



Water temperature criteria for native aquatic biota

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Water temperature criteria for aquatic native biota

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1 Introduction

Water temperature affects all aspects of freshwater ecosystems, from primary producers through to fishes. Altered water temperature regimes can alter the physical habitat conditions (e.g. algal blooms) and cause a wide variety of behavioural and physiological responses with the most dramatic being death (Carveth et al. 2007; De Vries et al. 2008). Consequently, maintaining suitable thermal conditions is critical to achieve instream management objectives, such as the conservation of freshwater species. Management of water temperatures for the protection of aquatic species should consider more than just the critical thermal limits and should be based on the thermal requirements of all life stages of the species in question.

This report reviews the existing water temperature criteria for aquatic life, with emphasis on setting thresholds for effects. It includes the following:

1. A review and critique of field and laboratory methods used for setting temperature criteria for freshwater biota, highlighting information gaps necessary to determine environmental temperature thresholds for native freshwater biota.
2. Comments on the application of these criteria to native freshwater biota, including physiological effects, in relation to both point source (e.g., thermal inputs) and passive (e.g., loss of shade) thermal effects. We consider the relevance of criteria to:
 - i. effects over long and short time scales (including temperature fluctuations),
 - ii. effects of temperature in combination with other environmental stressors (i.e., cumulative effects), and
 - iii. effects associated with modified biotic (e.g., competition/predation with introduced species) and food-web (e.g., heat stress rendering native species more susceptible to predation) interactions.
3. Based on the above, we recommend appropriate environmental temperature criteria for aquatic life in streams and rivers, and/or describe the studies required to determine these.

2 Fundamentals for understanding thermal tolerance

Before starting with the body of this review, it is necessary to introduce some concepts and terminology relating to the study of the thermal tolerance of organisms. All species have a critical thermal range over which they function, grow and develop normally. Defining this range is critical for successful management of a population. The following section defines the terminology used to define the thermal limits of a species and the factors that may affect these limits

2.1 Terminology

All of New Zealand's freshwater animals are poikilotherms (commonly referred to as cold-blooded) meaning that their internal body temperature varies with that of their environment (Greek poikilos = changeable). Consequently, water temperature exerts a significant influence over many aspects of their biology and so understanding the thermal requirements of biota is an essential component of informed management of these systems. A glossary of relevant terms shown in bold in the text is included in Appendix 1.

2.1.1 Defining thermal tolerance limits

The critical thermal range of an organism is bounded above by the **upper and lower ultimate lethal temperature**, the temperatures at which death occurs almost instantaneously. Within these ultimate thermal limits is a **tolerance zone** – the thermal range over which the animal will survive for significant periods of time. The upper and lower limits of the tolerance zone are defined by the **upper and lower incipient lethal temperatures (UILT and LILT, respectively)**. The incipient lethal temperature is usually defined as the temperature at which 50% mortality occurs in experiments conducted over a set period of time. It should be noted that the incipient lethal temperature is dependent on the exposure time, thus a higher incipient lethal temperature would be derived from an experiment conducted over a short time period rather than a long one. Because the UILT varies with acclimation temperature (Figure 1), the **ultimate upper incipient lethal temperature (UUILT)**, the point at which the upper incipient lethal temperature no longer increases with acclimation temperature (Figure 1), is often used to estimate the temperature at which significant mortality is expected to occur.

The **stress zone** is between the incipient lethal temperature and the ultimate lethal temperature. This is where thermal stress occurs and will ultimately kill the animal, with the time until death being a function of exposure time to the thermal stress. Within the tolerance zone is the **growth zone**, the temperature range over which normal (i.e. positive) growth can occur given sufficient availability of food. And within the growth zone is the **thermal growth optimum (Topt)**, the thermal range over which the greatest rate of growth occurs. It should be noted that the above limits and zones may change over the life-cycle of the species, with food availability (e.g. for the growth optimum in fish), and preceding thermal conditions (due to **acclimation/acclimatisation**). For instance, the **final preferendum** refers to the temperature at which acclimation and preferred

temperature are equal. The thermal tolerances and requirements of a species across a range of different acclimation temperatures can be represented as a **thermal tolerance polygon** (Figure 1).

To illustrate the various critical temperatures outlined above, the thermal tolerance polygon for brown trout (*Salmo trutta* L.) is shown in Figure 1. The brown trout was chosen as this example because there is detailed scientific information about its thermal requirements, largely due to the exhaustive experimental work done by J.M. Elliott (see review in Elliott 1994). Gathering these data requires a concerted experimental effort and at present sufficient information has not been collected to present such information for a New Zealand native species. In Figure 1, it should be noted that the ultimate and incipient lethal temperatures are affected by the acclimation temperature. It should also be noted that brown trout do not appear to have reached their lower ultimate lethal temperature at 0°C, as long as they do not become entombed in ice (Figure 1, Elliott 1994).

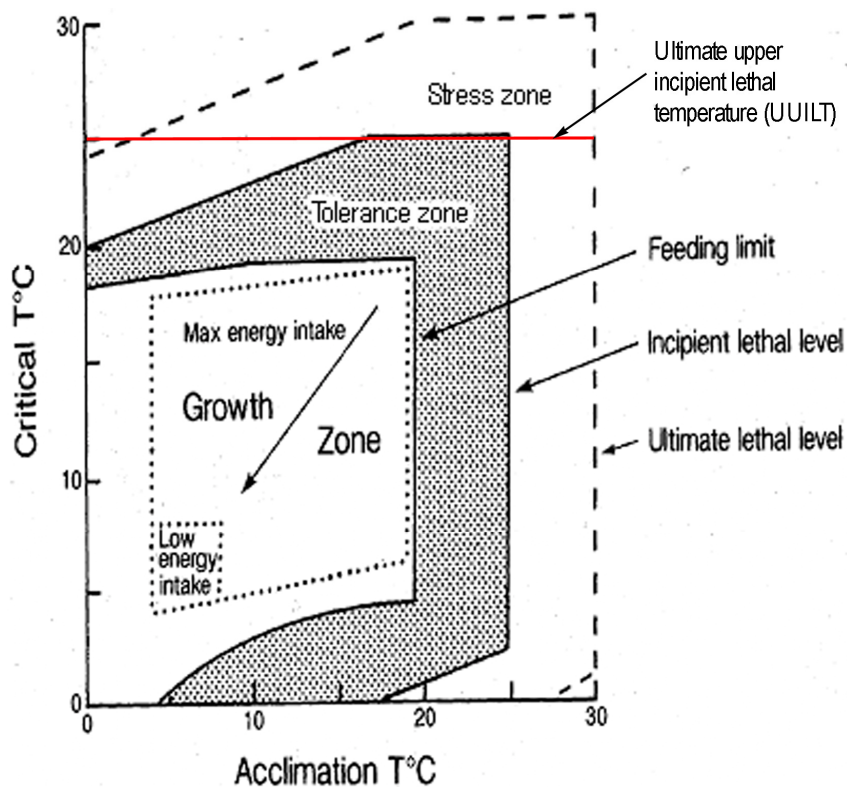


Figure 1.
Thermal tolerance polygon for brown trout from Elliott (1994).

2.1.2 Acclimation and acclimatisation

A key feature of the thermal tolerance polygon in Figure 1 is that the various critical temperatures (ultimate and incipient lethal, feeding limit and growth zone) are affected by the acclimation temperature; the temperature at which the animal was held and allowed to adjust to, prior to experiments being carried out. In Figure 1, the effect of acclimation has been determined based on experimental studies where temperature is the only variable being altered. Whilst this is the correct approach in conducting such experiments, such controlled changes in only one variable rarely occur in natural settings. Instead, in many natural settings water temperature varies considerably along with other variables (e.g., food availability) may also change. Reversible and adaptive physiological responses to changes in multiple variables are referred to as acclimatisation and, while it is a physiological response, it may also affect the behaviour of the organism.

2.2 Sub-lethal effects of temperature

'Sub-lethal effects' is a broad heading that could be used to encapsulate any effect that does not result in immediate mortality. For the purposes of this review, sub-lethal effects are defined as any effect that reduces the fitness of the individual. In this context, fitness refers to the number of offspring produced that survive to maturity and reproduction. Growth is an important sub-lethal response to temperature, since body size is directly related to fecundity in many species (e.g. Sweeney & Vannote 1978; Vannote & Sweeney 1985; Honěk 1993) and large size may convey advantages over smaller individuals (e.g. Taylor et al. 1998). Other measures of fitness indicate the likely reproductive output of an individual, which may be measured by gonad development as well as the viability and number of gametes produced. Such measures are reflected in Natural Resources legislation in Wisconsin, where sub-lethal effects have been defined as "...effects resulting in inadequate gonad development, gamete production and viability, spawning or growth." (https://docs.legis.wisconsin.gov/code/admin_code/nr/102/11/25).

