

Water temperature and riverine ecosystems: An overview of knowledge and approaches for assessing biotic responses, with special reference to South Africa

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Abstract

Available information pertaining to water temperature in riverine ecosystems is examined and consolidated into an overview that describes the spatial and temporal variation in water temperature, the importance of water temperature in lotic ecosystems, the measurement and modelling of water temperature, anthropogenic factors that modify water temperature, the effects of temperature changes on the physical and chemical characteristics of water; and on aquatic organisms and ecosystems. Methods for assessing the effects of temperature changes on aquatic organisms are discussed and current water temperature guidelines for the protection of aquatic ecosystems are outlined. This paper highlights the complexity of water temperature in the aquatic environment and the importance of understanding the spatio-temporal variability in water temperature and the variable responses of aquatic organisms to thermal stress. Anthropogenic modifiers of the thermal regime, which include heated discharges, flow modifications, riparian vegetation removal and global climate change; present ongoing threats to aquatic ecosystems. Whilst Northern Hemisphere information on water temperature is plentiful, this overview 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. The risk of increasingly harsh conditions caused by greater water demands and climate change 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. Future directions for thermal research are described.

Keywords: water temperature, riverine ecosystems, rivers, thermal regimes, biotic responses, aquatic organisms

Introduction

Natural thermal characteristics of riverine ecosystems are dependent on hydrological (e.g. source of water, relative contribution of groundwater, rate of flow or discharge, volume of water, inflow from tributaries); regional (e.g. latitude, altitude); climatological (e.g. air temperature, solar radiation, cloud cover, wind speed, vapour pressure, precipitation, evaporation); and structural features (e.g. topographic features, aspect and slope, riparian vegetation cover, channel form, geology, substratum, water depth, turbidity, percentage of pool habitat) of the region, catchment and site (Fig. 1). The relative importance of these features differs amongst rivers and river reaches.

Spatial and temporal variation in water temperature

At the catchment scale, differences are driven by variation in climate, geography, topography and vegetation (Poole et al., 2001). At a river scale, variation occurs longitudinally down a river system with headwaters typically cooler than lowland areas. Maximum temperatures increase downstream (Ward, 1985), while the maximum range is often found in the middle reaches (Vannote and Sweeney, 1980). At a site scale, differences are often determined by geomorphic variation, i.e. laterally across the channel

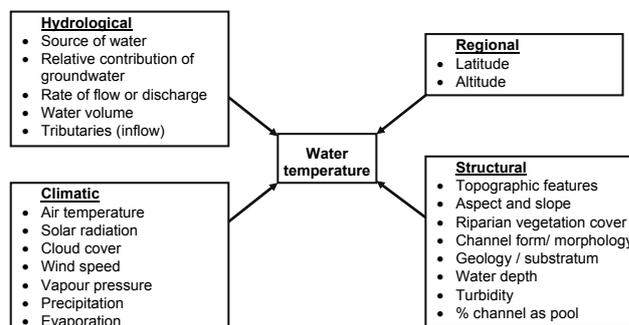


Figure 1

Hydrological, regional, climatic and structural factors influencing water temperature in riverine ecosystems

and in relation to different habitats (Ebersole et al., 2003; Poole et al., 2001), with different habitats having different temperature profiles (e.g. Appleton, 1976; Harrison and Elsworth, 1958; Allanson, 1961; Nordlie and Arthur, 1981).

Lotic systems in regions of seasonal climates exhibit diel (daily) and annual (seasonal) temperature periodicity patterns (Ward, 1985). Hourly temperatures are generally lowest during the night time or early morning and highest in the mid to late afternoon, although this may shift with season (e.g. Hopkins, 1971) and size of river. 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; Constantz et al., 1994). Seasonally, temperatures generally exhibit a sinusoidal pattern with temperatures highest

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Box 1

Examples of spatial and temporal variation in water temperature 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 = 671m), 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. 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, 1965). Values per zone were: Mountain Torrent zone (8.9 to 22.8°C), Upper Foothill (9.0 to 29°C), Lower foothill stony run zone (9.0 to 32.5°C), Foothill soft-bottom zone (10.0 to 31.7°C) and the Flood plain zone (9.0 to 25.5°C).
- The Buffalo River in the **Eastern Cape** had average minimum and maximum temperature 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 to 28°C), Umzintlaba (1 to 27°C), Kinira (9 to 28°C), Tina (12 to 25°C) and Tsitsa (11 to 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 160km 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.

in the summer and lowest in the winter. Inter-annual variation is less predictable with variation in temperature regimes reflected as 'hot-dry' and 'cool-wet' years (Poole et al., 2001).

