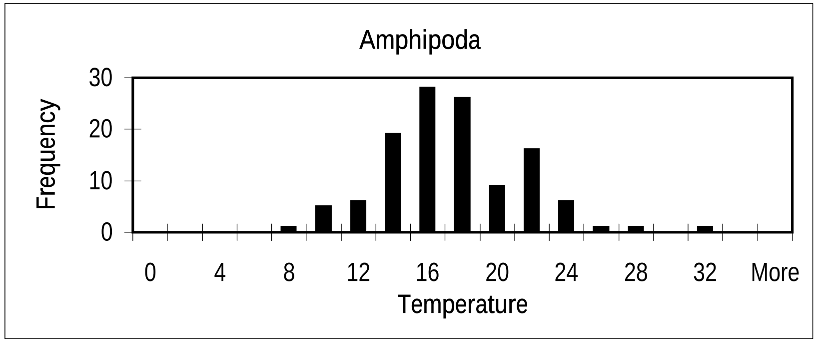


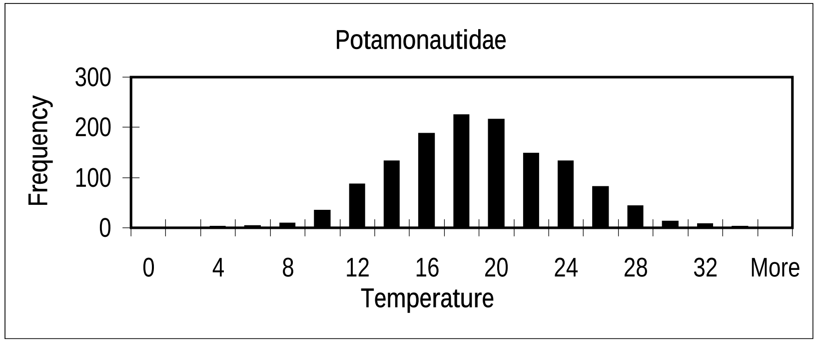


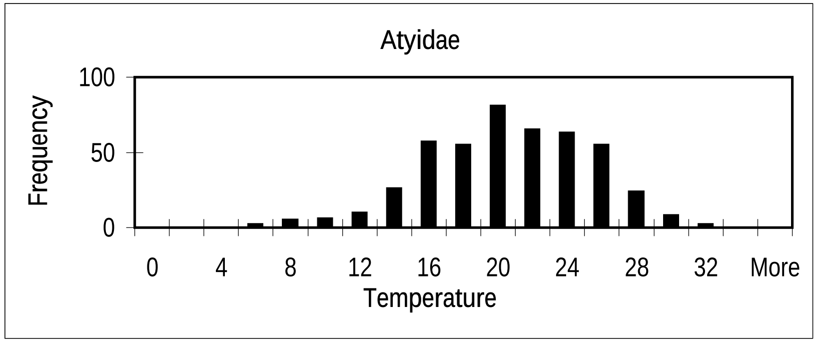


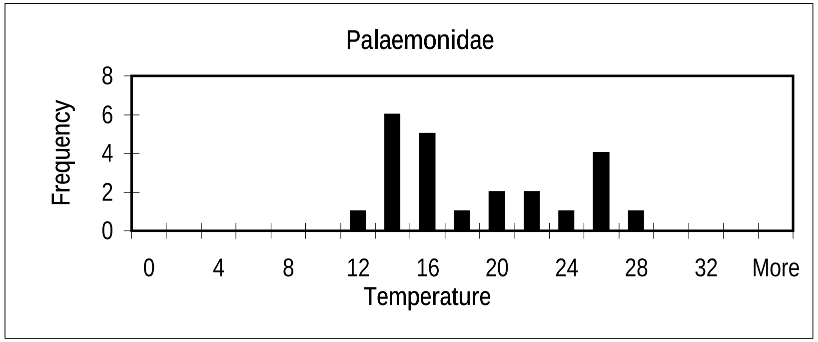


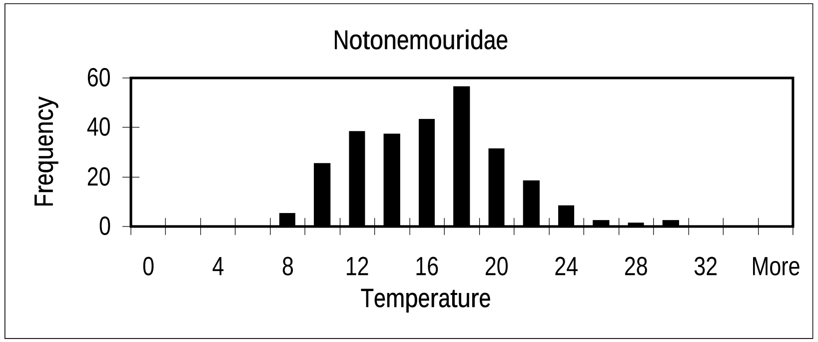
Appendix 1B. Temperature tolerance ranges based on recorded field temperatures in the Rivers Database (January 2007) Crustacea: Amphipoda, Potamonautidae, Atyidae and Palaemonidae and Plecoptera: Notonemouridae and Perlidae

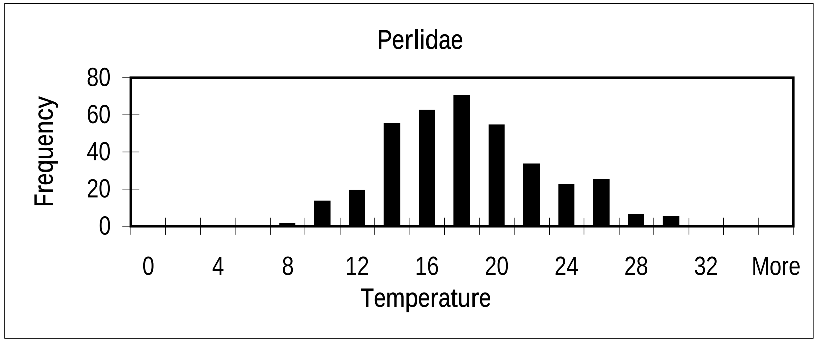




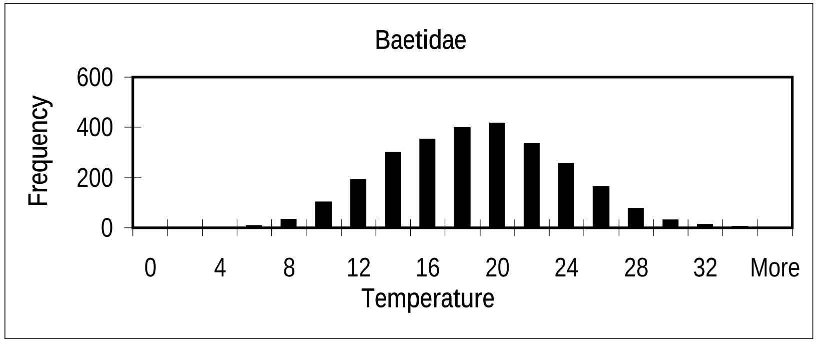


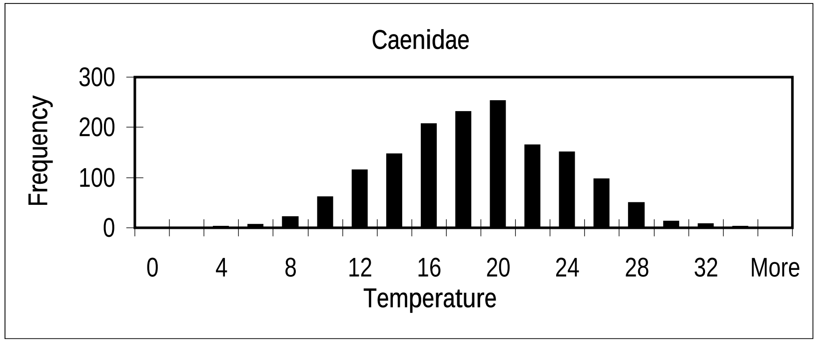


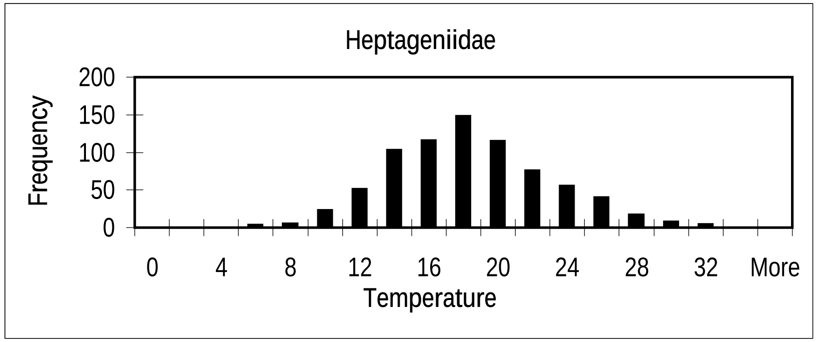


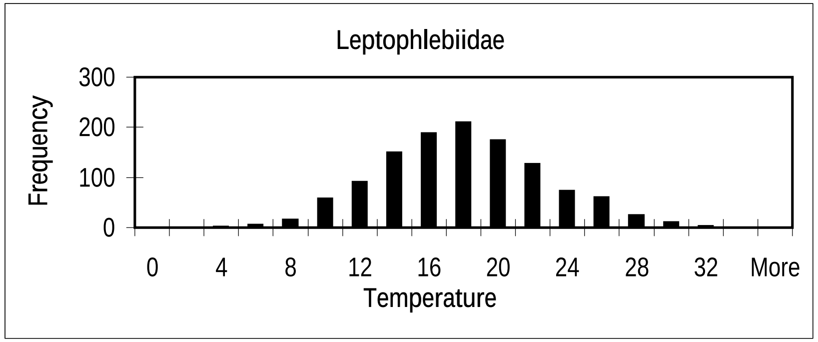


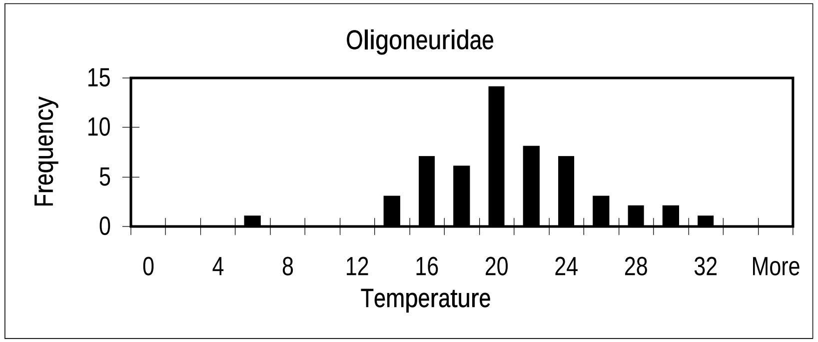
Appendix 1C. Temperature tolerance ranges based on recorded field temperatures in the Rivers Database (January 2007)
Ephemeroptera: Baetidae, Caenidae, Heptageniidae, Leptophlebiidae, Oligoneuridae and Polymitarcyidae

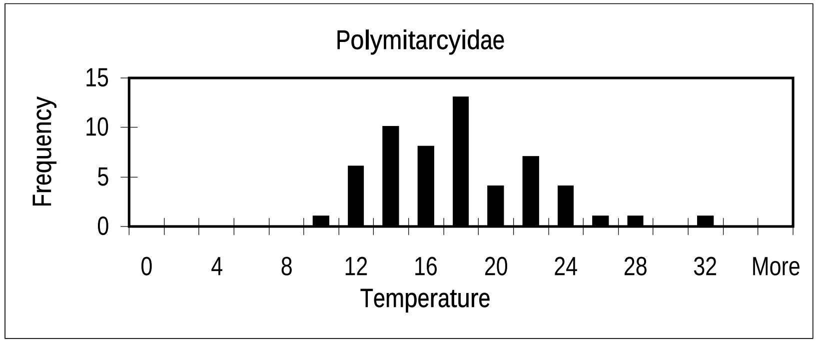




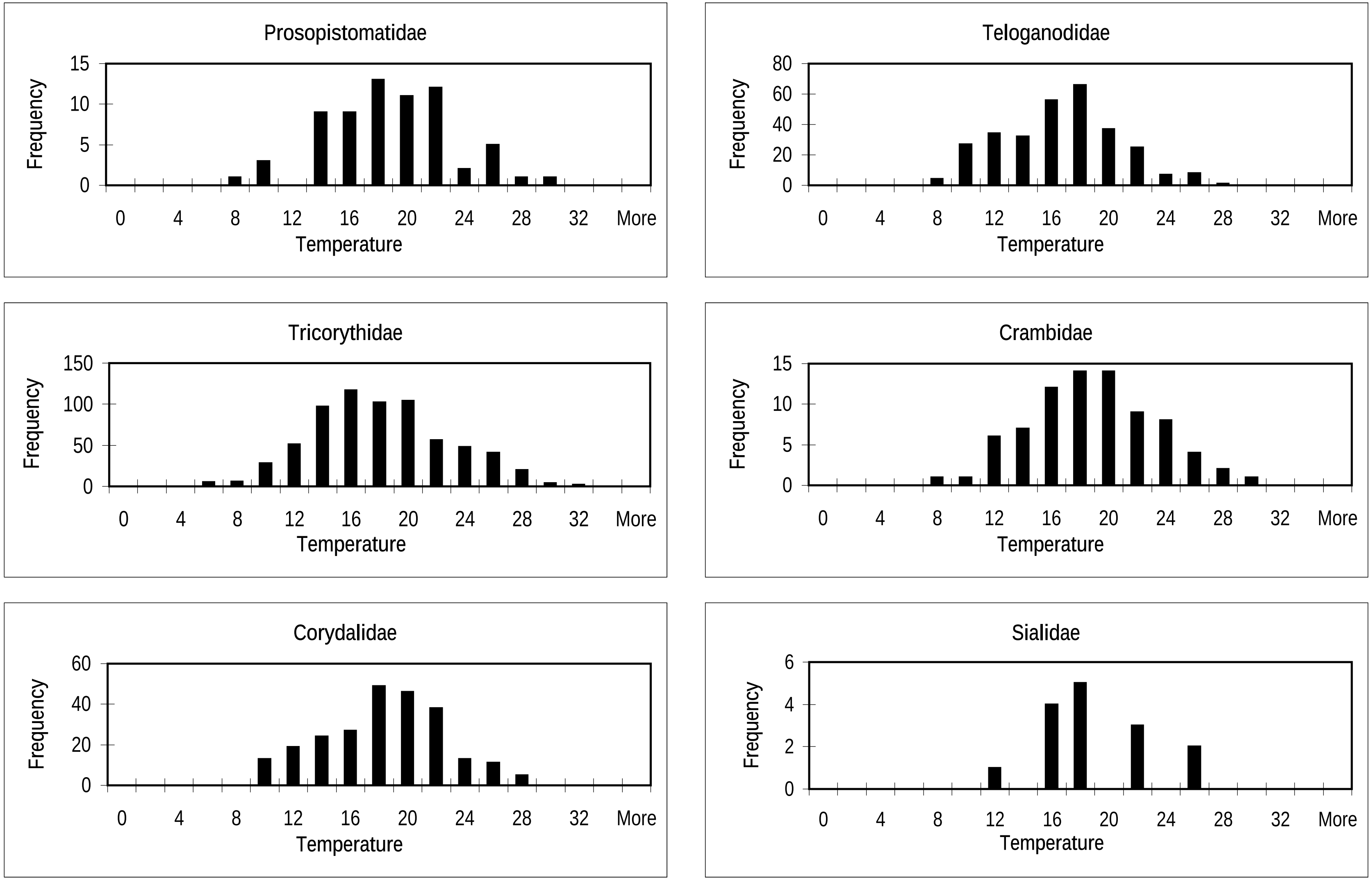




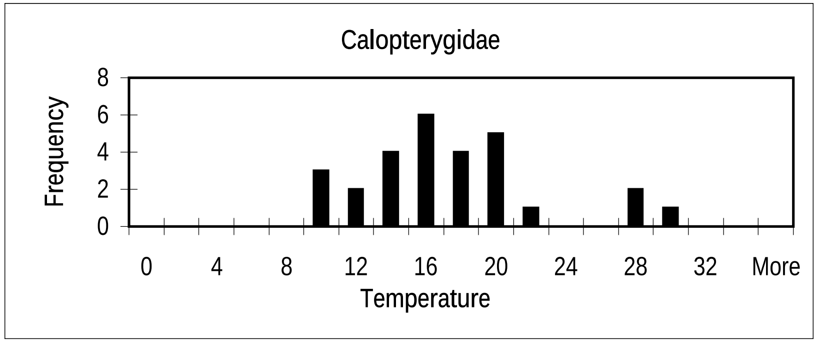


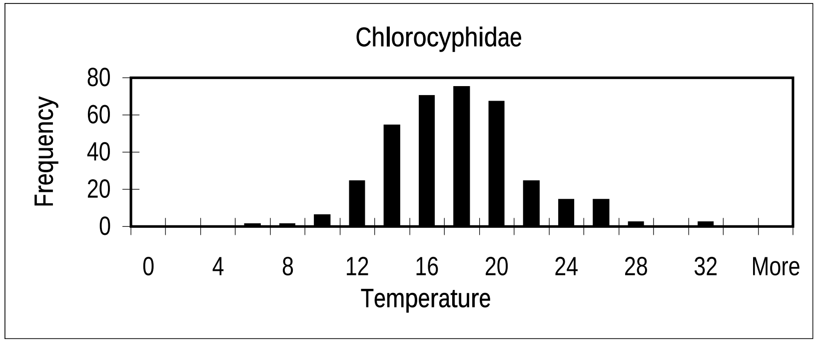


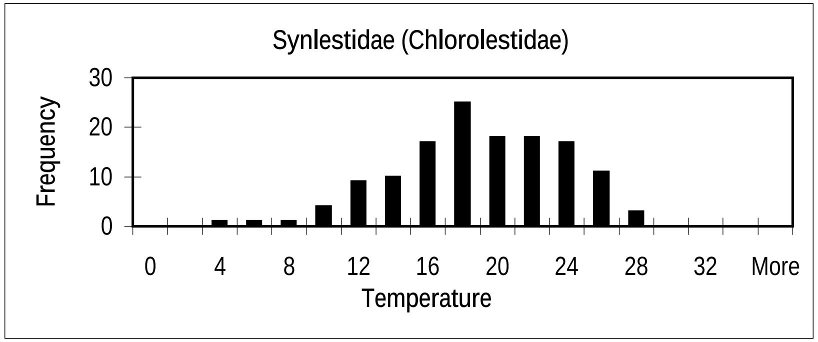
Appendix 1D. Temperature tolerance ranges based on recorded field temperatures in the Rivers Database (January 2007)
Ephemeroptera: Prosopistomatidae, Teloganodidae and Tricorythidae; Lepidoptera: Crambidae and Megaloptera: Corydalidae and Sialidae