2.3 Other factors affecting thermal tolerance

In most thermal tolerance experiments, fish are fed to satiation (i.e. on maximum rations). This removes a source of variability in experimental data but that variability is relevant to the management of wild populations. It is not uncommon for animals in natural environments to not achieve full rations (e.g. Cada et al. 1987; Gee 1988; Ensign et al. 1990; Burns & Dodds 1999; Young et al. 2000). Such food limitation may affect the thermal tolerance of organisms. For example, the thermal optimum for fish growth decreases on reduced rations (Elliott 1975; 1994; Elliott & Hurley 1999).

Elliott and Hurley (1999) also demonstrate that the optimal temperature for the growth of brown trout is dependent on the energy content of available food, with the optimal temperature for growth decreasing with decreasing energy content (see also Elliott 1975; 1994). The optimal temperature for growth of brown trout fed on an invertebrate diet is 14 °C while this increases to 17 °C in trout fed on a fish diet (Elliott & Hurley 1998; 1999; 2000).

Temperature fluctuations may also influence the thermal tolerances of fish and invertebrates. Experiments on rainbow trout (*Oncorhynchus mykiss*) showed that when growth was plotted against the mean daily temperature for fish exposed to daily fluctuations in water temperature of approximately 4°C, the growth curve shifted to the left of that obtained in constant temperature experiments (Hokanson et al. 1977). As a result, fluctuations resulted in higher growth rates at mean temperatures below the thermal growth optimum and retarded growth at temperatures above the thermal growth optimum (Hokanson et al. 1977). In addition, mortality of rainbow trout was higher when temperature fluctuated than when it was constant. (Hokanson et al. 1977). The thermal tolerance of two New Zealand invertebrates (*Deleatidium* and *Potamopyrgus antipodarum*) is also lower under fluctuating than constant temperature; Cox & Rutherford 2000 found that the incipient lethal limit for both taxa was reduced by 2.5°C under fluctuating temperatures (mean temperature \pm 5°C).

These studies have significant implications for applying the results of laboratory experiments on thermal tolerance to natural populations. The conditions present in most laboratory studies (constant temperature, abundant, high-energy content food) are unrealistic for most natural systems and are likely to over-estimate the real thermal tolerance of species under the conditions experienced in the natural environment. Consequently, this should be accounted for when applying experimentally-derived critical temperatures (e.g. UILT, critical thermal maximum, T_{opt}) to natural systems (see Section 6.3.1).

2.4 Behavioural thermoregulation

It should be kept in mind throughout this review that while cold-blooded, poikilotherms can nevertheless influence their body temperature through behaviour. Mobile organisms can thermoregulate by selecting areas with suitable temperatures. For behavioural thermoregulation to be effective, the environment must be thermally heterogeneous at an appropriate scale. In some rivers there may be significant longitudinal changes in water temperature due to altitude or changes in riparian vegetation, although such transitions are likely to occur over significant distances and would necessitate large-scale migration by organisms to utilise them. Whilst such migrations occur, smaller-scale thermal heterogeneity may provide resident fish with the opportunity to behaviourally thermoregulate without the large energetic investment and risk associated with long-distance migrations. Sources of such smaller-scale heterogeneity include thermal stratification in lakes, tributary inflows and groundwater inputs (such as springs) (e.g. Olsen & Young 2009).

During periods of thermal stratification in lakes, fish can influence their body temperature by residing at different depths and may move between different depths for different activities, such as foraging or resting. For example, a predatory fish may move into warmer water to forage if its prey has a higher thermal preference, but move back into cooler water to rest while digesting that prey. Conversely, prey may reside in water that is cooler or warmer than its preference to avoid predation.

2.5 Heat exchange between an organism and its environment

Aquatic organisms are in direct contact with water for much, if not all, of their lives (many aquatic invertebrates have terrestrial adults). Water has a very high volumetric heat capacity, resulting in the rapid transfer of heat from the bodies of aquatic organisms to the surrounding water. In the case of fish, the gills act as a heat-exchanger, but the majority of the heat transfer is via conduction through the body wall (Elliott 1981). In a practical sense, what this means is that the body temperature of a fish sitting in a body of water will change as the temperature of the water changes. However, changes in the body temperature of a fish will lag changes in the surrounding water (this lag is sometimes referred to as thermal inertia), with the change in body temperature relative to water temperature following Newton's law of cooling, which can be described as:

$$\frac{dQ}{dt} = -h \cdot A \Delta T(t)$$

where:

Q = thermal energy in joules,

h = heat transfer coefficient (assumed to be independent of T),

A = surface area of the heat being transferred,

$\Delta T(t)$ = time-dependent thermal gradient between environment and object.

Equation 1 shows that the key factors that affect the rate at which the body temperature of a fish are the surface area of the fish (inversely related to body size/weight) and the magnitude of the thermal gradient between the fish and the surrounding water.

Experiments conducted by Elliott (1994) confirmed this relationship for brown trout subjected to warming and cooling with the rate of change in body temperature being affected by the size and weight of the fish (Figure 4.1 of Elliott 1994). In addition, the rate change in body temperature was higher for warming than the rate of cooling (Figure 4.1 of Elliott 1994).

This is relevant to the thermal management of natural waterways, particularly those with substantial diel variation in water temperature, as the body temperature of a large fish will lag water temperature by more than that of a small fish resulting in large fish experiencing a lower maximum body temperature than a small fish. This will be a general pattern within and between fish species. One implication of this is that the risk from short-lived increases in water temperature is lower for large species (adult eels) than for a smaller species with similar upper thermal limits. This also has implications for the derivation of estimates of the upper ultimate lethal temperatures, since the experimental values derived for large fish may overestimate the ultimate lethal temperature due to the lag between changes in water temperature and changes in the body temperature of the fish (see Section 3.2).

3 Methods used to assess thermal tolerance

3.1 Field methods

3.1.1 Assessing thermal limits

Establishing thermal criteria from field-collected data has its limitations due to the inability of the observer to control all possible variables that contribute to the distribution of an organism.

Thermal springs offer an opportunity to gain some understanding of the upper thermal limits of taxa. However, thermal springs often represent strong gradients in factors other than temperature, and such factors (such as mineral content, salinity, and oxygen concentrations) may also define limits to animal distributions. In addition, the temperatures that organisms are exposed to may vary with time and the temperatures observed at the time of collection may not reflect preceding temperature conditions. Thus, field data cannot be used to definitively establish the thermal limits of organisms. However, sampling across strong thermal gradients, such as those found in the outlets of thermal springs, can be used to indicate the likely upper thermal tolerance of various species in the absence of experimental data.

3.1.2 Methods used to assess chronic thermal effects

Acute changes in water temperature generate a state of stress in fish. These changes trigger the heat shock response, which involves the action of several proteins, the heat shock proteins (HSPs) and transcription factors which, in turn, will increase the protection of the cell against the stressors. HSPs are a family of proteins expressed in response to a wide range of stressors, including temperature, but also exposure to oxidants, heavy metals, and bacterial and viral infections. HSPs are involved in essential cell roles such as protein assembly, correct folding and translocation, as well as in regulating interactions between hormones and their receptors (Lopez-Olmeda & Sanchez-Vazquez 2011).

The increase in temperature stimulates all metabolic processes; it enhances oxygen consumption and, therefore, may increase reactive oxygen species (ROS) (i.e., free radical) production as side-products of intensified metabolism resulting in oxidative stress (Lushchak 2011). Under normal conditions, ROS production is a dynamic process under steady-state concentrations where the amount of ROS produced is continuously eliminated. However, stressors such as temperature can alter ROS concentrations leading to disturbance of redox status called oxidative or reductive stress. Oxidative stress is a situation when steady-state ROS concentration is transiently or chronically enhanced, disturbing cellular metabolism and its regulation and damaging cellular constituents (Lushchak 2011).