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 m² (site or reach) and over a time period of hours (diel)]; meso-scale [operating between 10 m² to 10 km² (longitudinal) and over a time period of days (seasonal)]; and macro-scale [operating at areas > 10 km² (regional) and over a time period of years (inter-annual)]. Understanding spatial and temporal trends and variation in water temperature is necessary if the ecological responses of aquatic organisms to changes in water temperature are to be determined. Aquatic organisms, which are poikilothermic, are susceptible to changes in water temperature and it is recognised as a key environmental variable structuring aquatic communities (Arscott et al., 2001). Studies that have included water temperature as a variable indicate that spatial and temporal variation occurs in South African rivers (Box 1).

The importance of water temperature in lotic ecosystems

The importance of water temperature in river ecosystems 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).

Measuring water temperature in aquatic ecosystems – *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 has not been routinely measured in South African rivers although spot measurements of water temperature are available for many rivers (Department of Water Affairs and Forestry, 2008). 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. More recently Rivers-Moore et al. (2004) conducted a study to determine the intra-annual thermal patterns in the main rivers of the Sabie River 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, 2006).

Modelling water temperature

Studies aimed at developing water temperature models are widespread (e.g. Smith, 1981; Mackey and Berrie, 1991) and are broadly classified into three groups: regression, stochastic and deterministic models (Cassie, 2006). The subject is reviewed extensively by Cassie (2006). 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. 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., while logistic models account for groundwater and evaporative cooling (Mohseni and Stefan, 1999; Webb et al., 2003). More realistic but data intensive models are the stochastic and deterministic models. 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 (Stefan and Sinokrot, 1993). Rivers-Moore et al. (2005) tested five different regression water temperature models using maximum daily water temperatures for the Sabie River in 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).

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 (Table 1, next page). Elevated water temperature is more common and widely documented in the literature, although examples for South African rivers are relatively scarce. 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), inter-basin 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, although, it is likely that all modifiers are present within the country. Certainly, agricultural practices, flow modifications (both regulation and inter-basin water transfer) and afforestation are widespread within the country, although the extent of each is likely to vary geographically. More broadly, global warming is of significance for Southern Africa and is likely to have consequences for riverine ecosystems and the associated biota, although the severity of the effect may also vary geographically.

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 (Dallas and Day, 2004). Higher temperatures reduce the solubility of dissolved oxygen in water, decreasing its concentration and thus its availability to aquatic organisms. 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). If the organic loading is high oxygen depletion is further accelerated by greater microbial activity at the higher temperature.

Biological effects of temperature changes on aquatic organisms and aquatic ecosystems

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 metabolism, growth, behaviour, food and feeding habits, reproduction and life histories, geographical distribution and community structure, movements and migrations, and tolerance to parasites, diseases and pollution; of aquatic organisms. Vannote and Sweeney's (1980) '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). There is some debate on the validity of this hypothesis for Southern Hemisphere Rivers. 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

TABLE 1
Anthropogenic factors that modify water temperature in lotic ecosystems

Modifier	Characteristics and effects on aquatic organisms and riverine ecosystems
Thermal discharges	Sources of heated discharges include heated industrial discharge, heated cooling waters from power stations, and returning irrigation waters. Effects are variable, dependent on season (Wellborn and Robinson, 1996) and on the degree to which the heated effluent mixes with the receiving water (Mann, 1965). Heated industrial discharges are frequently linked to other forms of pollution (e.g. chemical pollution) and the toxicity of chemicals may be significantly increased when released in association with elevated temperatures.
Flow modification (river regulation)	In a natural river, 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). Decreasing flow is therefore likely to increase daily water temperatures, including daily maxima due to the lower corresponding depth of flow (Sinokrot and Gulliver, 2000). 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, 1993; 1997), as well as delayed seasonal temperature maximum (Ward, 1982). 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'Keefe, 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). Specifically, reduced water temperatures resulting from a hypolimnetic discharge, delayed spawning in direct proportion to the proximity to the dam (Paller and Saul, 1996), while epilimnetic releases resulted in early spawning.
Inter-basin water transfer (IBT)	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). 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 internationally is given in Snaddon et al. (2000).
Modification to riparian vegetation	Riparian vegetation affects water temperature by adsorbing some of the incoming radiation, emitting long-wave radiation and creating a microclimate, which in turn affects evaporation, conduction, ground and water temperature (Rutherford et al., 1997). Removal of riparian vegetation exposes water to increased direct solar radiation, which leads to higher temperatures, particularly during summer low flows, and greater temperature ranges and fluctuations. Smaller streams with canopy-like vegetation are more likely to experience significant temperature changes if the vegetation is removed, while reduction in riparian shading in larger rivers has less of an effect on water temperature (Quinn et al., 1992). Riparian vegetation is also important in influencing air temperatures which affect adult insects (Collier and Smith, 2000).
Climate change and global warming	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). 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°C) and least at the coast (0.5 to 1.0°C). 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 and decreasing rainfall in some regions is likely to lead to increased water temperatures. Northern Hemisphere studies on the potential impact of global warming on invertebrates (e.g. Hogg et al., 1995) and fish populations (e.g. Eaton and Scheller, 1996) indicate that changes in developmental rates growth rates and emergence times may result in changes in community structure and density of invertebrates. Higher temperatures may lead to a reduction in suitable habitat for cold and cool water fish species (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). No studies have been undertaken in South Africa, although it is likely that similar scenarios may occur. 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 factors such as flow modifications, land use changes, and 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.