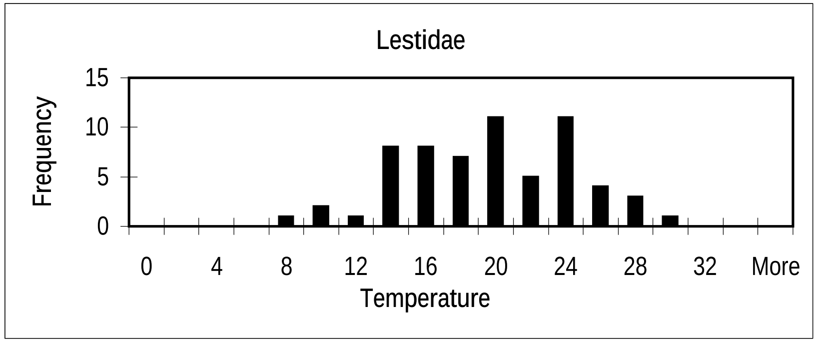


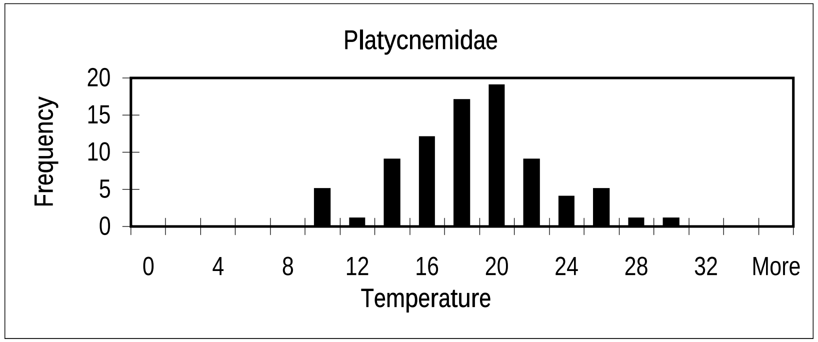
Appendix 1E. Temperature tolerance ranges based on recorded field temperatures in the Rivers Database (January 2007) Odonata: Calopterygidae, Chlorocyphidae, Synlestidae (Chlorolestidae), Lestidae, Platycnemidae and Protoneuridae

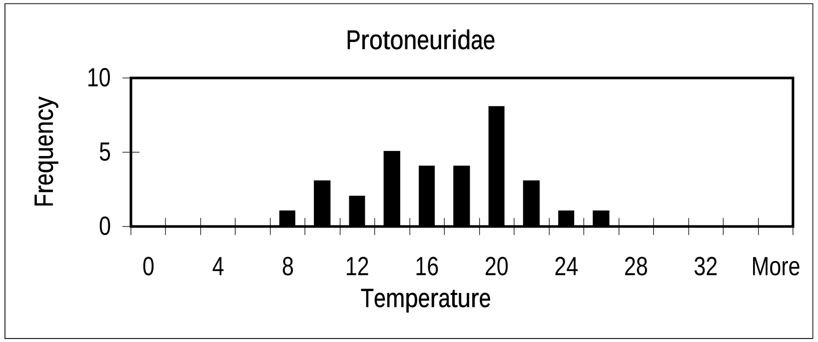




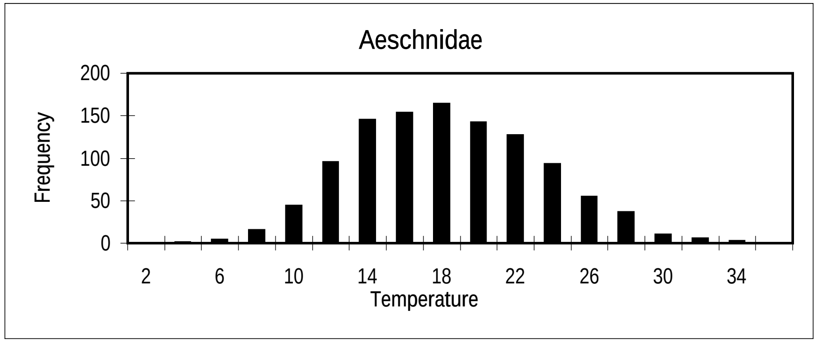


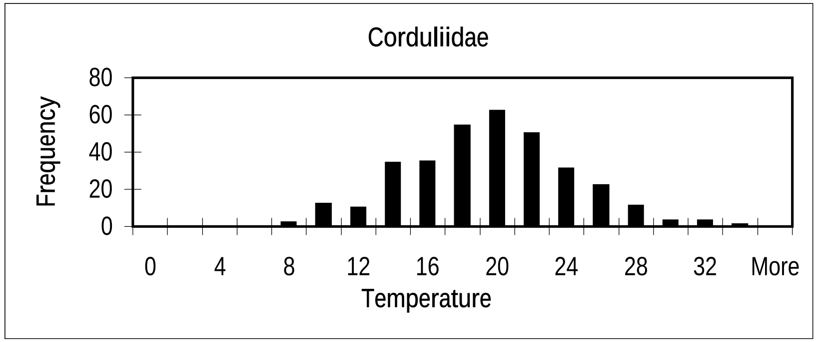


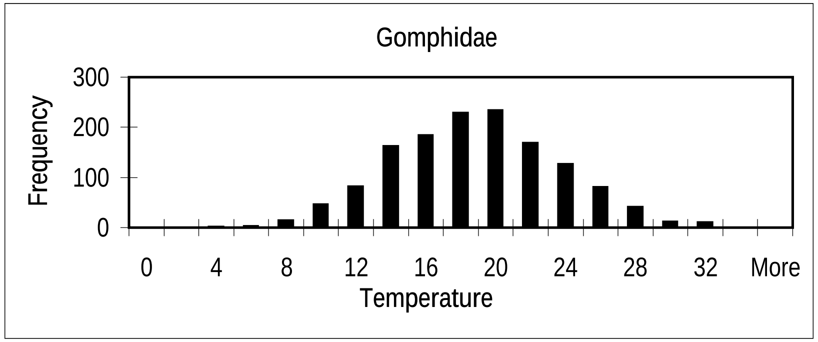


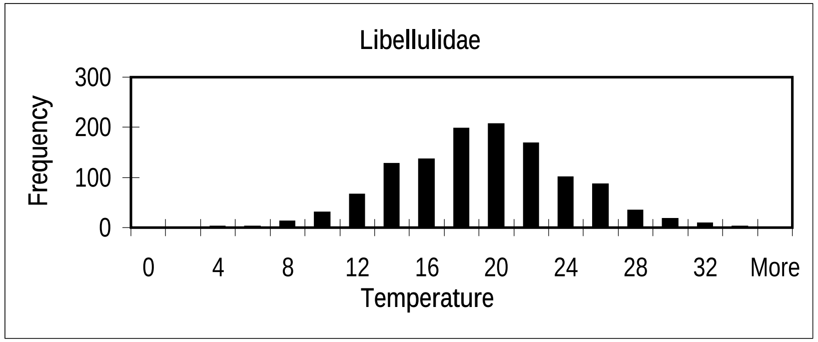


Appendix 1F. Temperature tolerance ranges based on recorded field temperatures in the Rivers Database (January 2007) Odonata: Aeschnidae, Corduliidae, Gomphidae and Libellulidae



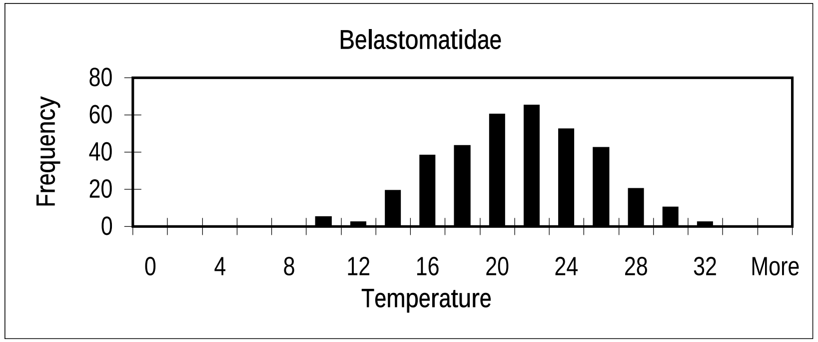


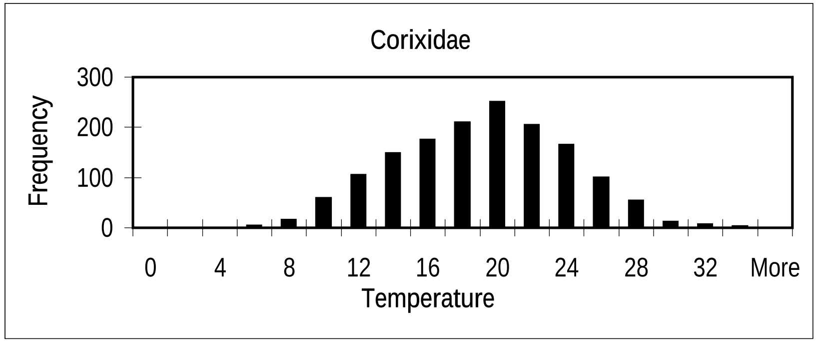


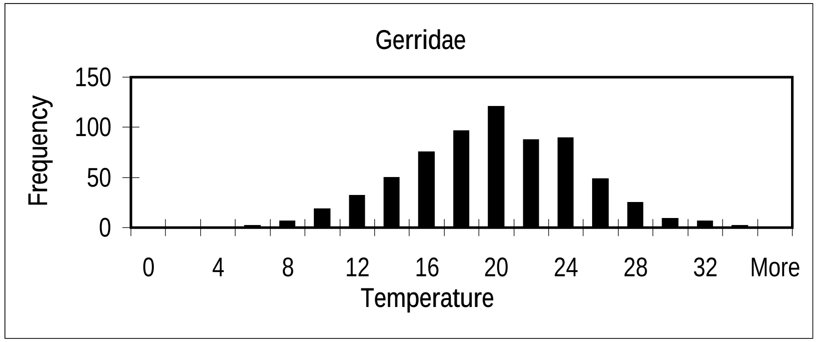


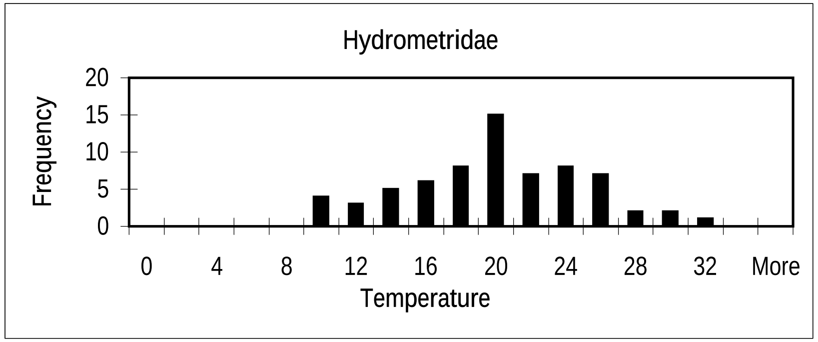
Appendix 1G. Temperature tolerance ranges based on recorded field temperatures in the Rivers Database (January 2007)

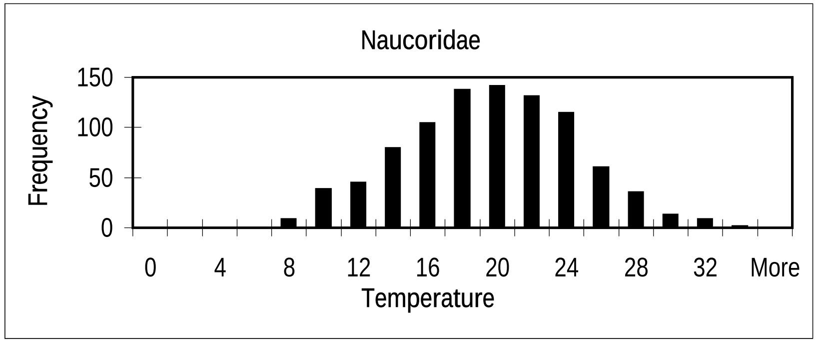
Hemiptera: Belastomatidae, Corixidae, Gerridae, Hydrometridae, Naucoridae and Nepidae

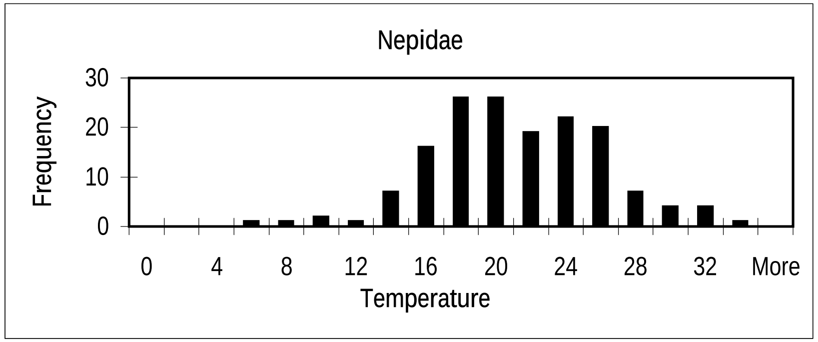




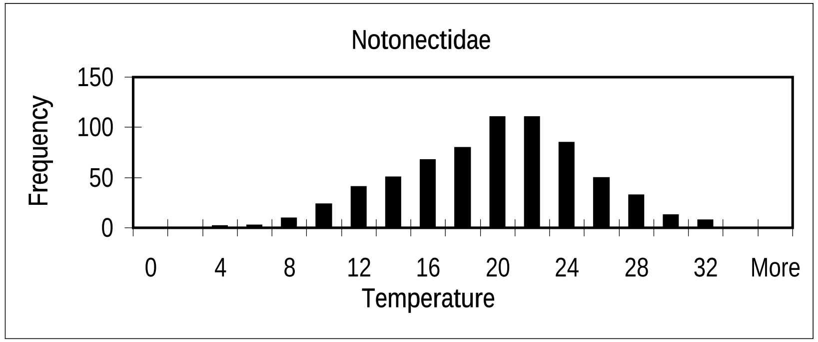


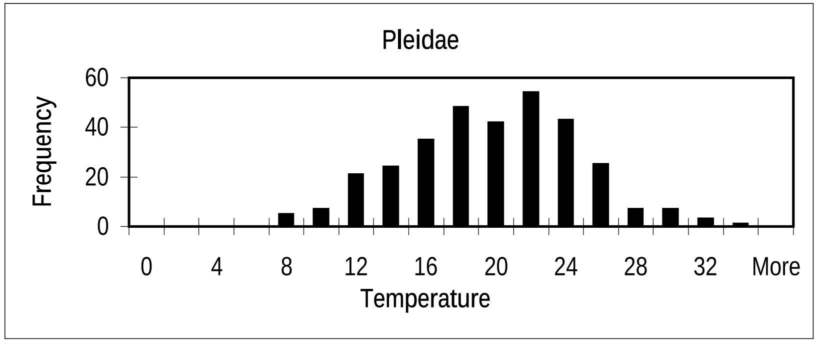


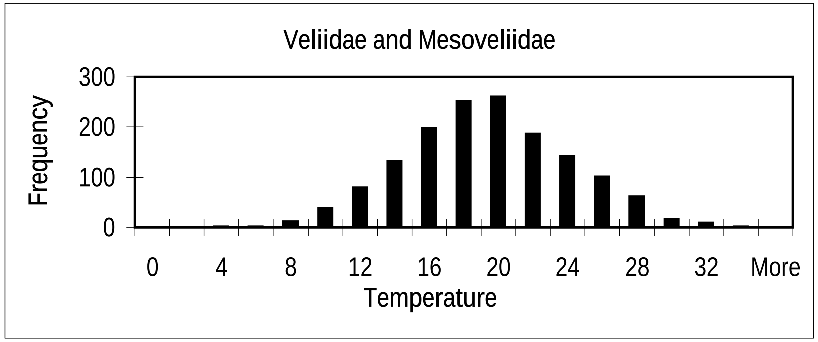




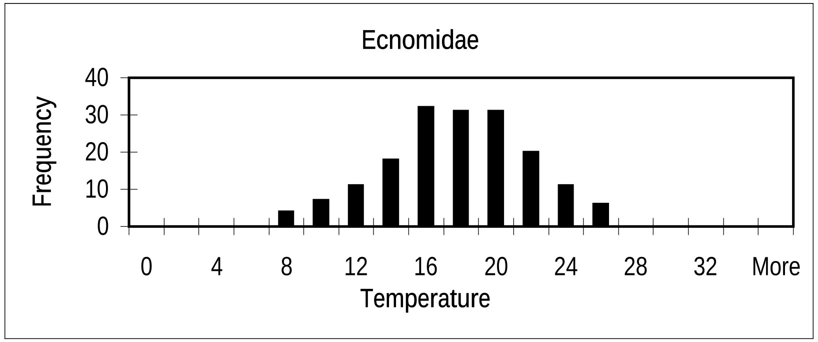
Appendix 1H. Temperature tolerance ranges based on recorded field temperatures in the Rivers Database (January 2007) Hemiptera: Notonectidae, Pleidae and Veliidae (Mesoveliidae)