3.2 Laboratory methods – lethal effects

3.2.1 Critical thermal maximum (CTM) method

The CTM method involves taking an acclimated individual and placing it in an experimental apparatus that allows the user to increase the water temperature in the apparatus at a constant rate until the end-point of the experiment (=the CTM) (Hutchison 1961). The CTM is usually defined as the temperature at which the animal's movement becomes disorganised and the animal would be unable to actively escape the warm water (Cowles & Bogert 1944). This method has commonly been employed for native fish species in New Zealand (Simons 1984; Simons 1986c; Teale 1986; Main 1988).

Determining the appropriate rate of heating used in the CTM approach is a trade-off. If the rate of temperature increase is too fast, there is the potential for a substantial lag between water temperature and the body temperature of the animal, resulting in an over-estimation of the CTM. If the rate of temperature increase is too slow, there is the potential that the experimental animals will acclimate as the experiment progresses, again over-estimating the CTM. Simons (1984) compared the CTM obtained for shortfin eel elvers at three different rates of heating: 1 °C per 2, 5 and 10 minutes. His experiments yielded CTMs of 35.6 °C at 1 °C/2 min, 35.0 °C at 1 °C/5 min and 31.4 °C 1 °C/10 min (Simons 1984). These differences may be caused by greater opportunity for acclimation at slower rates of temperature increase or a lag between the temperature of the water and the body temperature of the elvers.

Advantages of the CTM method include the relatively simple experimental set-up, short duration of tests and because the CTM method has been employed for a large number of species, inter-species comparisons are possible. However, CTM values are of limited applicability in understanding the tolerance of organisms in natural systems, since the rapid rate of temperature increase usually employed is unrealistic in such settings.

Modified CTM method

Due to the criticisms outlined above, a modified CTM method has been developed, in which a much slower rate of temperature increase is employed (e.g. 1 °C/day, Winterbourn 1969 – experiment 2), enabling experimental subjects to acclimate to temperature changes. However, neither of the CTM methods allows assessment of the effect of exposure time on tolerance because temperatures increase throughout the experiment.

3.2.2 Incipient lethal temperature (ILT) method

The incipient lethal temperature is usually calculated as the temperature at which 50% mortality occurs over a set time period, often referred to as the LT50. The duration of such experiments has varied widely, ranging from 10 minutes to 14 days. In the case of Richardson et al. (1994), fish were transferred from a tank held at the acclimation temperature to a water bath heated to the experimental temperature where they were immersed for 10 minutes before being returned to the acclimation tank.

The LT50 approach has the advantage that it takes account of the length of exposure to the experimental temperatures, with LT50s expressed for various exposure times. A disadvantage of this approach is that the abrupt change in temperature from the acclimation tank to experimental tank precludes acclimation and may cause shock. The evaluation of LT50 values can be challenging and depends on the acclimation temperature (T_a) as the effect of a sudden temperature increase in test systems with different water temperatures will differ. Consequently, recently a modified method has emerged that involves a slower transition from the acclimation temperature to the experimental temperature (Smith & Fausch 1997).

3.2.3 Acclimated chronic exposure (ACE) method

The ACE method was developed by Zale (1984 in Selong et al. 2001), and can be seen as a hybrid between the CTM and LT50 methods. After acclimation, the water temperature in the test tank is gradually increased (e.g., 1 °C/day) until it reaches the test temperature. Once the test temperature is reached, it is maintained for 60 days or until the death of the experimental subject. Unlike the CTM and ILT methods, which employ rapid or instantaneous temperature shifts, the ACE method allows test organisms to acclimate to environmentally realistic temperature changes. For each test temperature, median resistance times are recorded and plotted using exponential regression, and the resulting formula is then used to calculate the ultimate incipient lethal temperature (i.e., the temperature at which 50% of the test fish survive for 60 day) (Selong et al. 2001). Seelong (2001) claimed that by more closely mimicking the thermal conditions that fish experience in nature, the ACE method increases the applicability of laboratory results.

Advantages of the ACE method include the experimental subjects being given the opportunity to acclimate fully to the experimental temperature, the ability to use the results to evaluate chronic thermal effects, and the ability to assess the sub-lethal effects of the test temperature (fish growth, health) (Selong et al. 2001). It is argued that the long duration of ACE tests provides a more robust estimates of the temperature at which test taxa can survive indefinitely than shorter-term tests (such as 7-day LT50 tests). For example, Seelong (2001) observed delayed mortality of bull trout, which began up to 31 d after initial exposure to test temperatures, suggesting that a 7-day ultimate upper incipient lethal temperature (UUILT) may not accurately reflect the temperature at which 50% of the population can survive indefinitely.

Compared with the methods outlined above (CTM, LT50), the major disadvantages of the ACE method are the time, effort and resources required to conduct these tests. Chronic exposure tests require maintenance of experimental apparatus and experimental subjects for more than 60 d. The cost and effort required in conducting such experiments may restrict the number of animals used in the experiments, or may preclude the use of the ACE method altogether.

3.3 Laboratory methods – sub-lethal effects

In contrast to many of the experimental approaches to assessing the lethal effects of temperature, assessments of sub-lethal effects generally require long-term experiments.

This is because the ultimate measure of the sub-lethal effect of temperature is fitness, which requires experiments conducted over the life-time of an individual and its offspring.

Such experiments generally involve experimental organisms being held under temperature-controlled conditions (usually constant temperature, but may be subject to daily temperature fluctuations) under standardised light and food conditions for a set experimental period. Of the experimental approaches to assess lethal effects of temperature outlined above, the ACE method (Section 3.2.3), which is conducted over a 60 d period, allows some sub-lethal effects to be assessed.

3.3.1 Growth

The effects of temperature on growth can be assessed by comparing the weight and length of fish after experimental incubation with pre-experiment values. The duration of such experiments should be long enough to allow fish to settle after any initial stress that may occur at the start of the experiment (e.g. handling stress) and to ensure that any differences in growth over the experiment are measurable.

3.3.2 Reproductive indicators

Several measures of reproductive development and likely success have been developed. These include: levels of reproductive hormones, sexual characteristics and behaviour, fecundity, egg weight or size, gonadosomatic index, gamete viability, gamete abnormalities, age at maturity and developmental abnormality (Adams 2002). While many of these measures have been found to respond to a variety of stressors, this is of less concern under controlled experimental conditions.

3.3.3 Fitness

Growth and reproductive indicators are indirect measures of the likely effects of temperature on fitness. This is often necessary due to the difficulty in gaining direct estimates of fitness itself. Estimation of the effects of temperature on fitness require experiments that span almost two full generations – because fitness measures the survival and whole lifetime reproductive output of the experimental subject and the survival of its offspring to reproduction. Consequently, the effect of temperature on fitness has rarely been measured directly, particularly in long-lived species and is likely to be practical only in species with short life-cycles, such as zooplankton.

4 Existing information on thermal requirements of native biota

4.1 Fish – lethal effects

Upper lethal temperatures have been determined for 12 native fish species (Table 1). Most of these studies used the CTM method (Section 3.2) with a reasonably rapid rate of temperature increase (1 °C per 2-5 minutes). Consequently, the results of most of these studies provide estimates of the upper ultimate lethal temperature and are most relevant to assessments of the impacts of acute thermal stress. Several longer-term studies have also been conducted and can be used to estimate the incipient lethal temperature, the temperature at which prolonged thermal stress begins to lead to substantial mortality within a population

4.1.1 Ultimate lethal temperatures

Of the species considered, adult eels appear to have the highest upper thermal limit, with CTMs of 39.7°C for adult shortfin eels (*Anguilla australis*) and 37.3°C for adult longfin eels (*Anguilla dieffenbachii*) (both at an acclimation temperature of 15°C) (Table 1). The CTM for shortfin eel elvers rose from 33.4°C when acclimated at 12°C to 38.6°C when acclimated at 30°C) (Figure 2, Table 1).

The most sensitive species were adult banded kokopu (*Galaxias fasciatus*, CTM = 30°C, LT50 = 29.0°C, acclimated at 16°C), koaro (*Galaxias brevipinnis*, CTM = 28.0°C, LT50 = 27.0°C, both acclimated at 16°C) and common smelt (*Retropinna retropinna*, LT50 = 28.3°C, acclimated at 15°C) (Table 1).