environmental regimes (temperature and flow) are less predictable (McKie et al., 2004), such as South Africa.

Aquatic organisms may be broadly categorized 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); and eurytherms: those species with wide tolerance ranges, e.g. in temperate or sub-tropical regions (Langford, 1990). Temperature effects may be evident at the individual level through physiological and behavioural effects; the population level through development, fecundity and survival of individuals; and the community level by favouring temperature-tolerant taxa over temperature-intolerant ones leading to a shift in community structure (Mitchell, 1999).

Physiological and behavioural effects at the individual level

Aquatic organisms are very susceptible to changes in water temperature since a 10°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. The metabolic rate of invertebrates (e.g. Eriksen, 1964) and fish (e.g. Cech et al., 1990) increase in response to elevated water temperatures. Cech et al. (1990) in a study of fish in streams of the Mediterranean region (California) of the United States, suggest 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 their distribution. This region is climatically similar to the south-western Cape in South Africa. Studies on parasites and diseases have shown that fish become more susceptible to diseases when water temperature is elevated and fish are thermally stressed, and many parasites increase rapidly in response to elevated water temperatures. Water temperature plays a vital role in *Schistosoma* (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).

Temperature (and dissolved oxygen concentrations) has been shown to modify prey behaviour in some species (e.g. Kolar and Rahel, 1993) and influence predator-prey relationships (e.g. Cockrell, 1984). It has been shown to influence the rate of feeding of invertebrates and fish, with feeding rates varying significantly at different temperatures (Kishi et al. 2005), and highest feeding rates at intermediate temperatures (9 to 12°C), which coincided with mean summer water temperature. Some fish species also exhibit a temperature threshold below which they stop feeding or only feed sporadically (Keast, 1968 cited by Mohseni et al., 1998). Trophic interactions, such as predation, may be modified by water temperature as shown by Kishi et al. (2005) whose study highlighted the potential for trophic cascading effects resulting from changes in water temperature and provide evidence that thermal habitat alteration may affect not only thermally sensitive species like fish but also resistant species like caddis fly larvae and periphyton via indirect effects in food webs. Quinn et al. (1992) showed how changes in algal periphyton abundance and macroinvertebrate 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. Temperature may influence movement of aquatic organisms particularly fish, which 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. Torgersen et al., 1999; Elliot, 2000; Ebersole et al., 2001; Gardner et al., 2003). Thermal refugia, which include undercut banks and overhanging vegetation (Bell, 2006), coldwater patches associated with lateral seeps, cold side-channels, floodplain tail seeps, floodplain seeps and stratified pools (Mosley, 1983; Ebersole et al., 2001) are most numerous in intact riverine systems with riparian vegetation and groundwater (Torgersen et al., 1999). Vertical stratification in pools (Matthews and Berg, 1997; Elliot, 2000; Tate et al., 2006) may result in pools acting as thermal refugia with fish migrating to cooler bottom water when surface temperatures exceed their incipient lethal limit. These bottom waters are often lower in dissolved oxygen (DO) than the surface water resulting in a trade-off between high temperatures and low DO (Matthews and Berg, 1997; Elliot, 2000).