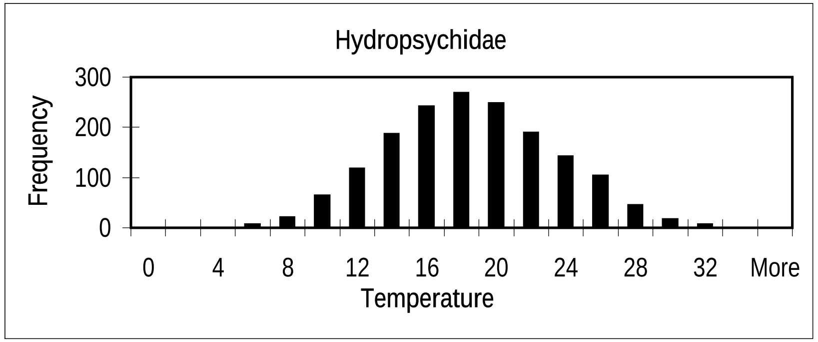


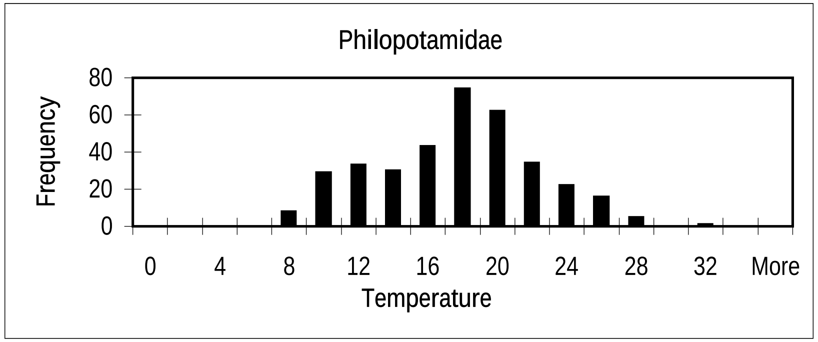


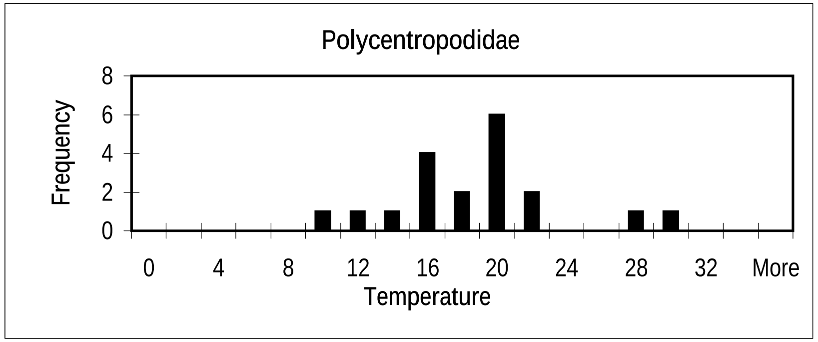


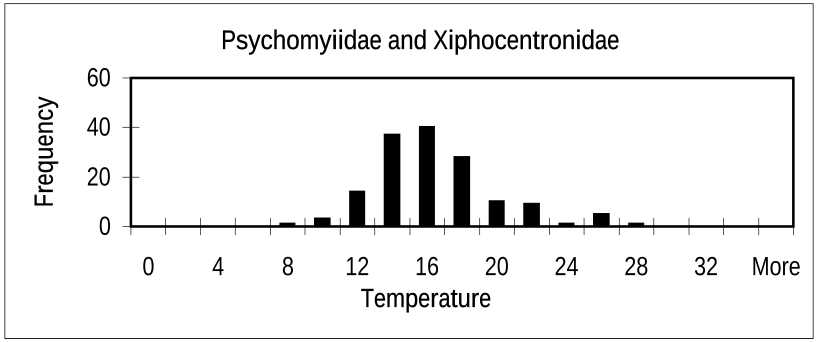
Appendix 1I. Temperature tolerance ranges based on recorded field temperatures in the Rivers Database (January 2007) Trichoptera: Ecnomidae, Hydropsychidae, Philopotamidae, Polycentropodidae and Psychomyiidae



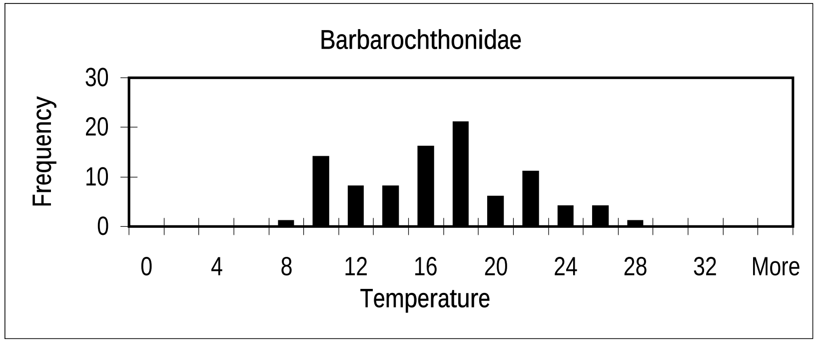


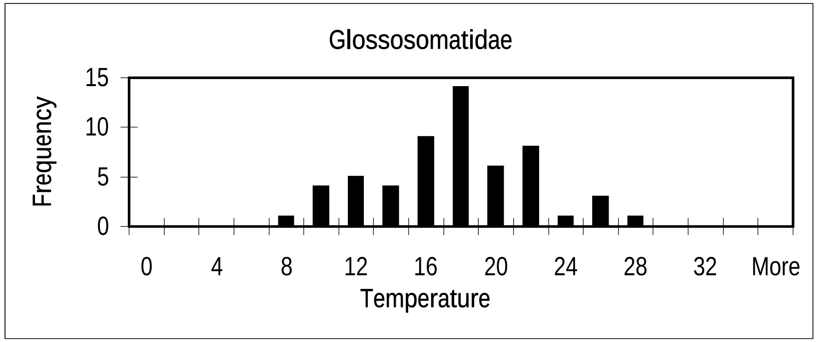


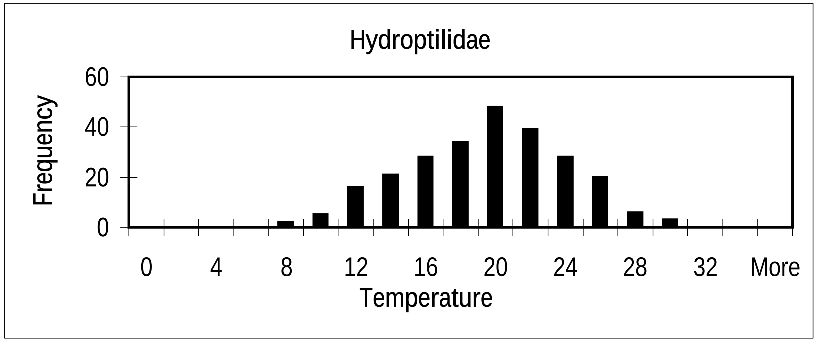


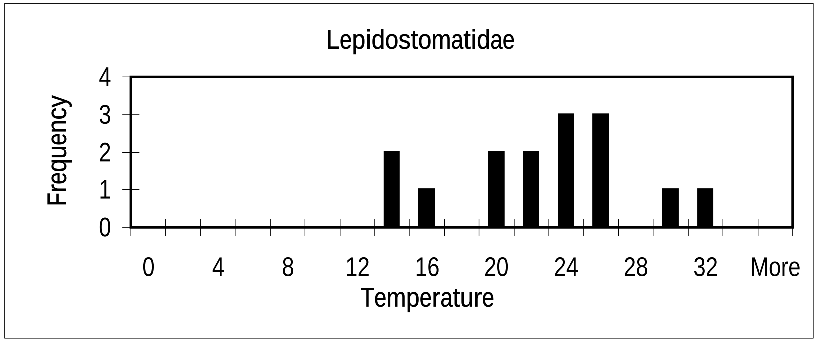


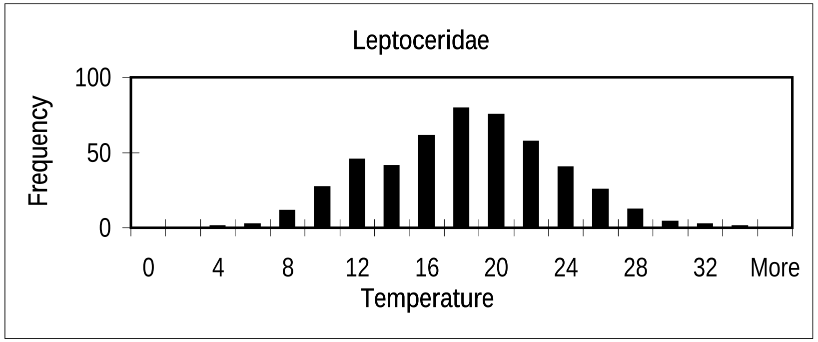
Appendix 1J. Temperature tolerance ranges based on recorded field temperatures in the Rivers Database (January 2007)
Trichoptera: Barbarochthonidae, Glossosomatidae, Hydroptilidae, Lepidostomatidae, Leptoceridae and Petrothrinicidae

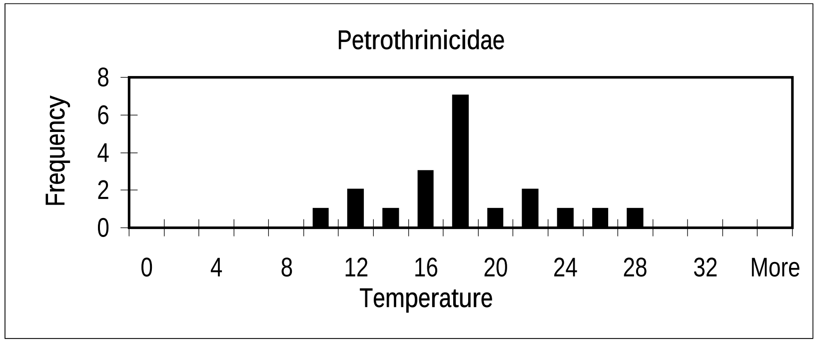

Barbarochthonidae


Glossosomatidae

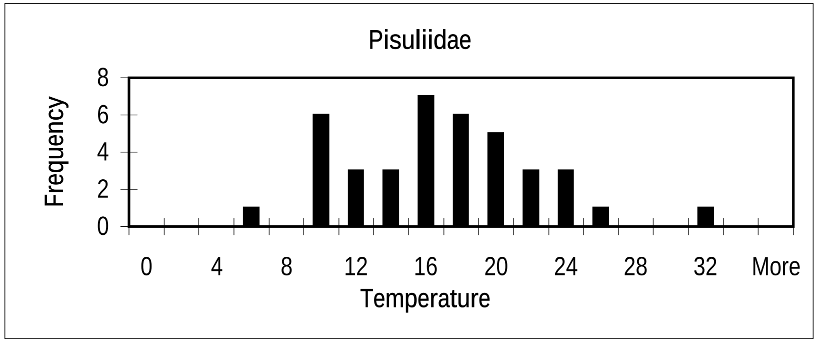

Hydroptilidae

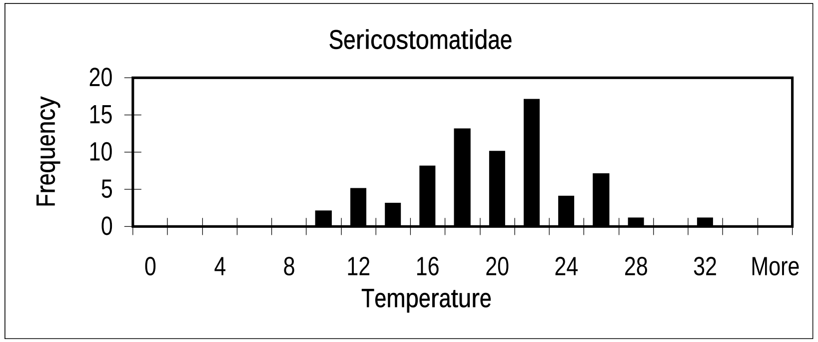

Lepidostomatidae

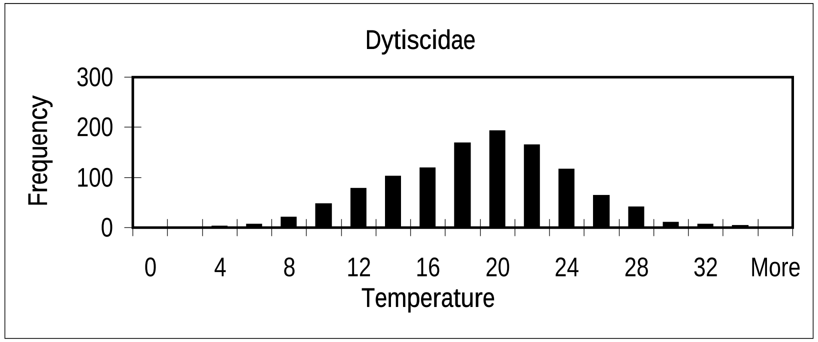

Leptoceridae

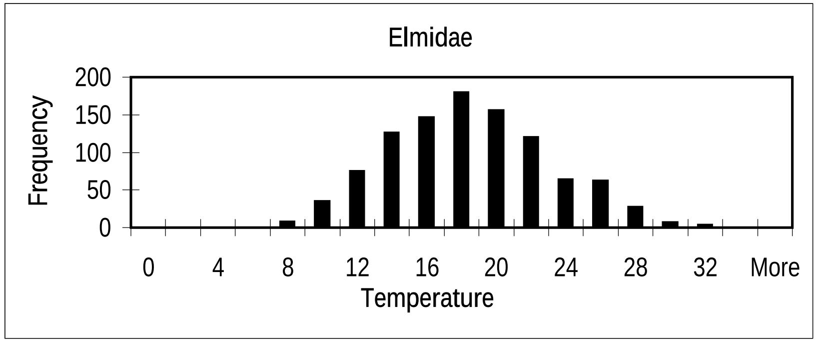

Petrothrinicidae

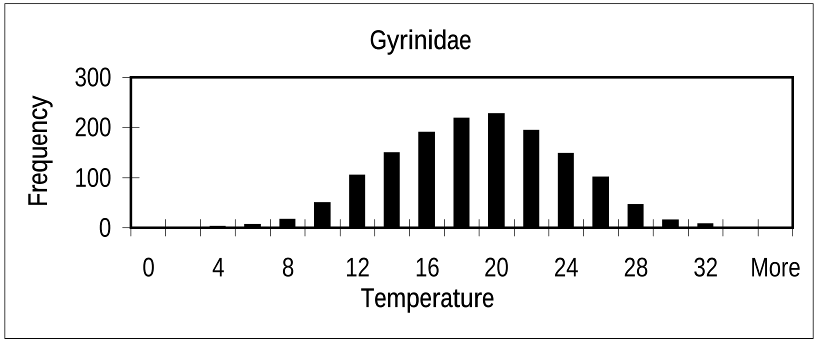
Appendix 1K. Temperature tolerance ranges based on recorded field temperatures in the Rivers Database (January 2007)
Trichoptera: Pisuliidae and Sericostomatidae; Coleoptera: Dytiscidae, Elmidae, Gyrinidae and Haliplidae