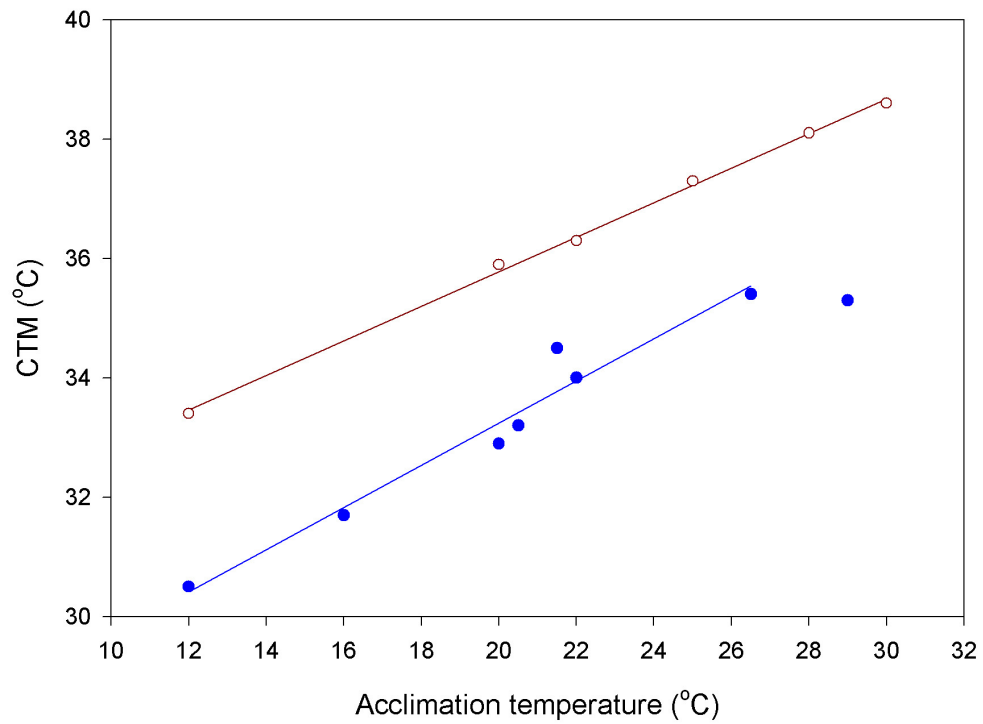


Figure 2

Relationships between critical thermal maximum (CTM) temperature and acclimation temperatures for shortfin eel elvers (maroon line, open circles) and inanga (blue line, closed circles). From Simons (1986c).

Table 1.

Summary of published estimates of upper ultimate lethal and preferred temperatures of twelve species of freshwater fish native to New Zealand. Fish used in preference experiment were acclimated at 15°C (Richardson et al. 1994).

Species	Life stage	Upper ultimate lethal temperature			Preferred temp. (°C) (quartiles)	Source
		Acclimation temperature (°C)	Temperature (°C)	Method		
<i>Anguilla australis</i> (Shortfin eel)	Elver	12	33.4	CTM, 1 °C/2 min	-	Simons 1986c
		15	35.7	LT ₅₀ , 10 minute exposure	26.9 (25.6-28.5)	Richardson <i>et al.</i> 1994
		20	35.9	CTM, 1 °C/2 min	-	Simons 1986c
		20	35.6	CTM, 1 °C/2 min	-	Simons 1984
		20	35.0	CTM, 1 °C/5 min	-	Simons 1984
		20	31.4	CTM, 1 °C/10 min	-	Simons 1984
		21.5	36.0	CTM, 1 °C/2 min	-	Simons 1986c
		22	36.3	CTM, 1 °C/2 min	-	Simons 1986c
		25	37.3	CTM, 1 °C/2 min	-	Simons 1986c
		28	38.1	CTM, 1 °C/2 min	-	Simons 1986c
		30	38.6	CTM, 1 °C/2 min	-	Simons 1986c
<i>Anguilla dieffenbachii</i> (Longfin eel)	Adult	15	39.7	LT ₅₀ , 10 minute exposure	-	Richardson <i>et al.</i> 1994
	Elver	15	34.8	LT ₅₀ , 10 minute exposure	24.4 (22.6-26.2)	Richardson <i>et al.</i> 1994
<i>Gobiomorphus basalis</i> (Cran's bully)	Adult	15	37.3	LT ₅₀ , 10 minute exposure	-	Richardson <i>et al.</i> 1994
<i>Gobiomorphus cotidianus</i> (Common bully)	Mixture	12	32.3	CTM, rate of increase: 1 °C/2 min	-	Simons 1984
		15	30.9	LT ₅₀ , 10 minute exposure	21.0 (19.6-22.1)	Richardson <i>et al.</i> 1994
		20	33.9	CTM, rate of increase: 1 °C/2 min	-	Simons 1984
<i>Gobiomorphus breviceps</i> (Upland bully)	Juvenile	12	32.7	CTM, rate of increase: 1 °C/2 min	-	Simons 1984
		15	30.9	LT ₅₀ , 10 minute exposure	20.2 (18.7-21.8)	Richardson <i>et al.</i> 1994
		20	34.0	CTM, rate of increase: 1 °C/2 min	-	Simons 1984
<i>Cheimarrichthys fosteri</i> (Torrentfish)	Adult	15	32.8	CTM	-	Teale 1986 – from Main 1988
			25.0	LT ₅₀	-	Teale 1986 – from Main 1988
			30.0	LT ₅₀ , 10 minute exposure	21.8 (20.1-22.9)	Richardson <i>et al.</i>

Species	Life stage	Upper lethal temperature			Preferred temp. (°C) (quartiles)	Source
		Acclimation temperature (°C)	Temperature (°C)	Method		
<i>Galaxias maculatus</i> (Inanga)	Whitebait	15	-	-	18.8 (18.0-19.8)	Richardson <i>et al.</i> 1994
		20	33.1	CTM	-	Simons 1986c
	Juvenile	12	30.5	CTM	-	Simons 1986c
		15	-	-	18.7 (17.3-20.0)	Richardson <i>et al.</i> 1994
		16	31.7	CTM	-	Simons 1986c
		20	32.9	CTM	-	Simons 1986c
		22	33.8	CTM	-	Simons 1986c
		26.5	35.4	CTM	-	Simons 1986c
<i>Galaxias argenteus</i> (Giant kokopu)	Adult	15	30.8	LT ₅₀ , 10 minute exposure	18.1 (17.2-19.1)	Richardson <i>et al.</i> 1994
	Juvenile	16	30.0	CTM, 1 °C/d	-	Main 1988
<i>Galaxias postvectis</i> (Shortjaw kokopu)	Juvenile	16	30.0	CTM	-	Main 1988
<i>Galaxias fasciatus</i> (Banded kokopu)	Whitebait	14	30.6	CTM	-	Simons 1986c
		15	-	-	16.1 (14.8-17.7)	Richardson <i>et al.</i> 1994
		16	30.0	CTM	-	Main 1988
		20	32.5	CTM	-	Simons 1986c
		22	31.2	CTM	-	Simons 1986c
		24	34.0	CTM	-	Simons 1986c
		26	31.1	CTM	-	Simons 1986c
	Adult	15	28.5	LT ₅₀ , 10 minute exposure	17.3 (16.3-18.3)	Richardson <i>et al.</i> 1994
<i>Galaxias brevipinnis</i> (Koaro)	Juvenile	16	28.0	CTM	-	Main 1988
		16	27.0	LT ₅₀	-	Main 1988
<i>Retropinna retropinna</i> (Common smelt)	Adult	15	28.3	LT ₅₀ , 10 minute exposure	16.1 (15.1-17.4)	Richardson <i>et al.</i> 1994
		20	31.9	LT ₅₀ , 10 minute exposure	-	Richardson <i>et al.</i> 1994
		20	31.8	CTM, rate of increase: 1 °C/2 min	-	Simons 1984
		20.5	33.4	CTM, rate of increase: 1 °C/2 min	-	Simons 1984

4.1.2 Incipient lethal temperatures

Jellyman (1974) found the 14-day LT₅₀ values for glass eels of shortfin and longfin eels to be 28 and 25 °C, respectively (Table 2). Simons (1986a) conducted experiments that considered the survival of inanga whitebait over a 24 h period, which he referred to as 'resistance time' experiments. These experiments yielded 24 h LT₅₀ values of 26.9 and 28.9 °C at acclimation temperatures of 12 and 14.5 °C, respectively (Table 2). Simons (1986c) observed higher than normal incidences of mortality, abnormal behaviour and reduced condition in inanga during acclimation at 26.5 and 29 °C. These observations are likely to be a result of the inanga being held at the upper incipient lethal temperature (UILT) values reported for inanga whitebait (Table 2).