Reproduction (fecundity), development, growth and life histories at the population level

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). Fish gonadal development and spawning may be triggered by temperature, photoperiod, water level or flooding, intra-specific interactions, and the presence of suitable spawning substrates (Lake, 1967; Jones et al., 1978 cited by Paller and Saul, 1996). 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 (Humphries et al., 1999). In the Northern Hemisphere several fish species spawn within 3 to 5°C of their critical thermal maximum. Several studies have examined the reproductive biology of fishes in South Africa (Box 2) and studies have shown that temperature is an important factor triggering spawning, with temperatures between 18 and 19°C triggering spawning of several of South Africa's indigenous fish species (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; Cambay et al., 1997; King et al., 1998).

The growth of aquatic insects has been shown to be strongly correlated with temperature in several taxa including mayflies (Markarian, 1980; Hury, 1996), stoneflies (Harper, 1973) and isopods (Thorup, 1973). Growth rates in aquatic invertebrates have rarely been studied in South Africa (e.g. Hart, 2001) although 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. Water temperature is considered to be the most important environmental factor affecting fish growth (Marine and Cech, 2004) with growth occurring within a limited thermal range and the temperature regime determining the length of the growth season. South African studies on fish growth 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,

Box 2

Examples of fish spawning in South African rivers

- In the Western Cape, *Barbus capensis* (Clanwilliam yellowfish), ascend rivers and spawn in gravel beds in relatively shallow water (Hey, 1947 cited by Cambray et al., 1997). Upstream migration occurs 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°C. In contrast, lower temperatures the following year due to late cold weather resulted in spawning bed temperatures between 16.6 to 17.5°C. No spawning occurred during this period (King et al., 1998). A thermal spawning threshold of 19°C has been proposed (King et al., 1998). In the Gouritz River system *Labeo umbratus* migrate upstream and spawn on the floodplain (Jackson and Coetzee, 1982). This has been observed in heavy floods in summer (Hamman and Thorne, 1982 cited by Tomasson et al., 1984). Larvae hatched after 30 h at 22°C (Mulder, 1971 cited by Tomasson et al., 1984). Various aspects related to seasonality, spawning and life history of fish in the Western Cape are currently being investigated (Paxton, 2008).
- In the Eastern Cape, *Oreochromis mossambicus*, usually spawn in late November when minimum water temperatures exceeded 18°C (James and Bruton, 1992) while *Barbus trevelyani* (Border barb) requires a minimum water temperature of 18°C for successful induced spawning (Bok and Heard, 1982).
- In the Northern Cape, 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. 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 4 to 6 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°C (Groenewald, 1951 cited by Tomasson et al., 1984) and fertilized eggs of *B. holubi* incubated for 3 to 8 d at 18 to 21.5°C (Le Roux, 1968 Mulder and Franke, 1973 cited by Tomasson et al., 1984).
- In Kwazulu Natal, *Barbus natalensis*, migrate upstream to spawn and are unable to breed in still water (Crass, 1964 cited by Tomasson et al., 1984). They spawn in clean, well circulated gravel in fast flowing water, when water temperature exceeds 19°C (Wright and Coke, 1975 cited by Tomasson et al., 1984).
- In neighbouring Lesotho, *Oreodaimon quathlambae* (Maluti minnow), is limited to the extreme upper area of the 2 300 km Orange River system. Adults' spawn and eggs are laid amongst boulders in mid-channel which is oxygen-rich (Cambray and Meyer, 1988).

1976). 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).

Temperature appears to be a determinant of synchrony of life history (Lake et al., 1985). 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. Macan, 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. In the Southern Hemisphere, Hart (1985), 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). The flexible life cycles are considered an adaptation to the unpredictable and highly variable climate in Southern Hemisphere regions such as Australia (Hynes and Hynes, 1975). Studies in South Africa are scarce, with information inferred from more generalist studies such as King (1981) and King et al. (1988). King et al. (1988) observed that abundance peaked in spring and late summer, while juvenile recruitment peaked in spring (November) in the Western Cape. 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). Many species emerged in summer, possibly to avoid high temperatures year (King, 1981).