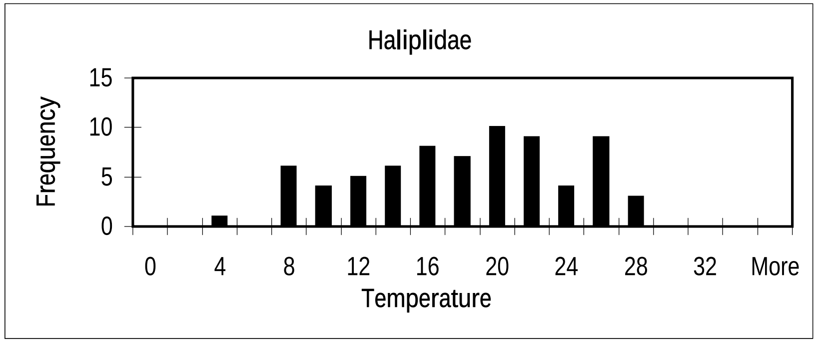




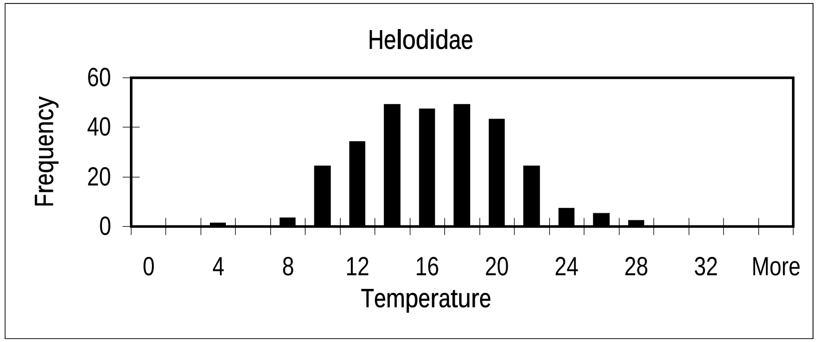


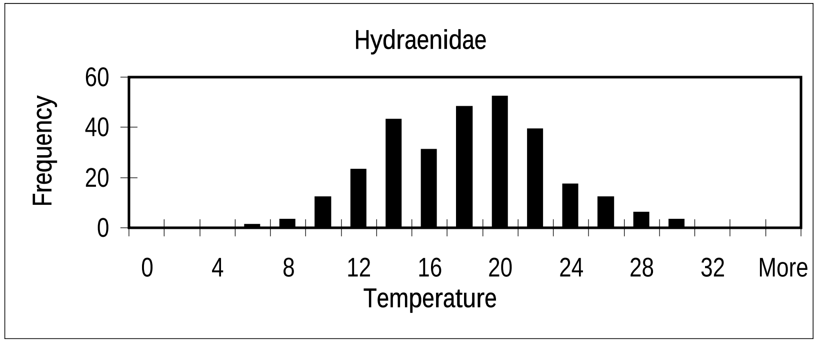


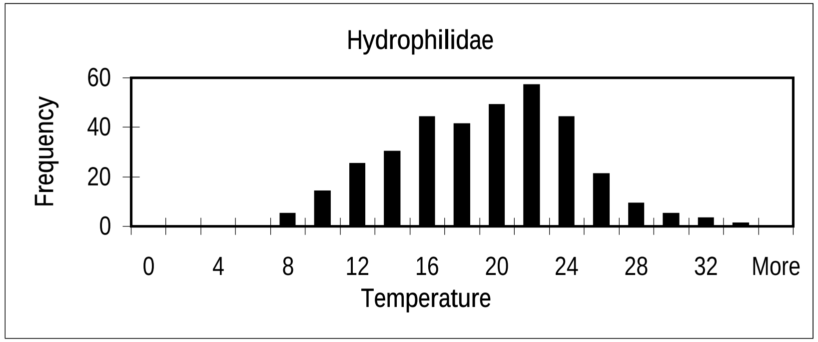


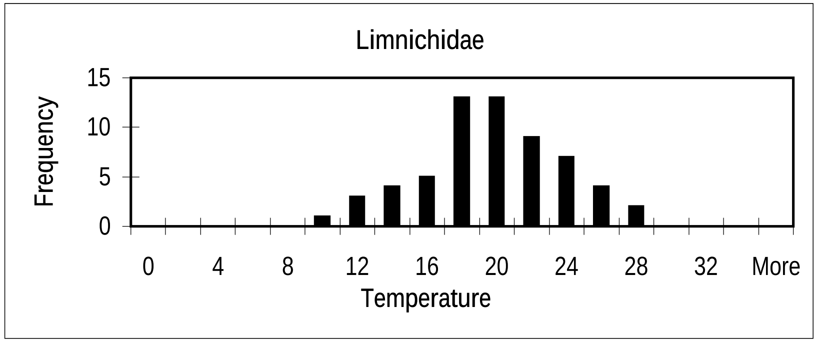


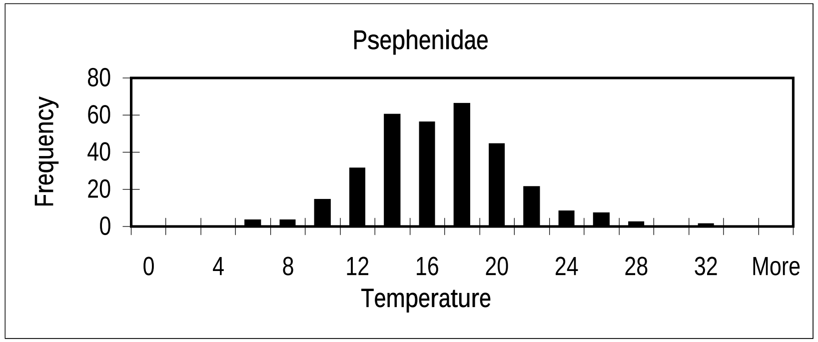
Appendix 1L. Temperature tolerance ranges based on recorded field temperatures in the Rivers Database (January 2007)
Coleoptera: Helodidae, Hydraenidae, Hydrophilidae, Limnichidae and Psephenidae



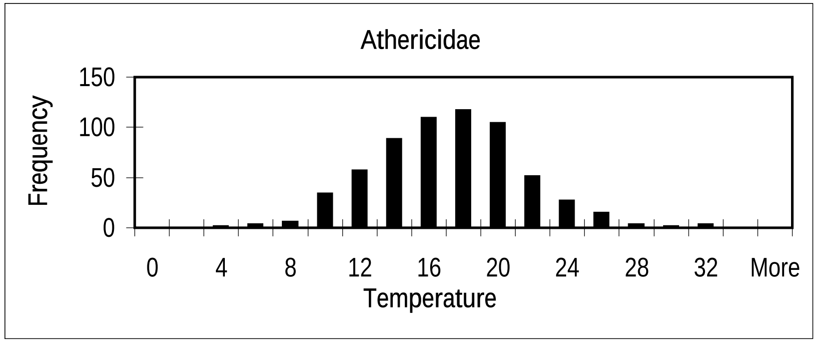


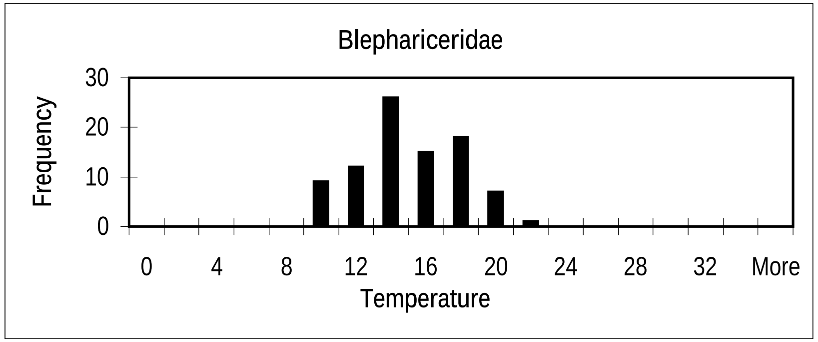


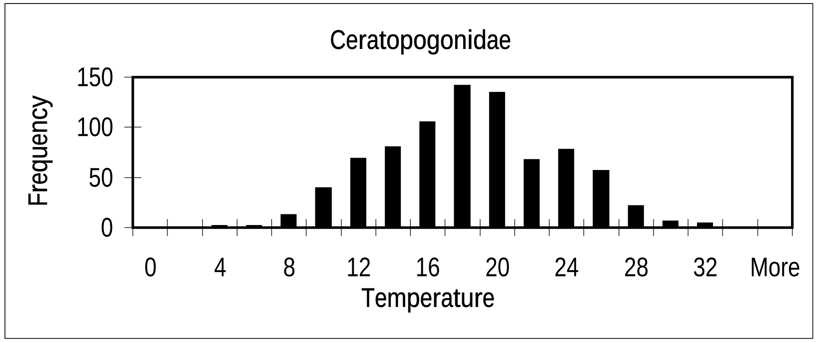


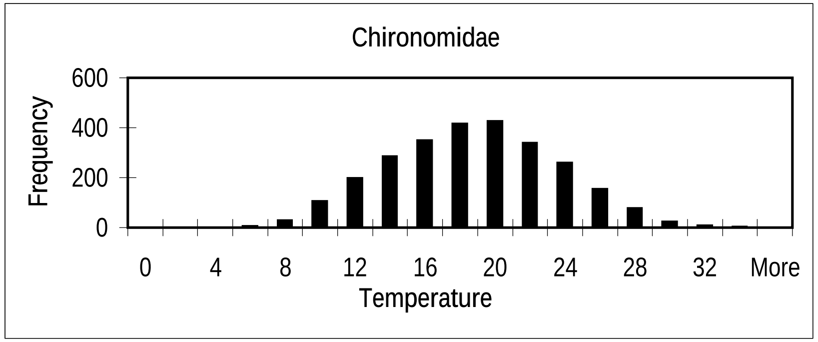


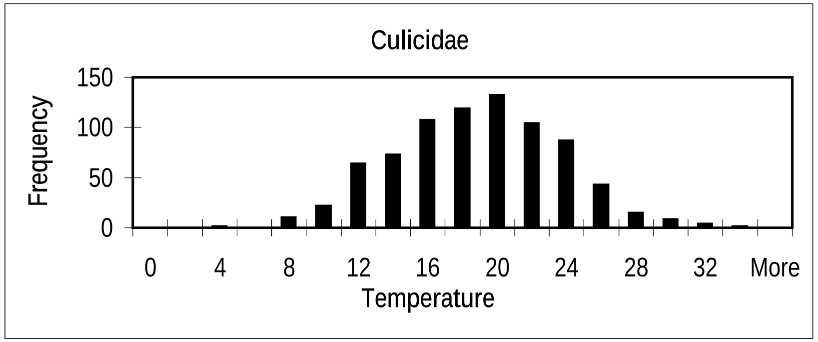
Appendix 1M. Temperature tolerance ranges based on recorded field temperatures in the Rivers Database (January 2007)
Diptera: Athericidae, Blephariceridae, Ceratopogonidae, Chironomidae, Culicidae and Dixidae

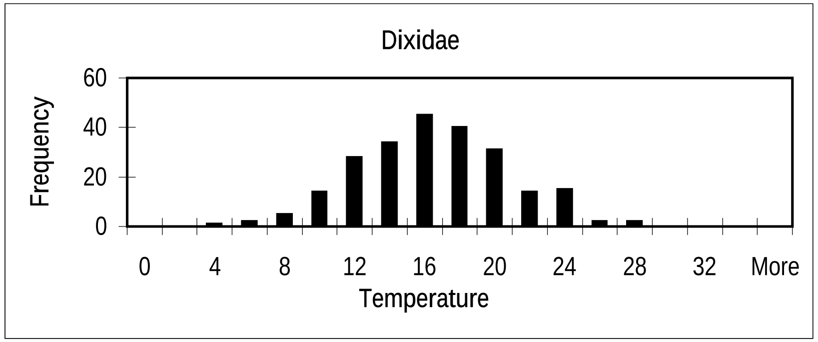






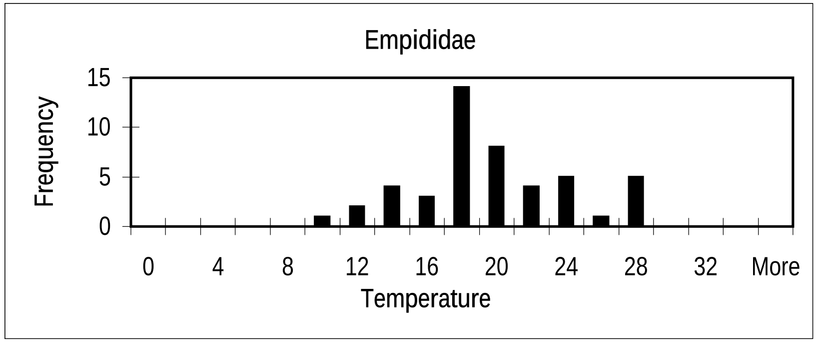


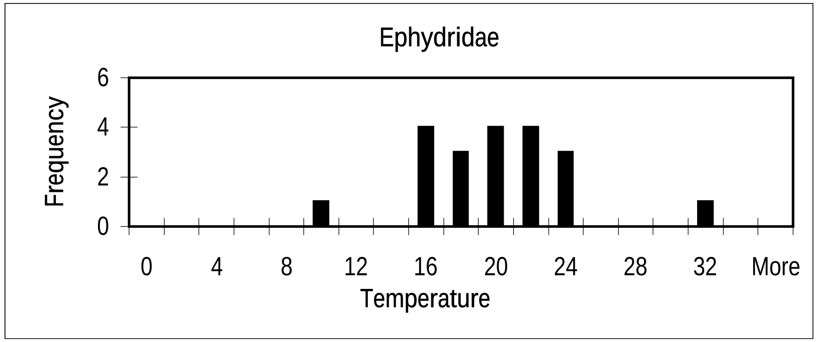


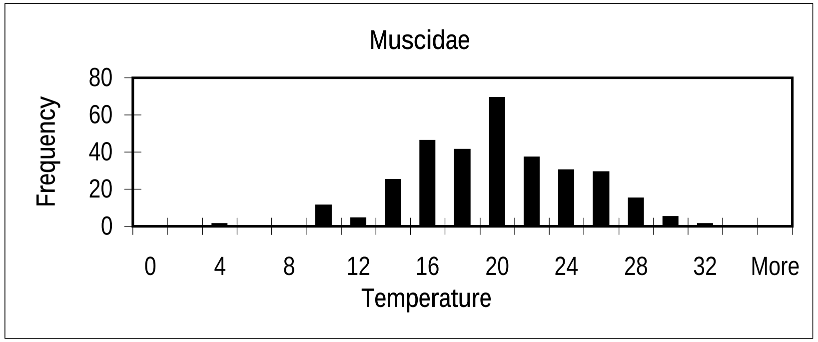


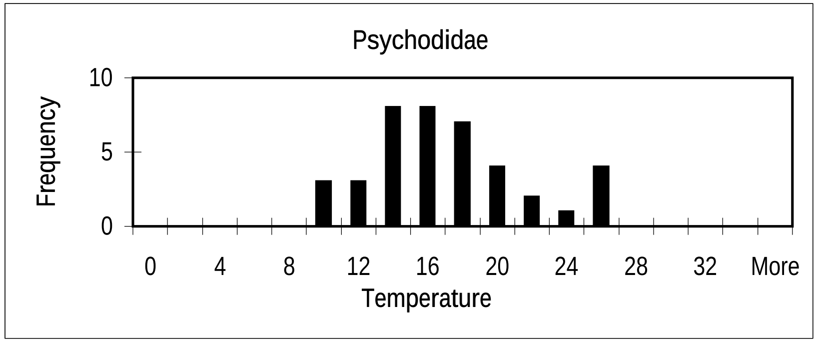
Appendix 1N. Temperature tolerance ranges based on recorded field temperatures in the Rivers Database (January 2007)

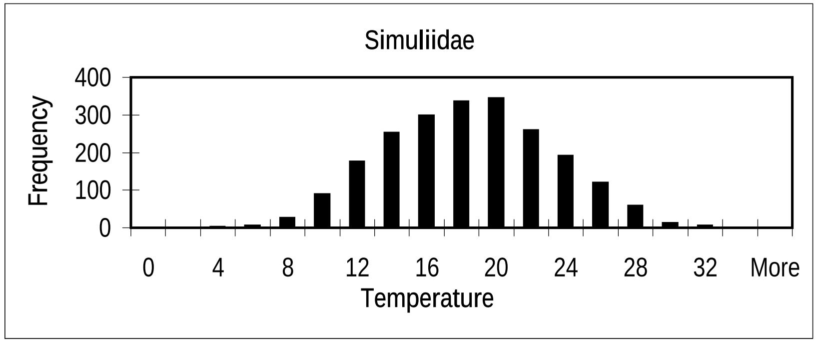
Diptera: Empididae, Ephydridae, Muscidae, Psychodidae, Simuliidae and Syrphidae

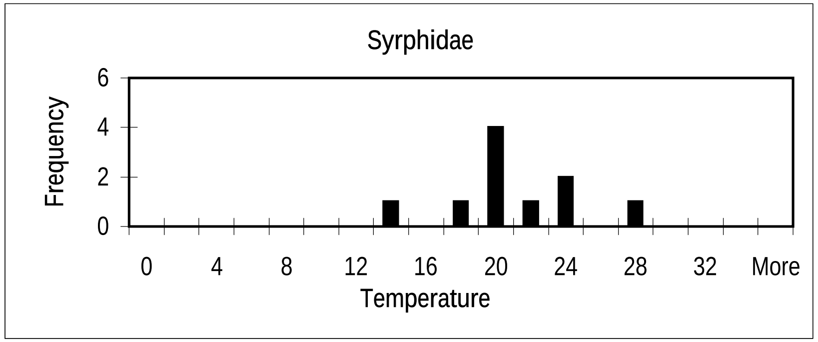




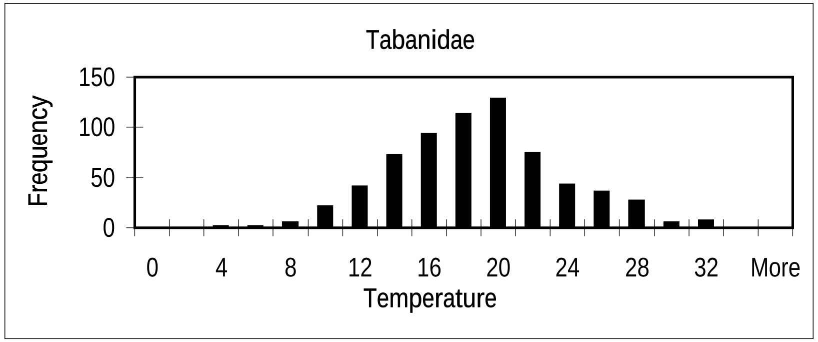


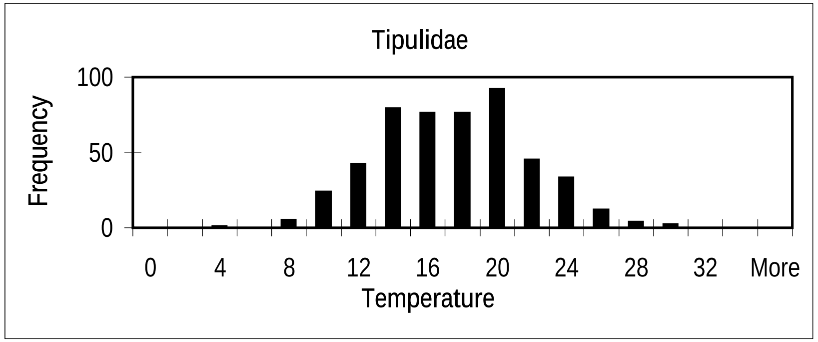


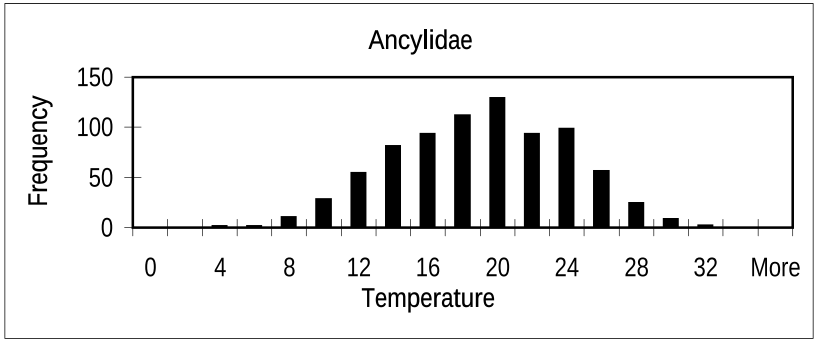


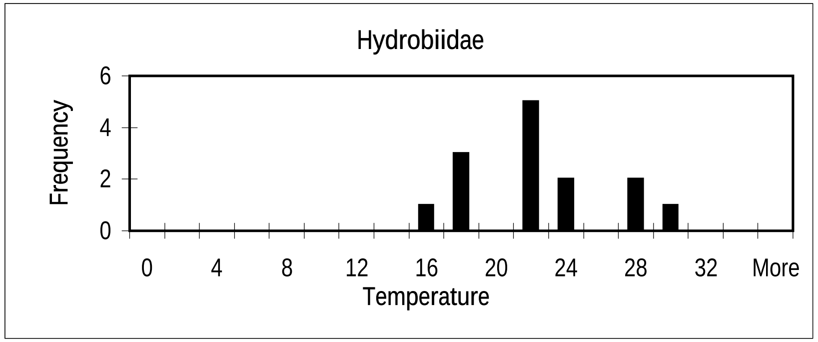


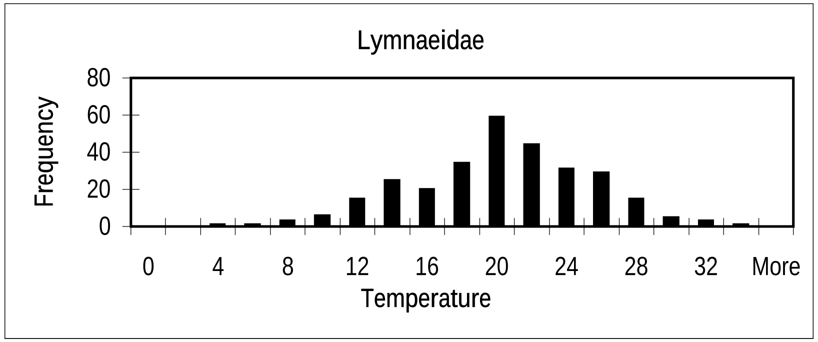
Appendix 1O. Temperature tolerance ranges based on recorded field temperatures in the Rivers Database (January 2007)
Diptera: Tabanidae and Tipulidae and Gastopoda: Ancylidae, Hydrobiidae, Lymnaeidae and Physidae