Several studies have yielded estimates of the incipient lethal temperature of common smelt. As for inanga, Simons (1986b) also conducted 'resistance time' experiments on smelt larvae. These experiments yielded 24 h LT₅₀ values that ranged from 25.2-28.5 °C depending on acclimation temperature (Table 2). Richardson et al. (1993) found 5-day LT₅₀ values for common smelt to be 26.8-27.5 °C for adult fish acclimated at 20 °C, while a repeat of these experiments with fish acclimated to 22 °C yielded 5-day LT₅₀ values of 26.1-26.5 °C (Richardson & West 1998) (Table 2). Simons (1986c) also reports that most banded kokopu died after 5-6 d at 26 °C, suggesting that the 5 day incipient lethal temperature for banded kokopu may be between 24-26 °C.

Table 2.

Summary of published estimates of the upper incipient lethal temperatures of four species of freshwater fish native to New Zealand.

Species	Life stage	Upper incipient lethal temperature		Method	Source
		Acclimation temperature (°C)	Temperature (°C)		
<i>Anguilla australis</i> (Shortfin eel)	Glass eel	15	28.0	LT ₅₀ , 14 d experiments	Jellyman 1974
<i>Anguilla dieffenbachii</i> (Longfin eel)	Glass eel	15	25.0	LT ₅₀ , 14 d experiments	Jellyman 1974
<i>Galaxias maculatus</i> (Inanga)	Whitebait	12	26.9	LT ₅₀ , 24 h	Simons 1986a
<i>Retropinna retropinna</i> (Common smelt)	Whitebait	14.5	28.9	LT ₅₀ , 24 h	Simons 1986a
	Larvae	14.5	25.2	LT ₅₀ , 24 h	Simons 1986b
	Larvae	18	26.5	LT ₅₀ , 24 h	Simons 1986b
	Larvae	22	28.5	LT ₅₀ , 24 h	Simons 1986b
	Adult	20	26.8-27.5	LT ₅₀ , 5 days	Richardson <i>et al.</i> 1993
	Adult	22	26.1-26.5	LT ₅₀ , 5 days	Richardson & West 1998

4.2 Fish – sub-lethal effects

4.2.1 Thermal needs for different life stages

New Zealand's fish species exhibit a wide range of migratory behaviours, including species that do not undergo large-scale migrations (e.g. non-migratory galaxiids such as dwarf galaxias) and others that undertake very large-scale migrations. Three different forms of diadromy (migration between the sea and freshwater) are recognised. These are (as defined by McDowall 2007):

1. Amphidromy – Species that spawn in freshwater, immediately after hatching, larvae move to sea to feed, returning a few weeks or months later as small juveniles. Most growth occurs in freshwater. No explicit migration for spawning (certainly not across biomes, i.e. freshwater to seawater or vice versa). Adults remain in freshwater after spawning. There are many examples of this in New Zealand – including smelt (*R. retropinna*), some bullies (*Gobiomorphus* spp.), some galaxiids (*Galaxias* spp.) and torrent fish (*Cheimarrichthys fosteri*).
2. Anadromy – Species that spawn in freshwater, progeny go to sea to feed and grow before returning to spawn. Migration from saltwater to freshwater is undertaken for the purpose of spawning. An example of this is the lamprey (*Geotria australis*).
3. Catadromy – Species that spawn in saltwater, progeny return to freshwater to feed and grow before returning to sea to spawn. Examples of this are the longfin (*A. dieffenbachii*) and shortfin eels (*A. australis*).

The complexity of the lifecycles of many native freshwater fish (Figure 3) means that they are found in a range of different habitats at different times and stages of development. Informed thermal management of a population relies on the provision of a thermal regime that is suitable for all life-stages and that temperatures are suitable at appropriate times and locations for each life-stage. For many native species, especially migratory species/populations, the level of knowledge needed for such an approach is much greater than is currently available.

Whilst limited data is available for native species, data on the thermal tolerances of various life-stages of spring Chinook salmon (*Oncorhynchus tshawytscha*) illustrate the depth of data required to understand and satisfy the thermal requirements of species with a complex life-history (Figure 4).

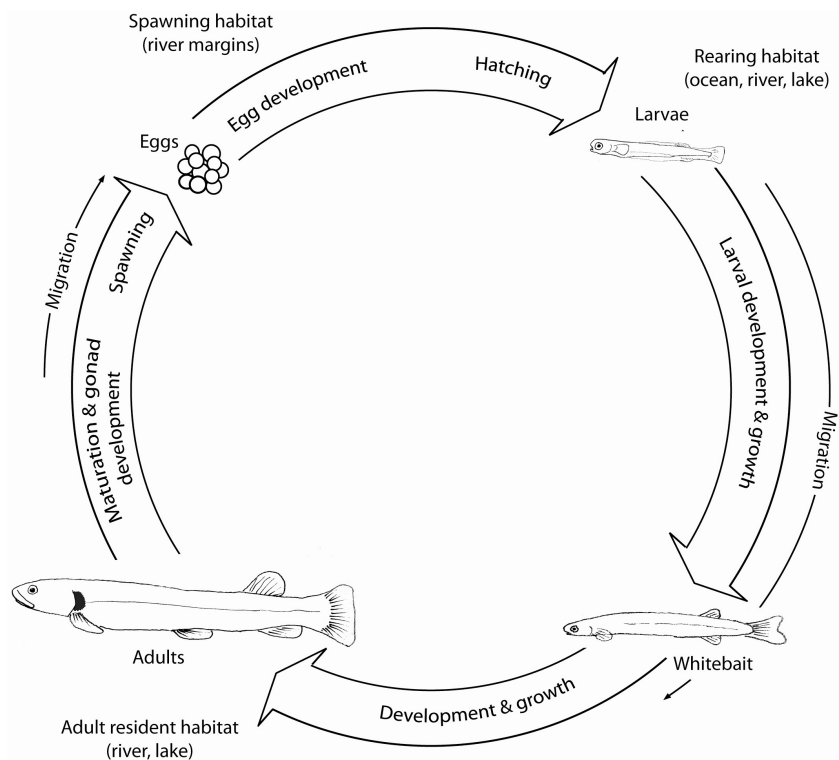


Figure 3

Life cycle of amphidromous galaxiid fish showing the habitats used by different life-stages, periods of migration and developmental stages.

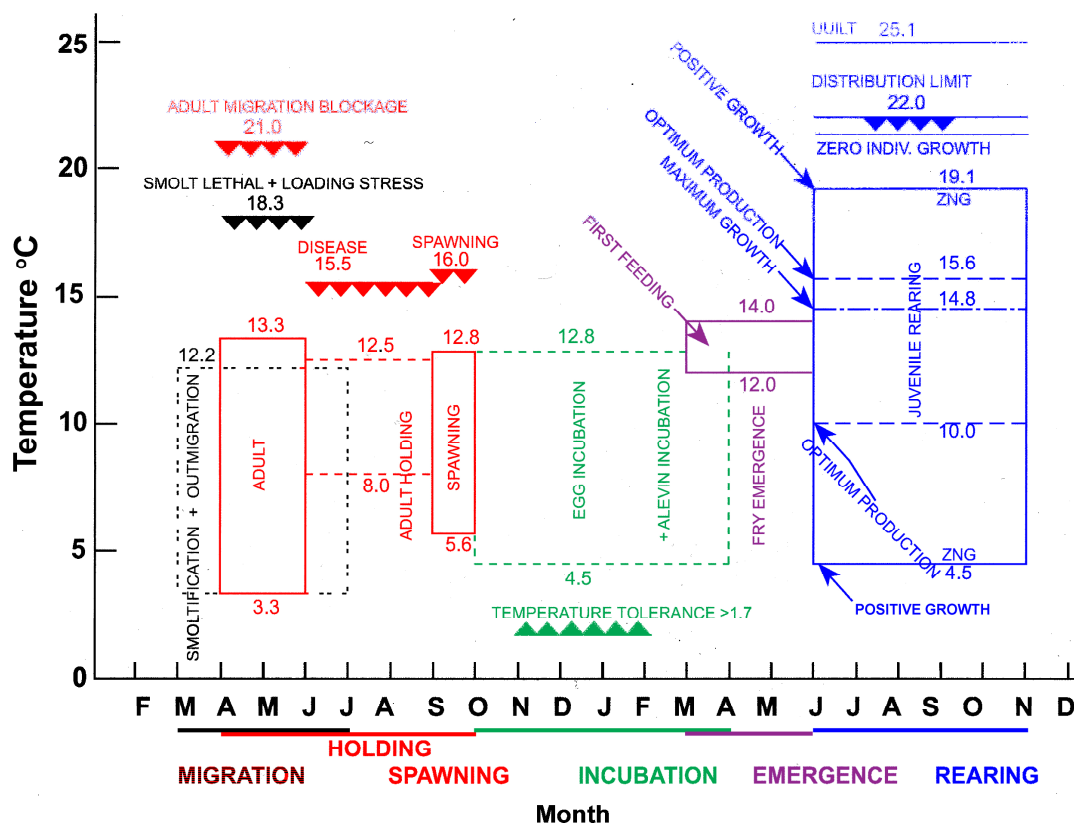


Figure 4

Thermal requirements of spring Chinook salmon in freshwater showing the thermal requirements of various life-history stages. Rows of triangles indicate thermal limits. Green = egg and alevin incubation, purple = fry, blue = juvenile, black = smoltification and out-migration, red = adult in-migration, holding and spawning. From McCullough 1999.