Functional and structural changes at the community level

Temperature regulates ecosystem functioning directly by influencing primary production. Studies have shown that primary production generally increases with temperature (e.g. Quinn et al., 1992; Kishi et al., 2005) and there is a shift in the dominance of algal classes from diatoms (<20°C) to green algae (15 to 30°C) to blue-green algae (>30°C) (DeNicola, 1996). Algal species diversity increases from 0 to 25°C and decreases at temperatures >30°C; while biomass increases with temperature from approximately 0 to 30°C and decreases at 30 to 40°C. The degree to which algal community composition changes with thermal input depends on the initial ambient temperature, with increases in temperature in environments near 25 to 30°C usually causing greater changes in community structure than in environments <25°C (DeNicola, 1996). Algal community structure usually recovers rapidly (<1 yr) when temperature stress is discontinued. In many natural communities temperature does not usually limit algal biomass and primary productivity but it does set an upper limit for production when other factors are optimal (DeNicola, 1996).

Water temperature strongly influences the geographic distribution of a species (Hart, 1985; Bell, 2006) and changes in water temperature may lead to structural 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) consider summer to be a critical season for many aquatic insect populations in that much of the biological production occurs when temperatures are highest. Several studies have shown a reduction in macroinvertebrate abundance and diversity following an average temperature increase of around 7°C (Coutant, 1962 cited by Mann, 1965; Wellborn and Robinson, 1996; Hogg et al., 1995).

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°C during the summer months (Skelton, 1993). Tropical fauna is restricted to areas where the water temperatures do not decline below 15 to 18°C during the cooler winter months (Skelton, 1993).

Assessing the effects of temperature changes on aquatic organisms

The effect of water temperature changes on aquatic organisms are assessed and monitored by direct measurement and observation in the field; and by laboratory studies, with the two methods often used in a complimentary way. Empirical data, derived from field observation, can provide useful information on the distribution of aquatic organisms. The potential problem with this method, however, is that it does not take into account microhabitat heterogeneity (Beitinger et al., 2000). Field data is

often used to calculate averages such as the 7 d average of daily maximum temperature (Huff et al., 2005), which may be related to thermal niches. In South Africa, water temperature data are 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). Water temperature data also exist for fish distribution records but these have not been captured into the distribution database (Bills, 2007). The utility of the two aquatic invertebrate databases in identifying thermally-sensitive taxa via calculation of the temperature ranges for different invertebrate families and selected genera or species was examined and is reported on in Dallas (2007).

Laboratory studies on the thermal tolerance of aquatic organisms are numerous particularly in the Northern Hemisphere. Effects may be assessed in terms of an organism's lethal limits (minimum and maximum), sublethal effects or behavioural avoidance preferences. For a comprehensive understanding of the effect of water temperature on aquatic organisms a combination of these methods is recommended although it is recognised that this is not always feasible.

Lethal effects on aquatic organisms

Lethal temperature is affected by several factors (Fig. 2, after Langford, 1990) including the rate of change of temperature, acclimatisation and acclimation (i.e. an organism's temperature history), duration of exposure (i.e. acute versus chronic), life history stage (e.g. eggs and larvae are often more susceptible than adult stages), multiple stresses (e.g. water quality impairment), and adaptive strategies that allow for behavioural thermoregulation or physiological adaptations. Laboratory studies include two approaches: lethal effects and critical thermal methodology. 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). LC_{50} is the temperature lethal to 50% of the test organisms, while the LT_{50} is the median lethal time, which is the duration eliciting 50% mortality at a specific temperature. The critical thermal methodology (CTM) is based on the exposure of an organism 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' (Cox, 1974 cited by Ernst et al., 1984). The CTM endpoint is the critical thermal

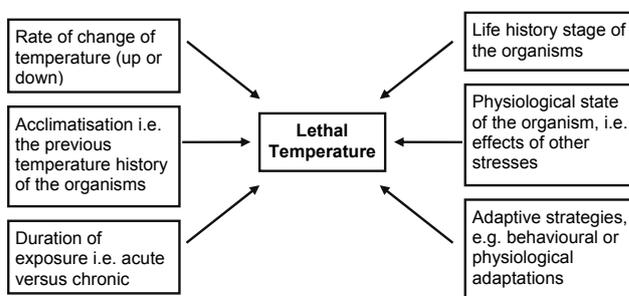


Figure 2
Factors affecting the lethal temperature for aquatic organisms
(adapted from Langford, 1990)

TABLE 2
Guidelines and criteria for water temperature in South Africa, Australia and New Zealand, Canada and the United States