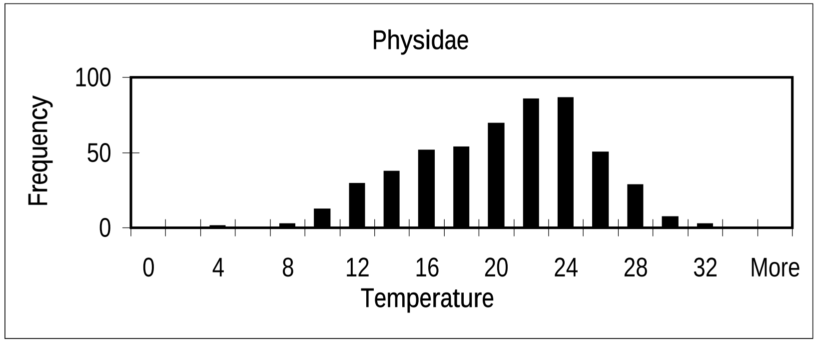




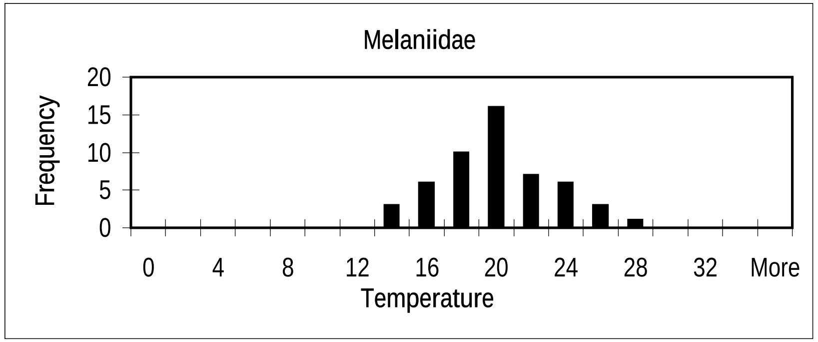


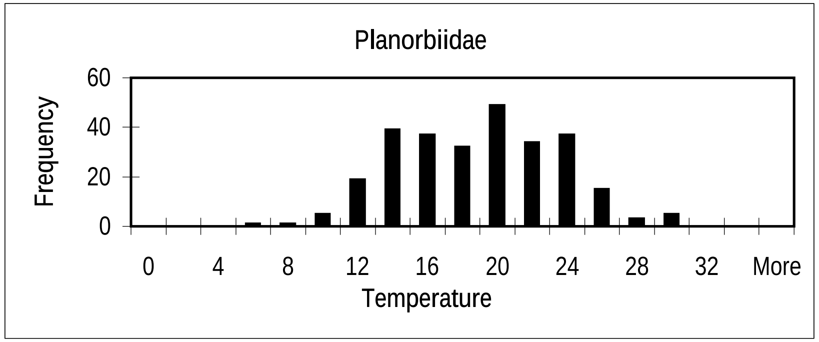


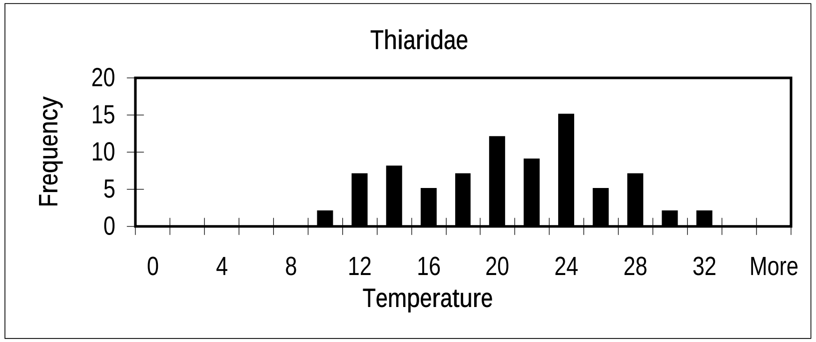


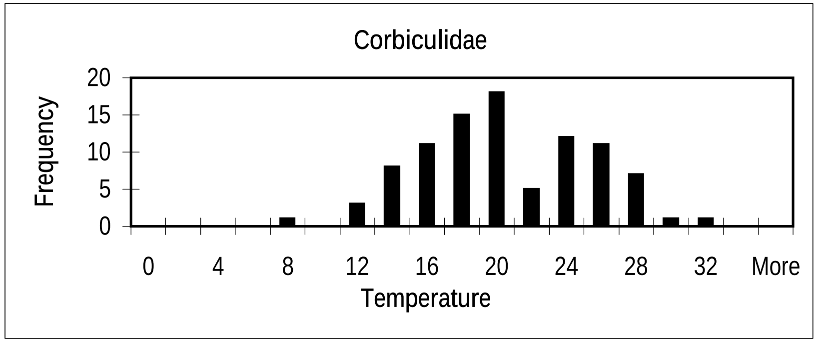


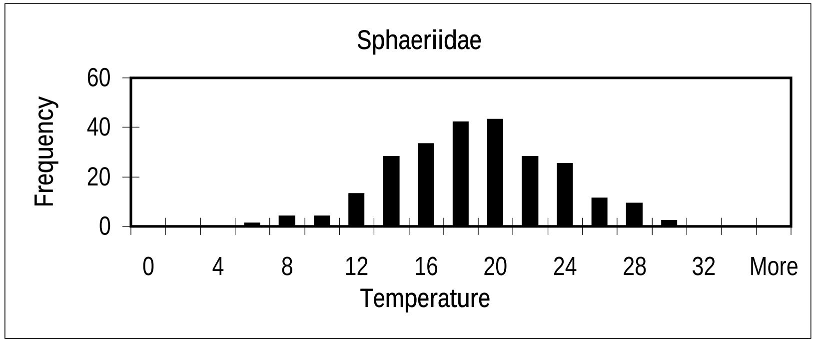
Appendix 1P. Temperature tolerance ranges based on recorded field temperatures in the Rivers Database (January 2007) Gastopoda: Melaniidae, Planorbiidae and Thiaridae and Pelecypoda: Corbiculidae, Sphaeridae and Unionidae

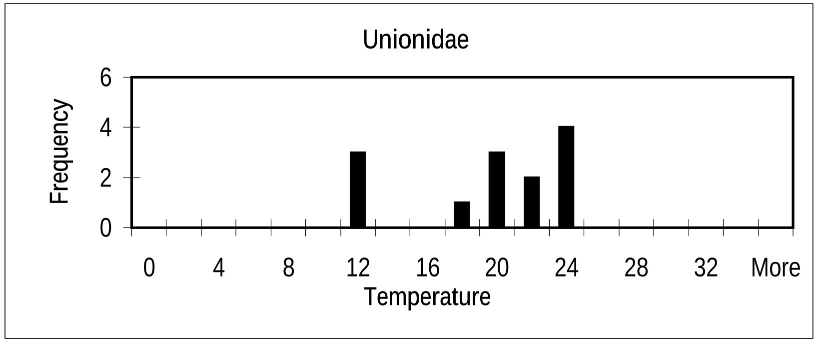












Appendix 2. Results of Kolmogorov-Smirnov test showing taxa which had significantly different recorded water temperatures compared to recorded water temperatures. Mean taxon temperature (N = number of records), significance levels (p-levels) and direction of change [i.e. lower (-) or higher (+) than water temperature] are given. Mean water temperature was 17.9^{o}C.

		Mean Taxon Temp	N	p-level	Direction of change
	Porifera	16.87	159	p < .01	-
	Coelenterata	16.79	11	p > .10	
Platyhelminthes	Turbellaria	17.26	878	p < .005	-
Annelida	Hirudinea	19.07	501	p < .001	+
Annelida	Oligochaeta	18.00	1587	p > .10	
Crustacea	Amphipoda	16.49	119	p < .001	-
Crustacea	Atyidae	19.70	460	p < .001	+
Crustacea	Palaemonidae	18.12	23	p > .10	
Crustacea	Potamonautidae	18.07	1305	p < .10	+
Arachnida	Hydracarina	17.90	822	p > .10	
Plecoptera	Notonemouridae	15.29	266	p < .001	-
Plecoptera	Perlidae	17.40	365	p < .01	-
Ephemeroptera	Baetidae	17.87	2653	p > .10	
Ephemeroptera	Caenidae	17.83	1508	p > .10	
Ephemeroptera	Ephemeridae	-	-	-	
Ephemeroptera	Heptageniidae	17.47	764	p < .001	-
Ephemeroptera	Leptophlebiidae	17.05	1186	p < .001	-
Ephemeroptera	Oligoneuridae	19.90	54	p < .025	+
Ephemeroptera	Polymitarcyidae	16.89	56	p < .025	-
Ephemeroptera	Prosopistomatidae	17.87	67	p > .10	
Ephemeroptera	Teloganodidae	15.72	297	p < .001	-
Ephemeroptera	Tricorythidae	17.18	681	p < .001	-
Odonata	Aeshnidae	17.40	1090	p < .01	-
Odonata	Calopterygidae	16.47	28	p > .10	
Odonata	Chlorocyphidae	16.86	354	p < .001	-
Odonata	Chlorolestidae	17.98	135	p > .10	
Odonata	Coenagrionidae	18.10	1731	p > .10	
Odonata	Corduliidae	18.67	330	p < .025	+
Odonata	Gomphidae	17.92	1392	p > .10	

		Mean Taxon Temp	N	p-level	Direction of change
Odonata	Lestidae	18.67	62	p > .10	
Odonata	Libellulidae	18.32	1184	p < .01	+
Odonata	Platycnemidae	17.70	83	p > .10	
Odonata	Protoneuridae	16.06	32	p > .10	
Lepidoptera	Crambidae	18.05	79	p > .10	
Hemiptera	Belastomatidae	20.36	358	p < .001	+
Hemiptera	Corixidae	18.17	1508	p < .05	+
Hemiptera	Gerridae	18.88	659	p < .001	+
Hemiptera	Hydrometridae	19.17	68	p < .10	+
Hemiptera	Naucoridae	18.65	914	p < .001	+
Hemiptera	Nepidae	20.32	157	p < .001	+
Hemiptera	Notonectidae	18.87	675	p < .001	+
Hemiptera	Pleidae	18.79	322	p < .005	+
Hemiptera	Veliidae/Mesoveliidae	18.44	1491	p < .001	+
Megaloptera	Corydalidae	17.43	245	p < .05	-
Megaloptera	Sialidae	18.00	15	p > .10	
Trichoptera	Barbarochthonidae	15.82	94	p < .001	-
Trichoptera	Calamoceratidae	14.60	2	p > .10	
Trichoptera	Dipseudopsidae	21.67	3	p > .10	
Trichoptera	Ecnomidae	16.93	171	p < .025	-
Trichoptera	Glossosomatidae	16.48	56	p < .10	-
Trichoptera	Hydropsychidae	17.66	1654	p > .10	
Trichoptera	Hydroptilidae	18.56	250	p < .05	+
Trichoptera	Lepidostomatidae	21.86	15	p < .025	+
Trichoptera	Leptoceridae	17.26	483	p > .10	
Trichoptera	Petrothrincidae	17.33	20	p > .10	
Trichoptera	Philopotamidae	16.73	357	p < .001	-
Trichoptera	Pisidiinae	22.90	5	p < .05	+
Trichoptera	Pisuliidae	16.11	39	p > .10	
Trichoptera	Polycentropodidae	17.80	19	p > .10	
Trichoptera	Psychomyiidae/Xiphocentronidae	15.55	149	p < .001	-
Trichoptera	Sericostomatidae	18.60	71	p > .10	
Coleoptera	Dytiscidae	18.01	1120	p > .10	
Coleoptera	Elmidae/Dryopidae	17.56	1009	p < .05	-
Coleoptera	Gyrinidae	18.04	1457	p > .10	

		Mean Taxon Temp	N	p-level	Direction of change
Coleoptera	Haliplidae	17.11	72	p > .10	
Coleoptera	Helodidae	15.62	288	p < .001	-
Coleoptera	Hydraenidae	17.27	290	p < .10	-
Coleoptera	Hydrophilidae	18.32	348	p < .10	+
Coleoptera	Limnichidae	18.93	61	p < .05	+
Coleoptera	Psephenidae	15.80	316	p < .001	-
Diptera	Athericidae	16.27	619	p < .001	-
Diptera	Blephariceridae	14.27	88	p < .001	-
Diptera	Ceratopogonidae	17.53	812	p < .10	-
Diptera	Chironomidae	17.82	2675	p > .10	
Diptera	Culicidae	17.93	790	p > .10	
Diptera	Dixidae	15.54	233	p < .001	-
Diptera	Empididae	18.78	47	p > .10	
Diptera	Ephydridae	19.08	20	p > .10	
Diptera	Muscidae	18.98	314	p < .001	+
Diptera	Psychodidae	16.28	40	p < .01	-
Diptera	Simuliidae	17.52	2167	p < .10	-
Diptera	Syrphidae	20.08	10	p < .10	+
Diptera	Tabanidae	17.96	667	p > .10	
Diptera	Tipulidae	16.59	491	p < .001	
Mollusca	Ancylidae	18.14	790	p > .10	
Mollusca	Hydrobiidae	21.44	14	p < .05	+
Mollusca	Lymnaeidae	19.27	292	p < .001	+
Mollusca	Melaniidae	19.14	52	p < .025	+
Mollusca	Physidae	19.46	512	p < .001	+
Mollusca	Planorbidae*2	17.97	269	p > .10	
Mollusca	Thiaridae	19.75	81	p < .01	+
Mollusca	Corbiculidae	19.45	93	p < .10	+
Mollusca	Sphaeriidae	17.97	243	p > .10	
Mollusca	Unionidae	18.63	13	p > .10	

Appendix 3. Mean, median, minimum, maximum, standard deviation (SD) range of water temperatures for each taxon (extracted from the Rivers database). N = number of records, Min = minimum and Max = maximum values