Data available for native species

Most of the available data on the thermal tolerance of native species is for one life stage only (Table 1). The exceptions to this are shorfin and longfin eels (elver, adult) and inanga (whitebait, juvenile and adult) (Table 1). Some data were also available for different life-stages of banded kokopu (whitebait and adults), but differences in experimental approach for each of these life-stages mean that such comparisons are not possible for this species. The available data suggests that adult eels have higher ultimate lethal temperatures than elvers and that inanga whitebait (33.1 °C) had a similar CTM to juveniles (32.9 °C) (Table 1). Richardson et al. (1994) also investigated the thermal preferences of different inanga life-stages and found that whitebait and juveniles had similar thermal preferences (18.8 °C and 18.7 °C, respectively) while adult inanga preferred slightly cooler water (18.1 °C) (Table 1). The issue of whether there are differences in thermal preferences between life stages for native fish remains unresolved and requires more study.

Egg development

Temperature is the primary variable affecting the rate of embryonic development in fish (e.g. Gillooly et al. 2002; Ojanguren & Brana 2003) as well as in other ectotherms (Gillooly et al. 2002). Consequently, within the thermal tolerance limits of individual species, development time will decrease with increasing temperature.

Benzie (1968b) reported that inanga eggs incubated at 4.4°C took approximately 31 days to develop compared with 10 days for eggs incubated at 17°C. Furthermore, Mitchell (1989) reported that inanga eggs incubated at 18°C hatched after 10 days, compared with 40 days at 8°C. However, because inanga spawn near the high water mark during spring high tides, embryonic development is aerial and therefore affected by air temperature rather than water temperature, meaning that thermal management in waterways is unlikely to be important for this life-stage of inanga and other species that have similar spawning behaviour.

The eggs of upland bully (*Gobiomorphus breviceps* Stokell), which stay submerged, take 25 days to develop at 17.5°C, compared with 33 days at 14.5°C (McDowall 1990). Mitchell (1989) found that hatching success and rates were poor at temperatures below 10°C, while the onset of hatching and hatching success was better at 12-16°C.

Mora & Boubée (1993) concluded that the optimum water temperature of smelt eggs was about 14-18°C and that temperatures greater than 25°C were detrimental to the survival and normal development of smelt eggs. Their experiments show that temperature affected the rate of embryonic development, with the time to hatching being shorter at higher temperatures, although the proportion of eggs hatching was lower at high temperatures (Mora & Boubée 1993).

Potential effects on population sex-ratios

Temperature can also affect the sex-ratio observed in fish populations, with extreme temperatures leading to skewed sex ratios in some species. In a review of the prevalence of temperature-dependent sex determination (TSD) in fish, Ospina-Álvarez & Piferrer (2008) concluded that TSD is less common than has been suggested previously, with many reported cases being mistakenly diagnosed. They distinguished three forms of sex determination: (1) genotypic sex determination (GSD), (2) GSD with a temperature effect, and (3) TSD. Of these, many species that have been suggested to exhibit TSD were actually defined as exhibiting GSD with a temperature effect (Ospina-Álvarez & Piferrer 2008). In species with TSD, temperature during the incubation and larval development is the primary determinant of the resultant sex ratio. Of the species that Ospina-Álvarez & Piferrer (2008) classified as having TSD, all exhibited a pattern of TSD where the percentage of males increased with increasing temperature. Despite it being unlikely that any of our native freshwater fish exhibit TSD, temperature may still play a part in determining sex ratios of some native species, via the second mechanism outlined above, GSD with a temperature effect. In this mechanism, the phenotypic (observed) sex of individuals is primarily determined by sex chromosomes, but with a potential effect of temperature on the phenotypic sex of some individuals, particularly if thermal extremes occur during the critical period for sex determination (Lukšienė et al. 2000; Delvin & Nagahama 2002; Ospina-Álvarez & Piferrer 2008). To date, the mechanisms of sex-determination of native fish have not been investigated in New Zealand, nor is there any evidence of sex determination in native fish being affected by temperature.

Effects on migration

Given that many of New Zealand's fish species are migratory, it is important to consider whether water temperature may affect the ability of fish to complete their life-cycle. One of the primary effects of temperature on migration is the potential for migrating fish to avoid entering a tributary stream due to high water temperature. Migrating inanga have been shown to completely avoid water temperatures of 29.5-31.5°C, depending on acclimation temperature (Boubee et al. 1991). Stancliff et al. (1989) reported that a temperature of 27°C caused a migration barrier to inanga which avoided the thermal plume of Huntly Thermal Power Station by moving to the other side of the river. They also observed that some common bullies migrated through the thermal plume of Huntly power station when temperatures were as high as 28.5°C and suggested that bullies and shrimp may be able to avoid the thermal plume by migrating along the bottom of the river channel.

Bannon (2006) considered the effect of water temperature and oxygen availability on the swimming ability of three life-stages of inanga (larvae, post-larvae and adults). Peak swimming ability was between 15-20°C for larvae (whitebait) (optimum = 17.7°C) and adults (optimum = 18.3°C), with swimming ability declining markedly at temperatures above 20°C. In contrast, maximum swimming ability for post larvae occurred at 9.4°C and swimming ability declined markedly above 10°C, which was suggested to result from temporary reduction in swimming ability during metamorphosis. Under mild hypoxia (75% saturation), the swimming performance of inanga whitebait was reduced at 15°C and 20°C, but not at 10°C when compared to normoxic conditions (96% saturation) (Bannon 2006).

Increases in water temperature can result in the loss of schooling behaviour in inanga (Table 3, Simons 1986c), which may affect the susceptibility of inanga whitebait to predation and increase migration thereby reducing migration distances.

Table 3

Approximate temperatures at which loss of schooling behaviour was observed in inanga (*G. maculatus*). Reproduced from Simons (1986c). ΔT = degree of heating prior to loss of schooling behaviour.

Acclimation temperature (°C)	Loss of schooling (°C)	ΔT (°C)
12	18-20	6-8
16	22-24	6-8
20	25-26	5-6
22	24-26	2-4
26.5	Only prior to heating	0-1
29	No schooling	-

The migration of glass eels is affected by water temperature too (Jellyman 1977; August & Hicks 2008; Jellyman et al. 2009), although the exact nature of this effect is not well understood. August & Hicks (2008) reported that glass eels preferred water temperatures of between 12 and 20°C, with an optimum of 16.5°C, and that temperatures <12°C and >22°C inhibited migration. Jellyman (2009) reported that glass eel catch was strongly inversely related to water temperature, with 99% of catch in the two years studied occurring at temperatures between 12.6 and 13.1 °C.

Spawning

The onset of spawning of the Canterbury galaxiid *Galaxias vulgaris* may be triggered by temperature (Cadwallader 1976). This is consistent with the observation of earlier spawning in the lower reaches of the Cass River than upstream areas (Benzie 1968a). After injection with a pituitary extract to initiate ovulation, inanga took 40-48 h at 15-18°C and 75-100 h at 9-11 °C (Mitchell 1989). The duration of motility of the sperm of freshwater fish declines with increasing water temperature (Clark 1981), which may reduce fertilization success.