Country	Guidelines or criteria	References
South Africa	Guidelines are site-specific and based on the deviation from “natural” (reference) conditions. A target water quality range is specified 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. Daily temperature data are however limited and the current approach used to estimate the natural distribution of temperature is by specifying a monthly temperature range characterised by the 10 th and 90 th percentile temperatures. Where actual data do not exist modelled temperature data for a reference site as close to the resource unit of interest is used to derive the “no-effect” range. The “no-effect” and “critical effect” levels thus respond to natural seasonal variation.	DWAF, 1996 Dallas et al., 1998 Jooste and Rossouw, 2000
Australia and New Zealand	Guidelines are site-specific and based on the derivation of trigger values (20 th and 80 th percentile). These values are based on site-specific biological effects data and are generally calculated from data at a reference site. It is recommended that trigger values be developed 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 is used for comparison. Trigger values may be modified depending on the management objective i.e. levels of ecosystem condition.	NWQMS, 2000
Canada	Guidelines are site-specific and largely based on the protection of important fish species. Criteria are based on Maximum Weekly Average Temperatures (MWAT), which take into account the physiological optimum temperature (usually for growth) in warmer months, the survival temperature in winter months, the reproductive functions (e.g. migration spawning egg incubation fry rearing) of important species during the reproductive season, and overall species diversity and prevention of undesirable growths of nuisance organisms.	CCRME, 1999
United States	Guidelines are numerous and often regionally focused with emphasis placed on fish populations. Temperature criteria generally specify a temperature threshold calculated over an averaging period. Various temperature indices are used including the 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.	McCullough et al., 2001 Poole et al., 2001)

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 Analysis of Variance (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 an organism's internal temperature to equal water temperature. The rate of 0.3°C/min has been recommended (Beitinger et al., 2000).

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 Dallas (2007) although Northern Hemisphere studies are exhaustive and only selected studies are included. Lethal limits varied from 16°C for a North American family of Perlidae to 38.4°C for a freshwater prawn acclimated to 32°C in Mexico. In the Southern Hemisphere lethal limits varied from 21.9°C for a leptophlebiid mayfly to 32.4°C for a hydrobid snail (New Zealand studies). Mean CTM varied from 31.5°C for a North America perlid to 40.7°C for freshwater prawns. No

Southern Hemisphere studies using traditional CTM were noted. Information on temperature tolerances of North American fish is numerous and approximately 80 studies provide tolerance data (see Beitinger et al., 2000 for a review). 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.

Sublethal effects

Sublethal (chronic) effects include those on reproduction, spawning, egg incubation and hatchability, development and growth, survival of fry, and emergence success, as well as sub-lethal physiological effects. The duration of exposure is important in assessing sublethal effects. Two common measures of chronic exposure are the maximum weekly average temperature (MWAT) and the maximum weekly maximum temperature (MWMT). Many studies have examined egg incubation and hatchability rates for aquatic insects (Elliot, 1972; Harper, 1973; Humpesch, 1980; Weatherley and Ormerod, 1990; Britain, 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; b; 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).

Behavioural preferences and avoidance

Studies on the behavioural effects 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 (Cherry and Cairns, 1982; Boubee et al., 1991; Richardson et al., 1994). 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 and allows ontogenetic shifts in temperature preferences to be calculated. Boubee et al. (1991) showed experimentally that the final preferred temperature of *Galaxias maculatus* resident in New Zealand is about 20°C and temperatures above 29.5°C were totally avoided.

Water temperature guidelines for the protection of aquatic ecosystems

An examination of the guidelines for water temperature in aquatic ecosystems highlights the importance of understanding natural spatial and temporal 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 variable 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 (Sullivan et al., 2000) include temperature thresholds that reflect biological effects (acute sublethal); temperature fluctuation characteristic (maximum mean minimum fluctuation); and averaging period (instantaneous maximum 7 d 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. Table 2 provides a brief 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.

Conclusions

This overview highlights the complexity of water temperature in the aquatic environment, 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 a country already 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 overview 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.

Such a programme has recently been initiated in South Africa (Dallas and Rivers-Moore, 2008) with the focus on lotic ecosystems, since these systems are subject to flow regulation and water abstraction to a much greater degree than lentic systems. The persistence of these ecosystems is more likely to be achieved through a better understanding of water temperature patterns and processes. Emphasis will be placed on the collection of long term data, which are necessary for extracting principles on water temperature relevant to South Africa. These will in turn inform policy. Research has indicated that there are likely to be significant differences between Northern and Southern Hemisphere aquatic thermal regimes (Dallas, 2007; Rivers-Moore, 2007). Thus, Northern Hemisphere practices cannot be blindly applied to management issues in Southern African rivers. 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. 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.

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