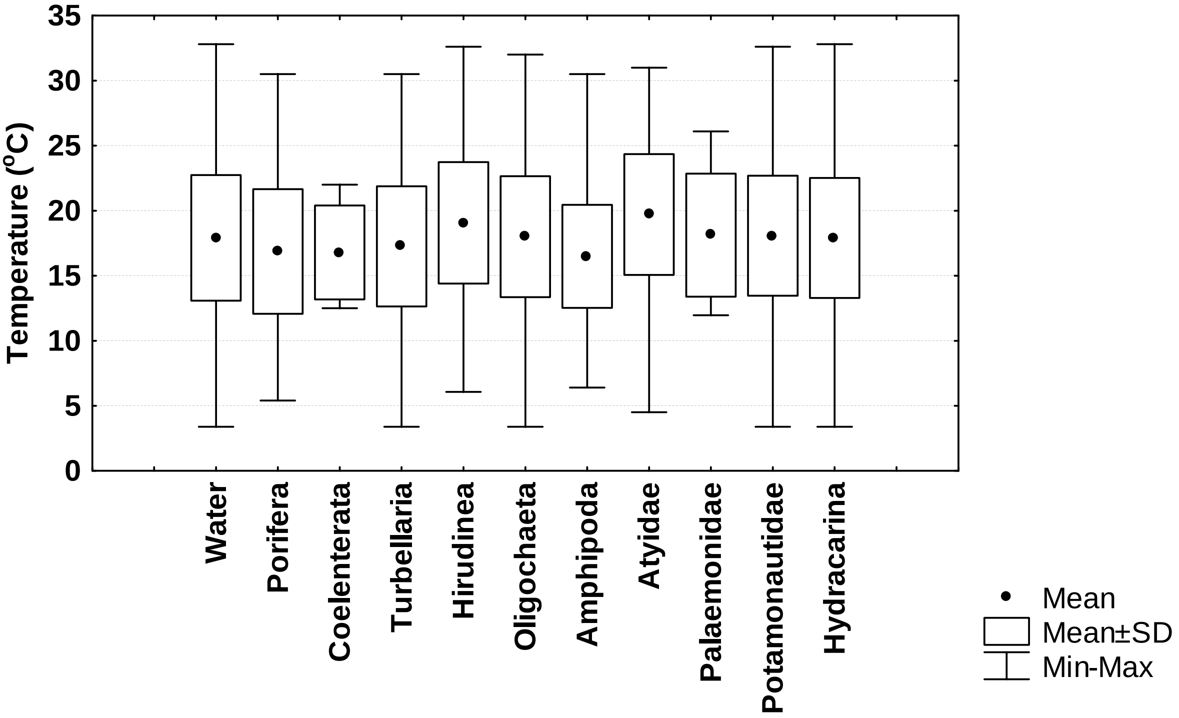
		N	Mean	Median	Min	Max	SD	Range
	Water	2949	17.9	18.0	3.4	32.8	4.8	29.4
	Porifera	159	16.9	16.7	5.4	30.5	4.8	25.1
	Coelenterata	11	16.8	16.7	12.5	22.0	3.6	9.5
Platyhelminthes	Turbellaria	878	17.3	17.4	3.4	30.5	4.6	27.1
Annelida	Hirudinea	501	19.1	19.4	6.1	32.6	4.7	26.5
Annelida	Oligochaeta	1587	18.0	18.0	3.4	32.0	4.6	28.6
Crustacea	Amphipoda	119	16.5	16.1	6.4	30.5	4.0	24.1
Crustacea	Atyidae	459	19.7	19.7	4.5	31.0	4.6	26.5
Crustacea	Palaemonidae	23	18.1	16.0	12.0	26.1	4.7	14.1
Crustacea	Potamonautidae	1305	18.1	18.0	3.4	32.6	4.6	29.2
Arachnida	Hydracarina	822	17.9	18.0	3.4	32.8	4.6	29.4
Plecoptera	Notonemouridae	266	15.3	15.5	6.4	29.5	4.0	23.1
Plecoptera	Perlidae	365	17.4	17.0	7.2	29.3	4.4	22.1
Ephemeroptera	Baetidae	2646	17.9	17.9	3.4	32.8	4.8	29.4
Ephemeroptera	Caenidae	1508	17.8	17.9	3.4	32.8	4.9	29.4
Ephemeroptera	Ephemeridae	1	21.6	21.6	21.6	21.6		
Ephemeroptera	Heptageniidae	764	17.5	17.0	4.5	31.0	4.6	26.5
Ephemeroptera	Leptophlebiidae	1186	17.1	16.9	3.4	30.6	4.6	27.2
Ephemeroptera	Oligoneuridae	54	19.9	19.5	5.7	31.0	4.7	25.3
Ephemeroptera	Polymitarcyidae	56	16.9	16.5	9.8	30.4	4.3	20.6
Ephemeroptera	Prosopistomatidae	67	17.9	17.4	7.8	28.4	4.3	20.6
Ephemeroptera	Teloganodidae	297	15.7	16.0	6.4	26.3	4.0	19.9
Ephemeroptera	Tricorythidae	681	17.2	16.8	5.2	31.0	4.7	25.8
Odonata	Aeshnidae	1090	17.4	17.2	3.4	32.8	5.0	29.4
Odonata	Calopterygidae	28	16.5	15.4	9.0	29.9	5.3	20.9
Odonata	Chlorocyphidae	354	16.9	16.8	4.5	31.0	3.8	26.5
Odonata	Chlorolestidae	135	18.0	18.0	3.4	27.7	4.8	24.3
Odonata	Coenagrionidae	1731	18.1	18.1	3.4	32.8	4.9	29.4
Odonata	Corduliidae	330	18.7	18.9	7.2	32.8	4.6	25.6
Odonata	Gomphidae	1392	17.9	17.9	3.4	32.0	4.7	28.6
Odonata	Lestidae	62	18.7	19.2	8.0	29.5	4.8	21.5
Odonata	Libellulidae	1184	18.3	18.3	3.4	32.8	4.7	29.4

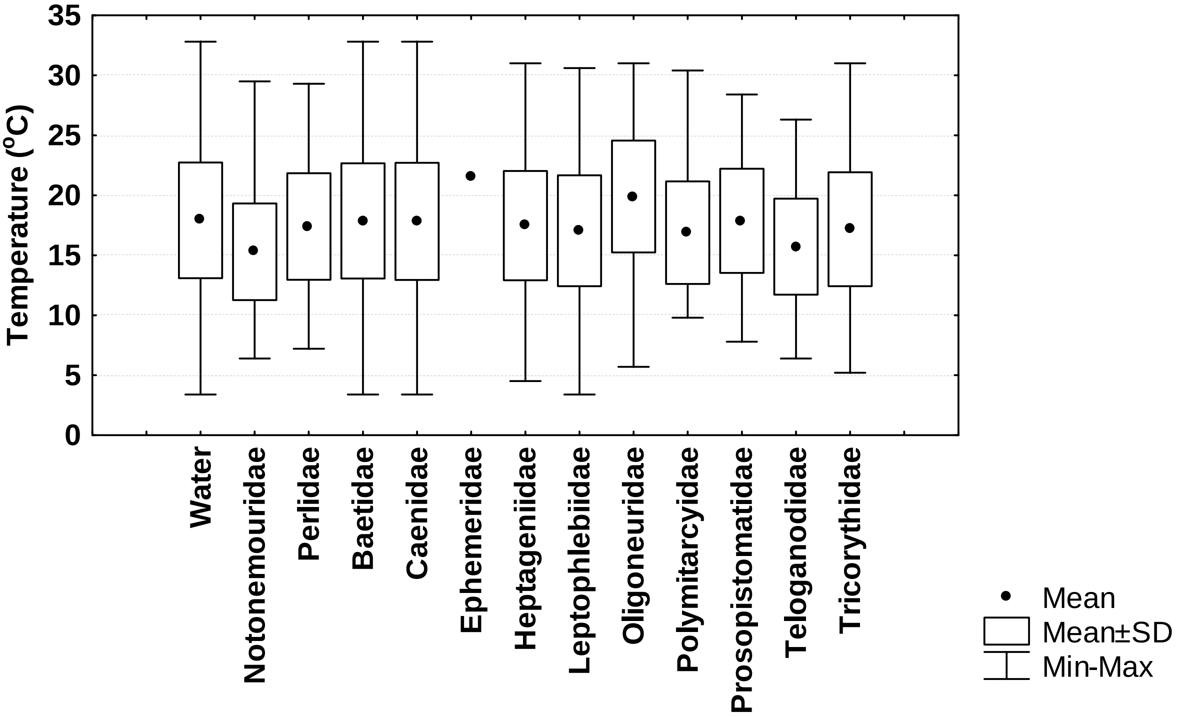
		N	Mean	Median	Min	Max	SD	Range
Odonata	Platycnemidae	83	17.7	17.9	8.2	28.9	4.1	20.7
Odonata	Protoneuridae	32	16.1	16.7	7.4	24.3	4.5	16.9
Lepidoptera	Crambidae	79	18.1	18.0	7.8	29.9	4.5	22.2
Hemiptera	Belastomatidae	358	20.4	20.5	8.7	31.0	4.3	22.3
Hemiptera	Corixidae	1508	18.2	18.4	4.5	32.8	4.8	28.3
Hemiptera	Gerridae	659	18.9	19.0	4.5	32.8	4.7	28.3
Hemiptera	Hydrometridae	68	19.2	19.3	9.0	32.0	5.1	23.0
Hemiptera	Naucoridae	914	18.6	18.6	6.4	32.8	4.9	26.4
Hemiptera	Nepidae	157	20.3	19.9	5.7	32.8	4.8	27.1
Hemiptera	Notonectidae	675	18.9	19.3	3.4	32.0	5.1	28.6
Hemiptera	Pleidae	322	18.8	19.1	6.7	32.8	4.9	26.1
Hemiptera	Veliidae/Mesoveliidae	1491	18.4	18.3	3.4	32.8	4.7	29.4
Megaloptera	Corydalidae	245	17.4	17.5	8.2	27.7	4.2	19.5
Megaloptera	Sialidae	15	18.0	17.1	12.0	25.2	3.7	13.2
Trichoptera	Barbarochthonidae	94	15.8	16.0	6.4	26.3	4.6	19.9
Trichoptera	Calamoceratidae	2	14.6	14.6	10.2	19.0	6.2	8.8
Trichoptera	Dipseudopsidae	3	21.7	23.7	17.0	24.4	4.1	7.4
Trichoptera	Ecnomidae	171	16.9	17.0	6.7	26.0	4.1	19.3
Trichoptera	Glossosomatidae	56	16.5	16.4	6.4	26.3	4.4	19.9
Trichoptera	Hydropsychidae	1653	17.7	17.5	4.5	31.0	4.8	26.5
Trichoptera	Hydroptilidae	250	18.6	19.0	6.6	29.9	4.5	23.3
Trichoptera	Lepidostomatidae	15	21.9	24.0	12.1	31.0	5.3	18.9
Trichoptera	Leptoceridae	483	17.3	17.3	3.4	32.8	5.0	29.4
Trichoptera	Petrothrincidae	20	17.3	16.6	10.0	26.3	4.3	16.3
Trichoptera	Philopotamidae	357	16.7	17.0	6.1	30.7	4.6	24.6
Trichoptera	Pisidiinae	5	22.9	22.8	20.0	25.2	2.1	5.2
Trichoptera	Pisuliidae	39	16.1	15.9	4.5	30.7	5.2	26.2
Trichoptera	Polycentropodidae	19	17.8	18.6	9.2	29.5	4.9	20.3
Trichoptera	Psychomyiidae/Xiphocentronidae	149	15.5	15.2	7.2	26.3	3.5	19.1
Trichoptera	Sericostomatidae	71	18.6	18.7	8.6	30.7	4.3	22.1
Coleoptera	Dytiscidae	1120	18.0	18.3	3.4	32.8	4.9	29.4
Coleoptera	Elmidae/Dryopidae	1009	17.6	17.3	6.4	31.0	4.5	24.6
Coleoptera	Gyrinidae	1457	18.0	18.1	3.4	31.0	4.8	27.6
Coleoptera	Haliplidae	72	17.1	17.2	3.4	27.8	6.0	24.4
Coleoptera	Helodidae	288	15.6	15.6	3.4	27.0	4.0	23.6
Coleoptera	Hydraenidae	290	17.3	17.5	5.2	29.5	4.5	24.3

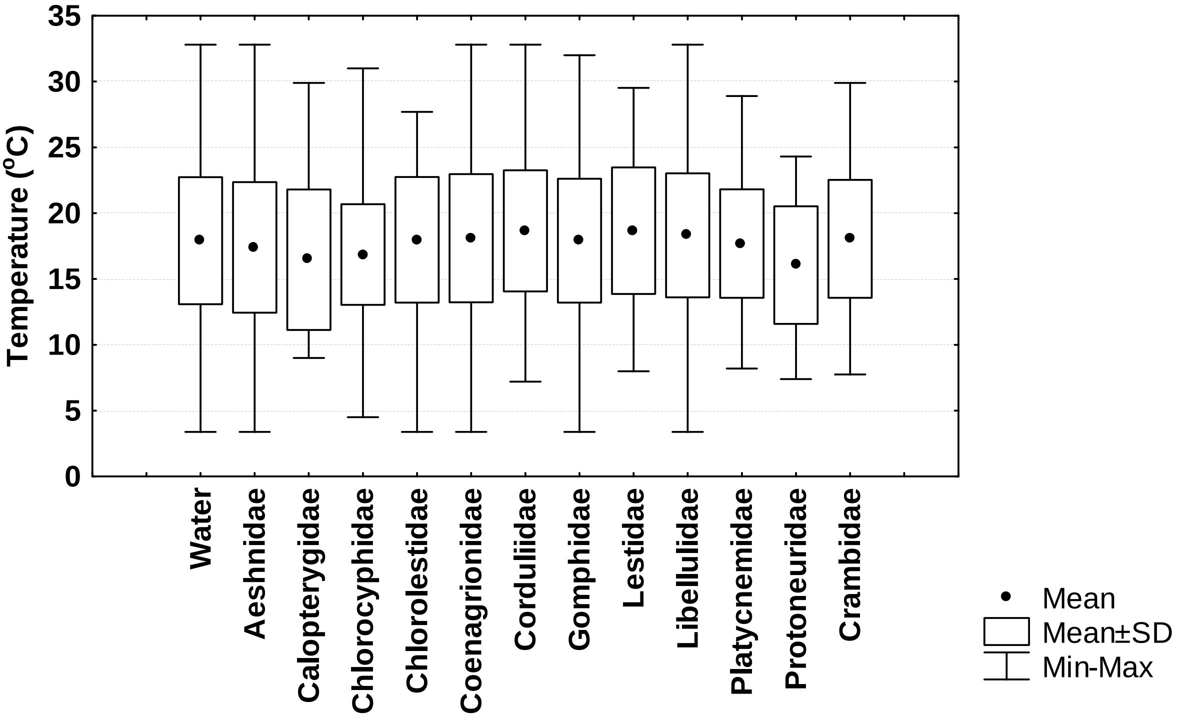
		N	Mean	Median	Min	Max	SD	Range
Coleoptera	Hydrophilidae	348	18.3	18.6	6.4	32.8	5.0	26.4
Coleoptera	Limnichidae	61	18.9	19.0	8.9	27.8	4.1	18.9
Coleoptera	Psephenidae	316	15.8	15.8	4.5	30.5	3.9	26.0
Diptera	Athericidae	619	16.3	16.3	3.4	31.0	4.2	27.6
Diptera	Blephariceridae	88	14.3	14.0	8.7	20.5	2.9	11.8
Diptera	Ceratopogonidae	812	17.5	17.4	3.4	31.0	4.9	27.6
Diptera	Chironomidae	2675	17.8	17.9	3.4	32.8	4.8	29.4
Diptera	Culicidae	790	17.9	18.0	3.4	32.6	4.7	29.2
Diptera	Dixidae	233	15.5	15.3	3.4	27.6	4.3	24.2
Diptera	Empididae	47	18.8	18.0	8.7	27.8	4.3	19.1
Diptera	Ephydridae	20	19.1	18.9	9.5	30.9	4.4	21.4
Diptera	Muscidae	314	19.0	18.9	3.4	30.5	4.5	27.1
Diptera	Psychodidae	40	16.3	15.7	8.3	25.8	4.5	17.5
Diptera	Simuliidae	2167	17.5	17.4	3.4	31.0	4.7	27.6
Diptera	Syrphidae	10	20.1	19.3	12.6	27.1	3.9	14.5
Diptera	Tabanidae	667	18.0	18.0	3.4	32.0	4.7	28.6
Diptera	Tipulidae	491	16.6	16.5	3.4	29.9	4.2	26.5
Mollusca	Ancylidae	790	18.1	18.3	3.4	31.0	4.9	27.6
Mollusca	Hydrobiidae	14	21.4	21.2	14.8	28.9	4.0	14.1
Mollusca	Lymnaeidae	292	19.3	19.6	3.4	32.8	5.1	29.4
Mollusca	Melaniidae	52	19.1	18.9	12.9	27.0	3.2	14.1
Mollusca	Physidae	512	19.5	20.1	3.4	30.6	4.8	27.2
Mollusca	Planorbidae*2	277	18.0	18.3	4.5	29.9	4.6	25.4
Mollusca	Thiaridae	81	19.8	20.0	8.2	31.0	5.5	22.8
Mollusca	Corbiculidae	93	19.4	19.0	6.7	31.0	4.7	24.3
Mollusca	Sphaeriidae	243	18.0	17.8	5.4	29.2	4.6	23.8
Mollusca	Unionidae	13	18.6	20.0	10.6	23.9	4.7	13.3

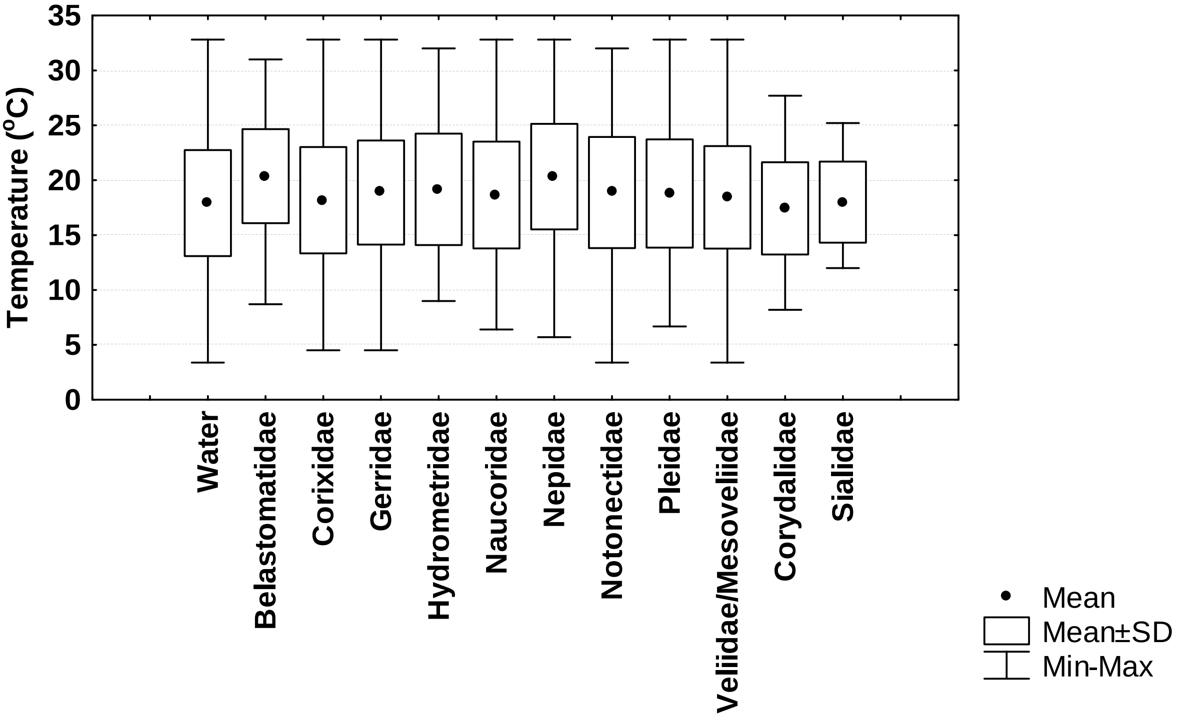
*2 includes Bulininae and Planorbinae

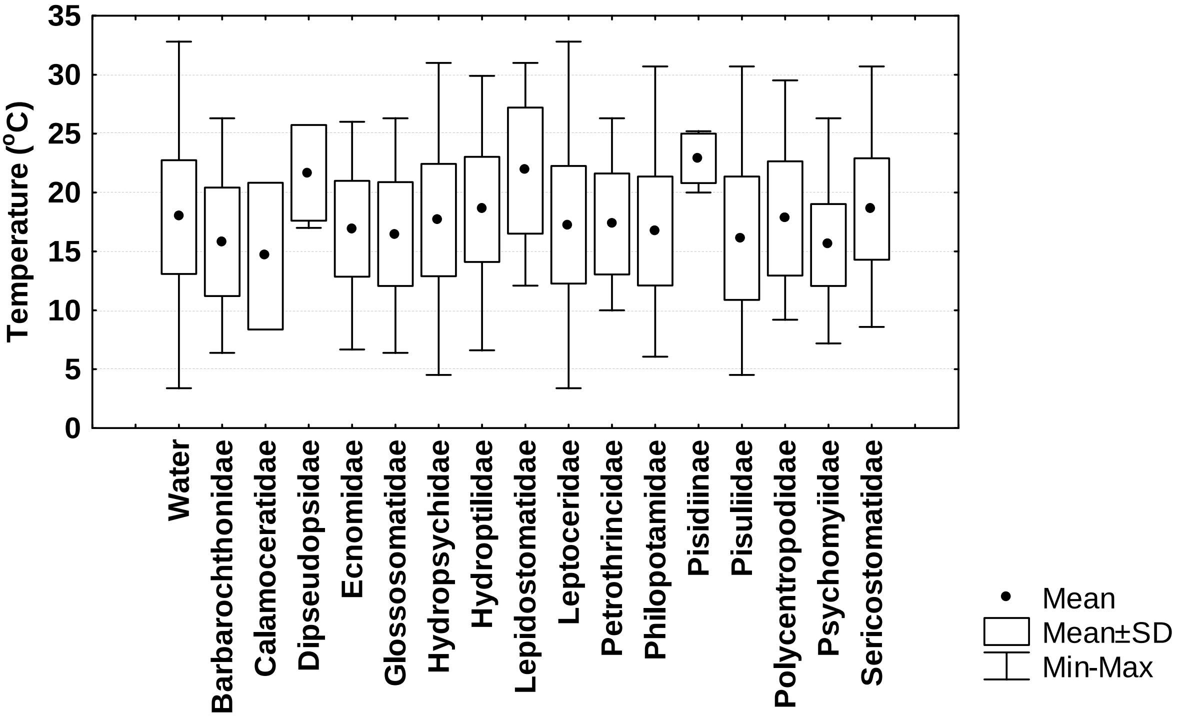
Appendix 4. Mean (standard deviation, minimum and maximum) temperatures for each invertebrate taxon (based on data extracted from the Rivers Database)