Whilst the mechanism triggering spawning in native fish is generally not well understood, thermal alteration of waterways may disrupt maturation and spawning. Monitoring of gonad development in smelt in the Waikato River as part of monitoring of the Huntly Thermal Power Scheme has indicated a general effect of temperature on gonad development, with smelt collected at warmer locations having less developed gonads than those at cooler water sites (Wilding et al. 2003; Wilding et al. 2004a; 2004b; Wilding et al. 2005; 2006). Increases in gonadal development at the warmest sites once water temperatures had cooled suggests that temperature rather than habitat suitability accounted for the reduced reproductive output at these sites (Wilding et al. 2004b; Wilding et al. 2005; 2006). However, while these results indicate a general effect of temperature on gonad development in smelt, no measurable effect of the plume from the Huntly Power Scheme on gonad development in smelt has been detected to date.

In a study of life history traits of upland bullies in seven Otago catchments, Hamilton & Poulin (2001) found no link between water temperature range and clutch size, egg size, age or size at maturity.

Growth

Temperature influences growth rates by affecting food consumption rates and metabolic rates (Elliott 1994). There is little information on thermal growth limits or growth optima for New Zealand native fish, probably because of the large experimental effort required to derive such values.

In the absence of experimental data on the temperature at which optimal growth rates are observed for each species, published relationships to estimate growth optima from the final preferendum and upper ultimate lethal temperatures, such as those of Jobling (1981), can be used to derive interim values (Table 4). Jobling's equation relating growth optimum to final preferendum temperatures suggests that these two variables are closely related (Table 4), although this is not always the case. For example, experiments conducted by Larsson (2005) found that the brown trout preferred temperatures close to their growth optimum, while Arctic charr, *Salvelinus alpinus* preferred temperatures about

4.5°C below their experimentally-derived optimal temperature for growth. We used Jobling's relationship to predict thermal growth optima for the eight native fish species for which preferred temperatures were estimated by Richardson et al. (1994) (Table 5). The predicted growth optima for shortfin (26.1 °C) and longfin (23.7 °C) eels are consistent with the value estimated by Graynoth & Taylor (2000) (25 °C) from previous studies of New Zealand eel species and the European eel (*Anguilla anguilla*).

Graynoth & Taylor (2000) reported that growth of shortfin eels ceased below 8.9°C for fish fed on maximum rations. This appears to be the sole estimate of a thermal minimum for growth for a New Zealand native fish species.

Table 4

Published linear regression equations between growth optimum, preferred, and upper ultimate lethal temperature. n indicates the number of fish species used to develop each set of regression equations.

<i>X</i>	<i>Y</i>	<i>n</i>	Regression equations		<i>r</i>	Source
Growth optimum	Final preferendum	19	$Y = 1.05X - 0.53$	$X = 0.95Y + 0.50$	0.937	Jobling (1981)
Growth optimum	Lethal temperature	22	$Y = 0.76X + 13.81$	$X = 1.32Y - 18.17$	0.886	Jobling (1981)
Final preferendum	Lethal temperature	38	$Y = 0.66X + 16.45$	$X = 1.52Y - 24.9$	0.88	Jobling (1981)
Final preferendum	Lethal temperature	46	$Y = 0.65X + 16.84$	$X = 1.54Y - 25.91$	0.878	Richardson et al. (1994) based on Jobling (1981) but with 8 NZ species included
Final preference	Lethal temperature	8	$Y = 0.68X + 17.11$	$X = 1.47Y - 25.16$	0.878	Richardson et al. (1994) based on 8 NZ species only

Table 5

Thermal growth optimum predicted from the upper lethal temperatures using the second equation of Jobling (1981) presented in Table 4. Acclimation temperature was 15 °C or 16 °C (for species marked *).

Common name	Scientific name	Life stage	Upper lethal temperature	Predicted growth optimum
Shortfin eel	<i>Anguilla australis</i>	Elver	35.7	29.0
Shortfin eel	<i>Anguilla australis</i>	Adult	39.7	34.2
Longfin eel	<i>Anguilla dieffenbachii</i>	Elver	34.8	27.8
Longfin eel	<i>Anguilla dieffenbachii</i>	Adult	37.3	31.0
Cran's bully	<i>Gobiomorphus basalis</i>	Mixture	30.9	22.6
Common bully	<i>Gobiomorphus cotidianus</i>	Mixture	30.9	22.6
Upland bully	<i>Gobiomorphus breviceps</i>	Juvenile	32.8	25.1
Torrent fish	<i>Cheimarrichthys fosteri</i>	Adult	30.0	21.4
Inanga	<i>Galaxias maculatus</i>	Adult	30.8	22.5
Giant kokopu	<i>Galaxias argenteus</i> *	Whitebait	30.0	21.4
Shortjaw kokopu	<i>Galaxias postvectis</i> *	Juvenile	30.0	21.4
Banded kokopu	<i>Galaxias fasciatus</i>	Adult	28.5	19.5
Koaro	<i>Galaxias brevipinnis</i> *	Juvenile	28.0	18.8
Common smelt	<i>Retropinna retropinna</i>	Adult	28.3	19.2

4.3 Macroinvertebrates – lethal effects

4.3.1 Ultimate lethal temperatures

Two studies have used the CTM method to determine the ultimate lethal temperature of macroinvertebrates (Table 6). Experiment 1 of Winterbourn (1969) used it to determine the ultimate lethal temperature of the mudsnail, *Potamopyrgus antipodarum*. Experiments were conducted with animals acclimated to 10 °C, 16 °C and 22-24 °C and resulted in CTM values of 32-33 °C (Table 6). Simons (1984) carried a series of experiments using the CTM method on the freshwater shrimp *Paratya curvirostris* and koura *Paranephrops planifrons* with animals acclimated to either 12 °C or 20 °C. This study yielded similar results for both species, with CTM values of 28.9-32.6 °C for *Paratya* and 28.8-31.9 °C for koura (Table 6).

Table 6

Upper ultimate lethal temperatures of three species of freshwater macroinvertebrate. Results from Winterbourn (1969) are from Experiment 1.

Species	Acclimation temperature (°C)	Upper lethal temperature		Source
		Temperature (°C)	Method	
<i>Potamopyrgus antipodarum</i>	22-24	33.0	CTM, rate of increase: 1 °C/5 min	Winterbourn 1969
(NZ mudsnail)	16	32.0	CTM, rate of increase: 1 °C/5 min	Winterbourn 1969
	10	33.0	CTM, rate of increase: 1 °C/5 min	Winterbourn 1969
<i>Paratya curvirostris</i>	12	28.9	CTM, rate of increase: 1 °C/2 min	Simons 1984
(Freshwater shrimp)	20	32.6	CTM, rate of increase: 1 °C/2 min	Simons 1984
<i>Paranephrops planifrons</i>	12	28.8	CTM, rate of increase: 1 °C/2 min	Simons 1984
(Koura/freshwater crayfish)	20	31.9	CTM, rate of increase: 1 °C/2 min	Simons 1984

4.3.2 Incipient lethal temperatures

In contrast to studies of native fish, most thermal studies that have been done on macroinvertebrates here have used LT50 experiments conducted over periods ranging from 24-96 h (Table 7, Table 8). Information for most species is from the experiments of Quinn et al. (1994) who conducted LT50 tests on 10 species of common macroinvertebrate, with these tests being carried out at three durations (24, 48 and 96 h). Further to these constant temperature experiments, Cox & Rutherford (2000) conducted LT50 tests on two of these macroinvertebrates (*Deleatidium* and *P. antipodarum*) with diurnally fluctuating water temperature (daily amplitude 10 °C).

In constant temperature experiments, the mayflies *Deleatidium* spp. and *Zephlebia dentata* were the most sensitive taxa studied, while the riffle beetle *Hydora*, the sand-cased caddis *Pycnocentria evecta* and the mudsnail *Potamopyrgus antipodarum* were the most tolerant (Table 7). LT50 values decreased with increases in the duration of the experiments for most taxa considered (Table 7). The exceptions to this were *P. evecta* and *P. antipodarum*, both of which had LT50 values of 32.4 °C at all experimental durations (Table 7, Quinn et al. 1994). This finding for *P. antipodarum* is consistent with those of Winterbourn (1969), who estimated the CTM to be 32-33 °C across the various acclimation temperatures considered.

Table 7

Summary of published estimates of the upper incipient lethal temperatures of species of six species of endemic freshwater insect. * indicates that experimental specimens were collected from the field and were used without acclimation.