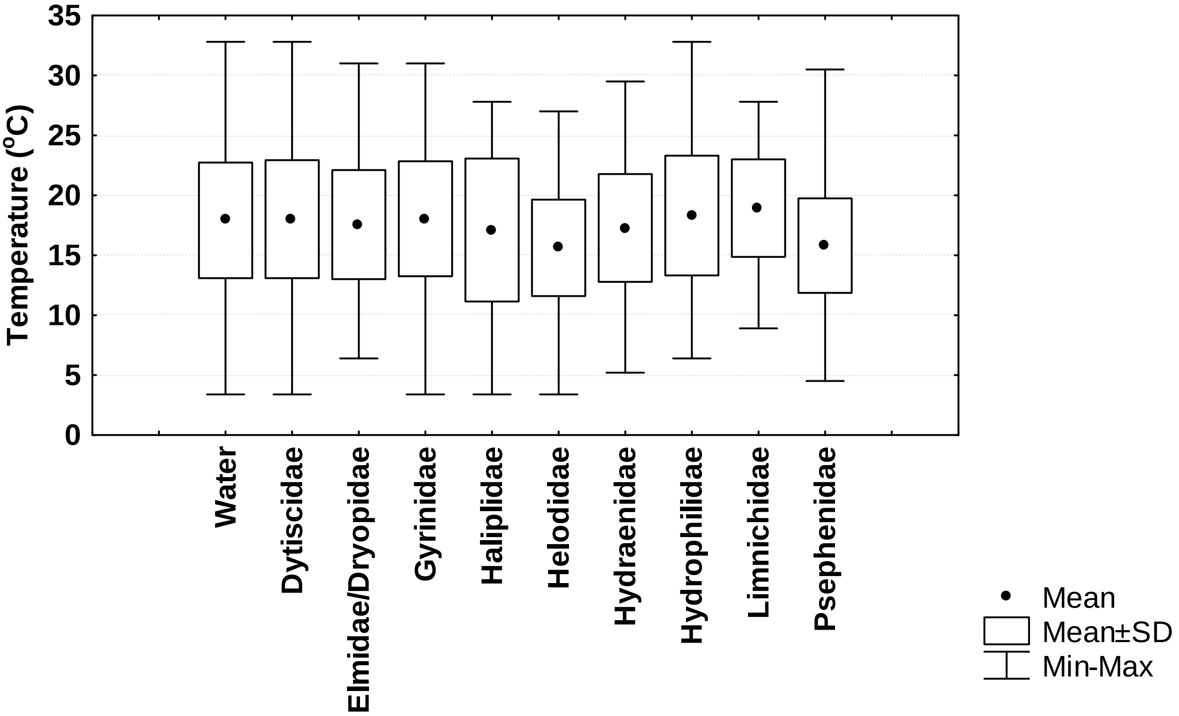


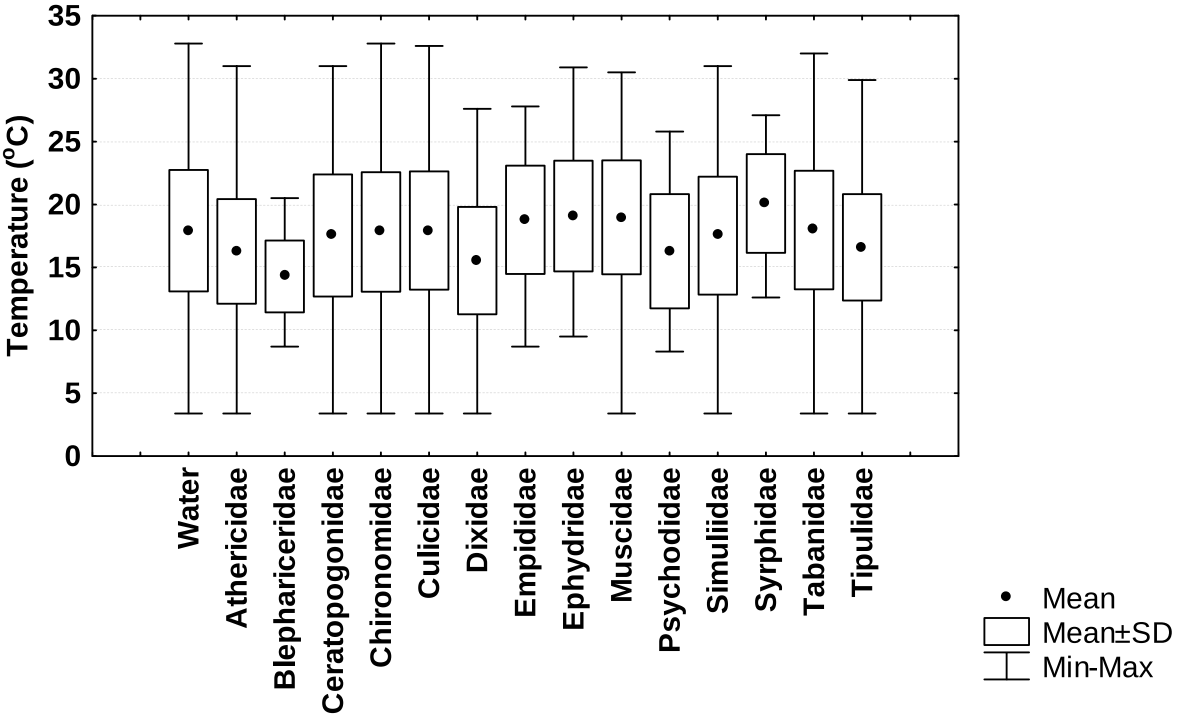


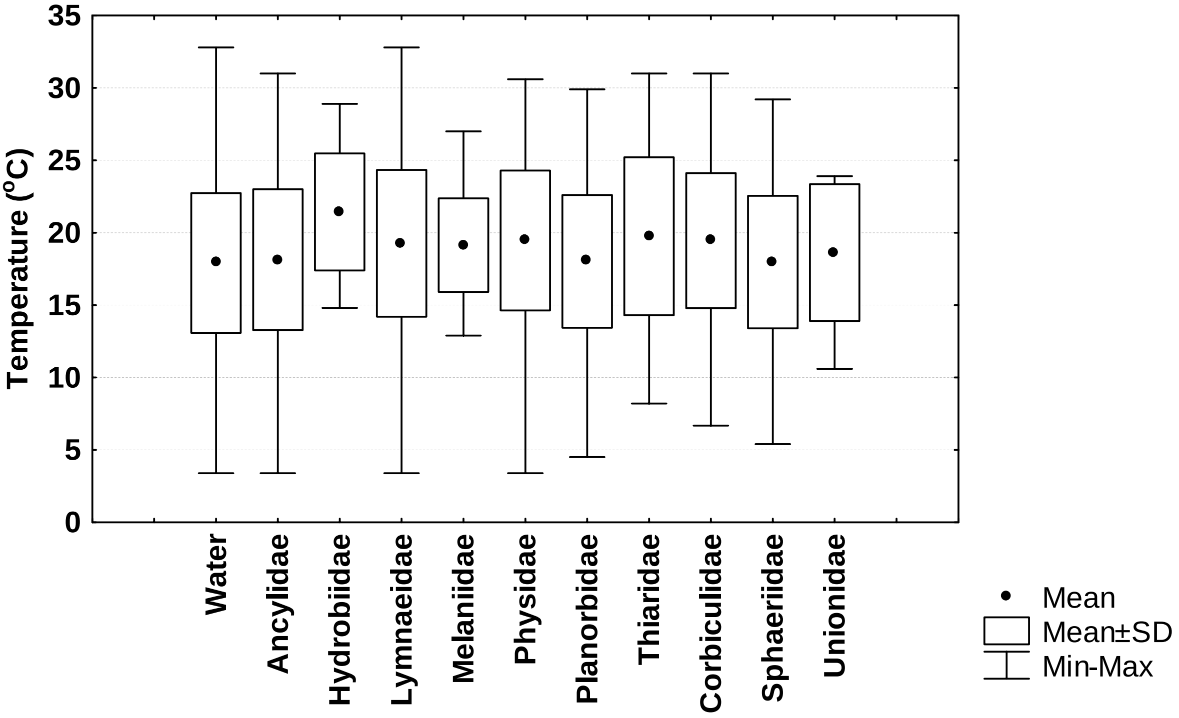

Temperature (°C)
35
30
25
20
15
10
5
0
Water
Aeshnidae
Calopterygidae
Chlorocyphidae
Chlorolestidae
Coenagrionidae
Corduliidae
Gomphidae
Lestidae
Libellulidae
Platycnemidae
Protoneuridae
Crambidae
Mean
Mean±SD
Min-Max


Temperature (°C)
35
30
25
20
15
10
5
0
Water
Belastomatidae
Corixidae
Gerridae
Hydrometridae
Naucoridae
Nepidae
Notonectidae
Pleidae
Velidae/Mesoveliidae
Corydalidae
Sialidae
Mean
Mean±SD
Min-Max


Temperature (°C)
35
30
25
20
15
10
5
0
Water
Barbarochthonidae
Calamoceratidae
Dipseudopsidae
Ecnomidae
Glossosomatidae
Hydropsychidae
Hydroptilidae
Lepidostomatidae
Leptoceridae
Petrothrincidae
Philopotamidae
Pisidiinae
Pisuliidae
Polycentropodidae
Psychomyiidae
Sericostomatidae
Mean
Mean±SD
Min-Max


Temperature (°C)
35
30
25
20
15
10
5
0
Water
Dytiscidae
Elmidae/Dryopidae
Gyrinidae
Haliplidae
Helodidae
Hydraenidae
Hydrophilidae
Limnichidae
Psephenidae
Mean
Mean±SD
Min-Max


Temperature (°C)
0
5
10
15
20
25
30
35
Water
Athericidae
Blephariceridae
Ceratopogonidae
Chironomidae
Culicidae
Dixidae
Empididae
Ephydridae
Muscidae
Psychodidae
Simuliidae
Syrphidae
Tabanidae
Tipulidae
Mean
Mean±SD
Min-Max


Temperature (°C)
0
5
10
15
20
25
30
35
Water
Ancylidae
Hydrobiidae
Lymnaeidae
Melaniidae
Physidae
Planorbidae
Thiaridae
Corbiculidae
Sphaeriidae
Unionidae
Mean
Mean±SD
Min-Max

Appendix 5. Mean (minimum, maximum, range) temperatures for each invertebrate taxon (based on data extracted from the Biobase, Dallas *et al.* 1999). N = number of records.

Order	Family	Genus species	Mean	Min	Max	Range	N
Amphipoda	Paramelitidae	*Paramelita nigroculus*	13.7	4.0	16.5	12.5	19
Amphipoda	Unspecified	*Unspecified*	15.6	11.0	21.1	10.1	15
Decapoda	Atyidae	*Caridina nilotica*	18.7	10.3	35.0	24.7	82
Decapoda	Atyidae	*Caridina typhus*	20.7	16.0	24.0	8.0	3
Plecoptera	Notonemouridae	*Aphanicerca sp.*	13.9	4.0	21.0	17.0	29
Plecoptera	Notonemouridae	*Aphanicercella sp.*	9.7	9.0	11.0	2.0	3
Plecoptera	Notonemouridae	*Unspecified*	18.0	3.9	22.5	18.6	29
Plecoptera	Perlidae	*Neoperla spio*	14.9	3.9	25.0	21.1	38
Plecoptera	Perlidae	*Neoperla spio complex*	26.0	22.0	28.0	6.0	4
Ephemeroptera	Heptageniidae	*Afronurus harrisoni*	16.3	11.0	22.2	11.2	12
Ephemeroptera	Heptageniidae	*Afronurus peringueyi*	19.7	10.0	27.0	17.0	7
Ephemeroptera	Heptageniidae	*Afronurus sp.*	16.8	3.9	30.0	26.1	65
Ephemeroptera	Heptageniidae	*Notonurus sp.*	16.9	6.8	29.0	22.2	11
Ephemeroptera	Heptageniidae	*Unspecified*	18.8	10.0	31.0	21.0	56
Ephemeroptera	Leptophlebiidae	*Adenophlebia auriculata*	14.9	10.5	17.8	7.3	5
Ephemeroptera	Leptophlebiidae	*Adenophlebia peringueyella*	14.2	11.7	21.0	9.3	4
Ephemeroptera	Leptophlebiidae	*Adenophlebia sp.*	15.4	12.0	19.8	7.8	18
Ephemeroptera	Leptophlebiidae	*Aprionyx peterseni*	14.3	4.0	21.0	17.0	21
Ephemeroptera	Leptophlebiidae	*Aprionyx rubicundus*	15.0	11.0	21.0	10.0	7
Ephemeroptera	Leptophlebiidae	*Aprionyx sp.*	12.7	8.0	15.5	7.5	4
Ephemeroptera	Leptophlebiidae	*Castanophlebia calida*	13.8	4.0	21.1	17.1	41
Ephemeroptera	Leptophlebiidae	*Castanophlebia sp.*	15.5	11.1	19.5	8.4	15
Ephemeroptera	Leptophlebiidae	*Choroterpes elegans*	17.1	3.9	29.0	25.1	71
Ephemeroptera	Leptophlebiidae	*Choroterpes sp.*	17.4	5.7	30.0	24.3	65
Ephemeroptera	Leptophlebiidae	*Euthraulus sp.*	24.2	18.0	31.0	13.0	23
Ephemeroptera	Leptophlebiidae	*Unspecified*	18.1	9.7	29.5	19.8	92
Ephemeroptera	Telagonodidae	*Ephemerellina barnardi*	14.1	11.0	19.7	8.7	3
Ephemeroptera	Telagonodidae	*Ephemerellina harrisoni*	16.2	11.0	24.5	13.5	8
Ephemeroptera	Telagonodidae	*Ephemerellina penicillata*	12.4	10.0	13.7	3.7	3
Ephemeroptera	Telagonodidae	*Ephemerellina sp.*	15.6	12.0	19.3	7.3	7
Ephemeroptera	Telagonodidae	*Lestagella spp.*	14.3	8.0	24.5	16.5	22
Ephemeroptera	Telagonodidae	*Lestagella penicillata*	14.0	8.0	24.5	16.5	15
Ephemeroptera	Telagonodidae	*Lithogloea harrisoni*	13.2	8.0	21.1	13.1	9
Ephemeroptera	Telagonodidae	*Lithogloea pennicillata*	13.7	4.0	16.5	12.5	19
Ephemeroptera	Telagonodidae	*Unspecified*	17.2	8.7	26.0	17.3	59
Ephemeroptera	Polymitarcyidae	*Ephoron sp.*	11.2	3.9	18.5	14.6	2
Ephemeroptera	Polymitarcyidae	*Povilla adusta*	29.3	28.0	31.0	3.0	3
Ephemeroptera	Tricorythidae	*Tricorythus discolor*	20.2	10.0	27.0	17.0	9
Ephemeroptera	Tricorythidae	*Tricorythus reticuatus*	22.2	13.0	31.0	18.0	37
Ephemeroptera	Tricorythidae	*Tricorythus sp.*	17.8	3.9	31.0	27.1	65
Ephemeroptera	Tricorythidae	*Unspecified*	18.8	9.5	28.0	18.5	33
Odonata	Aeschnidae	*Aeschna miniscula*	17.9	10.0	25.6	15.6	8
Odonata	Aeschnidae	*Aeschna sp.*	18.5	13.0	29.0	16.0	7
Odonata	Aeschnidae	*Anax imperator*	15.7	14.5	16.5	2.0	3
Odonata	Aeschnidae	*Anax sp.*	17.2	12.5	23.0	10.5	11
Odonata	Aeschnidae	*Unspecified*	21.2	13.0	31.0	18.0	51
Odonata	Chlorocyphidae	*Chlorocypha sp.*	17.0	7.9	22.2	14.3	12
Megaloptera	Corydalidae	*Unspecified*	19.3	11.0	27.0	16.0	43

Order	**Family**	**Genus species**	**Mean**	**Min**	**Max**	**Range**	**N**
Megaloptera	Corydalidae	*Chloroniella peringueyi*	14.3	4.0	25.6	21.6	26
Megaloptera	Corydalidae	*Platychauliodes sp.*	17.2	11.0	21.0	10.0	3
Megaloptera	Corydalidae	*Corydalus sp.*	12.3	11.9	12.7	0.8	2
Trichoptera	Ecnomidae	*Ecnomus sp.*	23.2	12.5	31.7	19.2	18
Trichoptera	Ecnomidae	*Ecnomus thomasseti*	19.8	12.0	29.5	17.5	22
Trichoptera	Ecnomidae	*Parecnomina resima*	17.5	11.7	21.0	9.3	3
Trichoptera	Ecnomidae	*Parecnomina sp.*	19.5	11.5	29.0	17.5	10
Trichoptera	Ecnomidae	*Unspecified*	18.4	8.7	28.0	19.3	47
Trichoptera	Philopotamidae	*Chimarra ambulans*	15.6	4.0	29.0	25.0	43
Trichoptera	Philopotamidae	*Chimarra sp.*	17.6	3.9	29.5	25.6	23
Trichoptera	Philopotamidae	*Dolophilodes sp.*	14.0	9.0	21.1	12.1	3
Trichoptera	Philopotamidae	*Unspecified*	18.6	9.5	29.5	20.0	68
Trichoptera	Barbarochthonidae	*Barbarochthon brunneum*	17.0	11.8	22.2	10.4	2
Coleoptera	Elmidae/Dryopidae	*Dryops sp.*	14.8	5.3	21.0	15.7	7
Coleoptera	Elmidae/Dryopidae	*Elpidelmis capensis*	15.0	4.0	25.6	21.6	32
Coleoptera	Elmidae/Dryopidae	*Haplelmis sp.*	15.3	15.0	16.0	1.0	3
Coleoptera	Elmidae/Dryopidae	*Helminthocaris sp.*	9.4	5.3	15.0	9.7	3
Coleoptera	Elmidae/Dryopidae	*Helminthopsis sp.*	16.2	3.9	29.0	25.1	34
Coleoptera	Elmidae/Dryopidae	*Leptelmis sp.*	18.4	7.9	30.0	22.1	8
Coleoptera	Elmidae/Dryopidae	*Lobelmis sp.*	14.9	5.3	21.0	15.7	12
Coleoptera	Elmidae/Dryopidae	*Microcylloepus sp.*	23.4	12.0	28.0	16.0	7
Coleoptera	Elmidae/Dryopidae	*Microdinodes sp.*	22.1	17.3	29.0	11.7	5
Coleoptera	Elmidae/Dryopidae	*Pachyelmis sp.*	17.6	3.9	30.0	26.1	32
Coleoptera	Elmidae/Dryopidae	*Peloriolus granulosus*	13.7	4.0	16.5	12.5	19
Coleoptera	Elmidae/Dryopidae	*Peloriolus sp.*	14.8	11.0	21.0	10.0	7
Coleoptera	Elmidae/Dryopidae	*Potamocares sp.*	12.0	9.0	16.0	7.0	3
Coleoptera	Elmidae/Dryopidae	*Potamodytes sp.*	14.0	3.9	21.0	17.1	18
Coleoptera	Elmidae/Dryopidae	*Potamogethes sp.*	11.4	3.9	17.0	13.1	9
Coleoptera	Elmidae/Dryopidae	*Protelmis sp.*	12.7	3.9	19.8	15.9	6
Coleoptera	Elmidae/Dryopidae	*Pseudancyronyx sp.*	12.9	3.9	19.5	15.6	10
Coleoptera	Elmidae/Dryopidae	*Pseudelmiddia sp.*	10.5	3.9	17.0	13.1	2
Coleoptera	Elmidae/Dryopidae	*Pseudelmidonia sp.*	12.7	3.9	19.8	15.9	3
Coleoptera	Elmidae/Dryopidae	*Stenelmis sp.*	18.3	3.9	31.0	27.1	55
Coleoptera	Elmidae/Dryopidae	*Unspecified*	18.0	3.9	31.0	27.1	246
Coleoptera	Helodidae	*Unspecified*	15.7	4.0	29.0	25.0	106
Coleoptera	Pspheniidae	*Eubrianax sp.*	14.5	3.9	21.0	17.1	15
Coleoptera	Pspheniidae	*Unspecified*	14.2	11.2	17.2	6.0	2
Diptera	Athericidae	*Atherix sp.*	13.7	3.9	19.8	15.9	37
Diptera	Athericidae	*Unspecified*	18.0	8.0	31.0	23.0	66
Diptera	Blephariceridae	*Elporia uniradius*	12.7	4.0	15.0	11.0	12
Diptera	Blephariceridae	*Unspecified*	14.2	3.9	21.0	17.1	36
Diptera	Dixidae	*Unspecified*	17.6	13.0	26.0	13.0	21
Diptera	Dixidae	*Dixa (Nothodixa) sp.*	12.8	7.5	23.5	16.0	6
Diptera	Tipulidae	*Antocha spp.*	14.8	3.9	19.8	15.9	10
Diptera	Tipulidae	*Eriocera spp.*	13.7	10.5	17.0	6.5	5
Diptera	Tipulidae	*Limnophila spp.*	15.8	6.8	24.0	17.2	28
Diptera	Tipulidae	*Limonia sp.*	17.5	6.8	25.6	18.8	15
Diptera	Tipulidae	*Prionocera sp.*	15.0	11.0	18.9	7.9	2
Diptera	Tipulidae	*Prionocerca sp.*	16.5	16.0	17.0	1.0	2
Diptera	Tipulidae	*Unspecified*	17.6	9.0	29.0	20.0	42

Appendix 6. Lethal (LC_{50}, LT_{50} or Critical Thermal Maxima - CTM) and sublethal (hatching success, growth rate, emergence) effects, preferred and optimum temperatures for aquatic invertebrates summarised from selected northern and southern hemisphere studies

Species	Family	Upper Lethal ^{o}C	Sublethal or preferred ^{o}C	Effect; Comment	Acclimation ^{o}C	Mean CTM ^{o}C	Rate of ^{o}C change	Test endpoint	Location	Reference
Turbellaria										
Dugesia dorotocephala	Planariidae	30.5	18 to 26	Lethal Limit; Optimal range	22				North America	Claussen *et al* . 2003
Oligochaeta										
Lumbriculus variegatus	Lumbriculidae	26.7		96h LT_{50} Constant ^{o}C					New Zealand	Quinn *et al.* (1994)
Crustacea										
Asellus aquaticus	Isopoda				9	34	1^{o}C/day	Inability to right themselves	Finland	Lagerspetz (2003)
Macrobrachium malcomsonii	Palaeomonidae			Juveniles; two acclimation temperatures 20 and 30^{o}C	20 (30)	37.1 (41.4)	0.3^{o}C/min	Loss of equilibrium	India	Selvakumar & Geraldine (2005)
Macrobrachium tenellum	Palaeomonidae	35.4 (38.4)	29.4 (27.7)	Preferred temperature at two acclimation temperatures	22 (32)				Mexico	Roderiguez & Ramirez (1997)
Macrobrachium rosenbergii	Palaeomonidae				25	Ct_{max}=40.7, Ct_{min}= 14.9	0.3^{o}C/min	Loss of equilibrium	India	Manush *et al.* (2004)
Palaemonetes kadiakensis	Palaeomonidae		28 to 32	Preferred temperature	20 to 28	37 to 40		Disorientaiton and tail fold	North America	Nelson & Hooper 1982
Paratya curvirostris	Atyidae	25.7		96h LT50 Constant oC					New Zealand	Quinn *et al.* (1994)
Paracalliope fluviatilis	Eusiridae (Amphipoda)	24.1		96h LT50 Constant oC					New Zealand	Quinn *et al.* (1994)
Paramelita nigroculus	Amphipoda	34.1			13.5				South Africa	Buchanan *et al* . 1988
Plecoptera										
Acroneuria californica	Perlidae	29	18 to 19	Lethal limit; Maximum growth rate					North America	Heiman & Knight 1975
Acroneuria lycorias	Perlidae	30							North America	Nebeker & Lemke 1968
Allocapnia granulata	Capniidae	23							North America	Nebeker & Lemke 1968
Austrocercella alpina	Notonemouridae		5 to 15	Hatching success					Australia	Brittain 1991a
Austrocercella hynesi	Notonemouridae		5 to 20	Hatching success					Australia	Brittain 1991a
Austrocercella illiesi	Notonemouridae		5 to 15	Hatching success					Australia	Brittain 1991a
Austrocercella tillyardi	Notonemouridae		5 to 20	Hatching success					Australia	Brittain 1991a
Cultus aestivalis	Perlidae	16							North America	Gaufin 1973 cited by Ernst *et al.* 1984

Species	Family	Upper Lethal ^{o}C	Sublethal or preferred ^{o}C	Effect; Comment	Acclimation ^{o}C	Mean CTM ^{o}C	Rate of ^{o}C change	Test endpoint	Location	Reference
Isogenus fontalis	Perlodidae	22.5	16	Lethal limit; Early emergence					North America	Nebeker & Lemke 1968, Nebeker 1971c
Isoperla namata	Perlodidae				6.5	33.2	0.34^{o}C/min	Loss of grip	North America	Ernst *et al.* 1984
Isoperla namata	Perlodidae				16	33.8	0.34^{o}C/min	Loss of grip	North America	Ernst *et al.* 1984
Leuctra spp.	Leuctridae		6.6 to 9.7	Optimum temperature for hatching					United Kingdom	Elliot 1987
Nemoura sp.	Nemouridae		16	Early emergence					North America	Nebeker 1971c
Paragnetina media	Perlidae	30.5							North America	Nebeker & Lemke 1968
Phasganophora capitata	Perlidae				6.5	33.4	0.34^{o}C/min	Loss of grip	North America	Ernst *et al.* 1984
Phasganophora capitata	Perlidae				17	36.3	0.34^{o}C/min	Loss of grip	North America	Ernst *et al.* 1984
Prostoia completa	Nemouridae				6.5	31.5	0.34^{o}C/min	Loss of grip	North America	Ernst *et al.* 1984
Pteronarcys dorsata	Pteronarcyidae	29.5	15	Optimum temp for feeding and emergence					North America	Nebeker & Lemke 1968, Nebeker 1971a
Pteronarcys californica	Pteronarcyidae	26.6							North America	Gaufin 1973 cited by Ernst *et al.* 1984
Pterocarcys badia	Pteronarcyidae	24.6							North America	Gaufin 1973 cited by Ernst *et al* . 1984
Soyedina carolinensis	Nemouridae		10	Maximum survival and larval growth					North America	Sweeney *et al.* 1986
Taeniopteryx maura	Taeniopterygidae	21							North America	Nebeker & Lemke 1968
Zelandobius furcillatus	Gripopterygidae	26.5		48h LT50 Constant oC					New Zealand	Quinn et al. (1994)
Ephemeroptera										
Baetis sp.	Baetidae		16	Early emergence					North America	Nebeker 1971c
Coloburiscoides spp.	Coloburiscidae		10 (84%), 25 (96%)	Hatching success - % in parenthesis					Australia	Brittain & campbell 1991
Deleatidium spp.	Leptophlebiidae	22.6		Constant temperature					New Zealand	Quinn *et al.* (1994)
Deleatidium autumnale	Leptophlebiidae	24.2		Constant temperature					New Zealand	Cox & Rutherford 2000
Deleatidium autumnale	Leptophlebiidae	21.9		Diurnally varying temperature (daily mean)					New Zealand	Cox & Rutherford 2000
Deleatidium autumnale	Leptophlebiidae	26.9		Diurnally varying temperature (daily max)					New Zealand	Cox & Rutherford 2000

Species	Family	Upper Lethal °C	Sublethal or preferred °C	Effect; Comment	Acclimation °C	Mean CTM °C	Rate of °C change	Test endpoint	Location	Reference
Dolania americana	Behningiidae		18	Lower limit for emergence					North America	Peters & Peters 1977
Ephemerella subvaria	Ephemerellidae	21.5	16	Lethal limit; Early emergence					North America	Nebeker & Lemke 1968, Nebeker 1971c
Ephemerella invaria	Ephemerellidae	22.9							North America	de Kozlowski & Bunting 1981
Hexagenia limbata	Ephemeridae		16	Early emergence					North America	Nebeker 1971c
Stenonema tripunctatum	Heptageniidae	25.5							North America	Nebeker & Lemke 1968
Stenonema ithaca	Heptageniidae	31.8							North America	de Kozlowski & Bunting 1981
Sephlebia dentata	Leptophlebiidae	23.6		96h LT50 Constant oC					New Zealand	Quinn *et al.* (1994)
Odonata										
Boyeria vinosa	Aeschnidae	32.5							North America	Nebeker & Lemke 1968
Ischnura elegans	Aeschnidae		8	Minimum temperature for growth					United Kingdom	Thompson 1978
Ophiogomphus rupinsulensis	Gomphidae	33							North America	Nebeker & Lemke 1968
Tetragoneuria (Epitheca) cynosura	Corduliidae		15	Maximum temperature for optimal development					North America	Lutz 1974
Hemiptera										
Sigara alternata	Corixidae		15	Accelerated development above this temperature					North America	Sweeney & Schnack 1977
Trichoptera										
Aoteapsyche colonica	Hydropsychidae	25.9		96h LT50 Constant oC					New Zealand	Quinn *et al.* (1994)
Brachycentrus americanus	Brachycentridae	29							North America	Nebeker & Lemke 1968
Brachycentrus lateralis	Brachycentridae	32.8							North America	de Kozlowski & Bunting 1981
Ceratopsyche morosa	Hydropsychidae				19	34.2	0.3°C/min	rolling	North America	Moulton *et al.* 1993
Cheumatopsyche campyla	Hydropsychidae		16	Early emergence					North America	Nebeker 1971c
Chiamarra aterrima	Philopotamidae				19	33.6	0.3°C/min	rolling	North America	Moulton *et al.* 1993
Chiamarra obscura	Philopotamidae				19	36.5	0.3°C/min	leg spasms and rolling	North America	Moulton *et al.* 1993
Hydropsyche beteni	Hydropsychidae		16	Early emergence					North America	Nebeker 1971c
Hydropsyche sp.	Hydropsychidae	30.3							North America	Gaufin & Hern 1971, cited by de Kozlowski & Bunting 1981
Hydropsyche simulans	Hydropsychidae				19	35.6	0.3°C/min	leg spasms and rolling	North America	Moulton *et al* . 1993
Symphitopsyche morosa	Hydropsychidae	30.4							North America	de Kozlowski & Bunting 1981
Pycnocentrodes aureola	Conoesucidae	32.4		96h LT50 Constant oC					New Zealand	Quinn *et al.* (1994)

Species	Family	Upper Lethal ^{o}C	Sublethal or preferred ^{o}C	Effect; Comment	Acclimation ^{o}C	Mean CTM ^{o}C	Rate of ^{o}C change	Test endpoint	Location	Reference
Pycnocentria eveta	Conoesucidae	25		96h LT50 Constant oC					New Zealand	Quinn *et al.* (1994)
Coleoptera										
Hydora spp.	Elmidae	32.6		96h LT50 Constant oC					New Zealand	Quinn *et al.* (1994)
Diptera										
Atherix variegata	Athericidae	32							North America	Nebeker & Lemke 1968
Australopelopia prionoptera	Chironomidae	20.1 to 23.9		LT$_{50}$, Temperate to tropical regions					Australia	McKie *et al.* (2004)
Echinocladius martini	Chironomidae	24.2 to 25.3		LT$_{50}$, Temperate to tropical regions					Australia	McKie *et al.* (2004)
Paramerina sp. "alpha"	Chironomidae	>32		LT$_{50}$, Tropical regions					Australia	McKie *et al* . (2004)
Polypedilum australotropicus	Chironomidae	24.6		LT$_{50}$, Tropical regions					Australia	McKie et al. (2004)
Nanocladius sp. "alpha"	Chironomidae	>32		LT$_{50}$, Tropical regions					Australia	McKie *et al.* (2004)
Tanytarsus dissimilis	Chironomidae		16	Year round emergence					North America	Nebeker 1971c
Simulium sp.	Simuliidae		16	Early emergence					North America	Nebeker 1971c
Mollusca										
Agriolimax reticulatus	Limacidae	17 to 18							North America	Dainton (1943) cited by Gerald & Spezzano (2005)
Helisoma trivolvis	Planorbiidae	17.0 to 22.5							North America	Kavaliers (1980) cited by Gerald & Spezzano (2005)
Lymnaea auricularia	Lymnaeidae	19.3	34 to 36	Lethal limit, Reduction in hatching success					North America, Middle East	Rossetti et al. (1989) cited by Gerald & Spezzano (2005), Salih et al. 1981
Potamopyrgus antipodarum	Hydrobiidae	30 to 32	28	Lethal limit, Inactivity					New Zealand	Winterbourn 1969
Potamopyrgus antipodarum	Hydrobiidae	32.4, 31.0		96h LT50 Constant oC					New Zealand	Quinn et al. (1994), Cox & Rutherford 2000
Potamopyrgus antipodarum	Hydrobiidae	28.6		Diurnally varying temperature (daily mean)					New Zealand	Cox & Rutherford 2000
Potamopyrgus antipodarum	Hydrobiidae	33.6		Diurnally varying temperature (daily max)					New Zealand	Cox & Rutherford 2000
Sphaerium novaezelanidiae	Sphaeridae	30.5		96h LT50 Constant oC					New Zealand	Quinn *et al.* (1994)
Melanoides tuberculata	Thiaridae		16.7 to 22.0	Thermal niche					North America	Gerald & Spezzano (2005)

References – Appendix 6

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