Species	Acclimation temperature (°C)	Temperature (°C)	Method	Source
<i>Deleatidium</i> spp. (mayfly)	12-14*	26.4*	LT ₅₀ , 24 h, constant temp.	Quinn <i>et al.</i> 1994
	12-14*	24.5	LT ₅₀ , 48 h, constant temp.	Quinn <i>et al.</i> 1994
	12-14*	22.6	LT ₅₀ , 96 h, constant temp.	Quinn <i>et al.</i> 1994
	15-16	24.2	LT ₅₀ , 96 h, constant temp.	Cox & Rutherford 2000
	15-16	21.9	LT ₅₀ , 96 h, <u>mean daily temp.</u> , time-varying temp.	Cox & Rutherford 2000
	15-16	26.9	LT ₅₀ , 96 h, <u>daily max. temp.</u> , time-varying temp.	Cox & Rutherford 2000
<i>Zephlebia dentata</i> (mayfly)	12-14*	26.9*	LT ₅₀ , 24 h, constant temp.	Quinn <i>et al.</i> 1994
	12-14*	25.3	LT ₅₀ , 48 h, constant temp.	Quinn <i>et al.</i> 1994
	12-14*	23.6	LT ₅₀ , 96 h, constant temp.	Quinn <i>et al.</i> 1994
<i>Aoteapsyche colonica</i> (net-spinning caddis fly)	12-14*	27.8	LT ₅₀ , 24 h, constant temp.	Quinn <i>et al.</i> 1994
	12-14*	27.0	LT ₅₀ , 48 h, constant temp.	Quinn <i>et al.</i> 1994
	12-14*	25.9	LT ₅₀ , 96 h, constant temp.	Quinn <i>et al.</i> 1994
<i>Pycnocentrodes aureola</i> (sand-cased caddis fly)	12-14*	32.4	LT ₅₀ , 24 h, constant temp.	Quinn <i>et al.</i> 1994
	12-14*	32.4	LT ₅₀ , 48 h, constant temp.	Quinn <i>et al.</i> 1994
	12-14*	32.4	LT ₅₀ , 96 h, constant temp.	Quinn <i>et al.</i> 1994
<i>Pycnocentria evecta</i> (sand-cased caddis fly)	12-14*	30.4	LT ₅₀ , 24 h, constant temp.	Quinn <i>et al.</i> 1994
	12-14*	26.8	LT ₅₀ , 48 h, constant temp.	Quinn <i>et al.</i> 1994
	12-14*	25.0	LT ₅₀ , 96 h, constant temp.	Quinn <i>et al.</i> 1994
<i>Hydora</i> sp. (Riffle beetle)	12-14*	>34	LT ₅₀ , 24 h, constant temp.	Quinn <i>et al.</i> 1994
	12-14*	>34	LT ₅₀ , 48 h, constant temp.	Quinn <i>et al.</i> 1994
	12-14*	32.6	LT ₅₀ , 96 h, constant temp.	Quinn <i>et al.</i> 1994

Table 8

Summary of published estimates of the upper incipient lethal temperatures of species of five species of endemic freshwater macroinvertebrate. * indicates that experimental specimens were collected from the field and were used without acclimation.

Group	Species	Acclimation temperature (°C)	Temperature (°C)	Method	Source
Mollusca	<i>Potamopyrgus antipodarum</i> (Mud snail)	12-14*	32.4	LT ₅₀ , 24 h, constant temp.	Quinn <i>et al.</i> 1994
		12-14*	32.4	LT ₅₀ , 48 h, constant temp.	Quinn <i>et al.</i> 1994
		12-14*	32.4	LT ₅₀ , 96 h, constant temp.	Quinn <i>et al.</i> 1994
			32.0	CTM, rate of increase: 1 °C/24 h	Winterbourn 1969- Experiment 2
		15-16	31.0	LT ₅₀ , 96 h, constant temp.	Cox & Rutherford 2000
		15-16	28.6	LT ₅₀ , 96 h, <u>mean daily temp.</u> , time-varying temp.	Cox & Rutherford 2000
		15-16	33.6	LT ₅₀ , 96 h, <u>daily max. temp.</u> , time-varying temp.	Cox & Rutherford 2000
	<i>Sphaerium novaezelandiae</i>	15*	32.8	LT ₅₀ , 24 h, constant temp.	Quinn <i>et al.</i> 1994
		15*	31.8	LT ₅₀ , 48 h, constant temp.	Quinn <i>et al.</i> 1994
		15*	30.5	LT ₅₀ , 96 h, constant temp.	Quinn <i>et al.</i> 1994
Crustacea	<i>Paratya curvirostris</i> (Freshwater shrimp)	14-15*	27.4	LT ₅₀ , 24 h, constant temp.	Quinn <i>et al.</i> 1994
		14-15*	26.5	LT ₅₀ , 48 h, constant temp.	Quinn <i>et al.</i> 1994
		14-15*	25.7	LT ₅₀ , 96 h, constant temp.	Quinn <i>et al.</i> 1994
	<i>Paracalliope fluviatilis</i> (Amphipod)	14-15*	27.5	LT ₅₀ , 24 h, constant temp.	Quinn <i>et al.</i> 1994
		14-15*	26.3	LT ₅₀ , 48 h, constant temp.	Quinn <i>et al.</i> 1994
		14-15*	24.1	LT ₅₀ , 96 h, constant temp.	Quinn <i>et al.</i> 1994
Oligochaeta	<i>Lumbriculus variegatus</i>	12-14*	30.1	LT ₅₀ , 24 h, constant temp.	Quinn <i>et al.</i> 1994
		12-14*	28.9	LT ₅₀ , 48 h, constant temp.	Quinn <i>et al.</i> 1994
		12-14*	26.7	LT ₅₀ , 96 h, constant temp.	Quinn <i>et al.</i> 1994

Table 9

Thermal limits of macroinvertebrates observed in various hydrothermal waters. L = larvae, P = pupae, A = adults.

Group	Species	Life stage	Maximum temperature observed (°C)	Locations	Source
Coleoptera (Beetles)	<i>Anacaena tepida</i>		44.5	Waipahihi Stream	James 1985
	<i>Enochrus tritus</i> (Hydrophilidae)		37	Waipahihi Stream	James 1985
	<i>Enochrus</i> sp. (Hydrophilidae)	L, A	45	Waipahihi Stream, Taupo; Waimangu Valley; Lake Rotowhero	Winterbourn 1968
	<i>Laccobius arrowi</i> (Hydrophilidae)		38	Copland Springs	Winterbourn 1973
	<i>Antiporus</i> sp. (Dytiscidae)	L, A	34	Lake Rotowhero	Winterbourn 1968
	<i>Laccobius mineralis</i>		29	Waipuwera Stream	James 1985
	<i>Liodessus plicatus</i> (Dytiscidae)	A	32	Copland Springs	Winterbourn 1973
	<i>Liodessus deflectus</i> (Dytiscidae)	L	32.5	Hurunui River Spring	Stark <i>et al.</i> 1976
	<i>Liodessus deflectus</i> (Dytiscidae)	A	35	Hurunui River Spring	Stark <i>et al.</i> 1976
Diptera (True flies)	Helodidae sp.	L	31	Copland Springs	Winterbourn 1973
	<i>Ephydrella</i> spp. (Ephydrella)	L, P	47	Waipahihi Stream (Taupo); Ketetahi Springs (Tongariro (Mangatipua Stream)); Orakei (Korako); Waimangu Valley; Ohinemutu	Winterbourn 1968
	<i>Ephydrella thermarum</i> (Ephydrella)		44.5	Copland Springs, Waipahihi Stream	Winterbourn 1973, James 1985
	<i>Neoscatella vittithorax</i>		44.5	Waipahihi Stream	James 1985
	<i>Scatella</i> sp. (Ephydrella)	L, P	45	Waipahihi Stream, Taupo	Winterbourn 1968
	<i>Scatella nitidifrons</i> (Ephydrella)	L, P	47	Hurunui River Spring	Stark <i>et al.</i> 1976
	<i>Chironomus</i> spp. (Chironominae)	L, P	40	Waipahihi Stream, Taupo; Ketetahi Springs, Tongariro (Mangatipua Stream); Orakei - Korako; Waimangu Valley; Lake Rotowhero	Winterbourn 1968
	<i>Gladopelma curtivalva</i> (Chironominae)		35	Waipahihi Stream	James 1985
	Tanytarsini (Chironominae)	L	41	Copland Springs, Hurunui River Spring	Winterbourn 1973, Stark <i>et al.</i> 1976
	<i>Syncricotopus pluriserialis</i> (Orthoclaadiinae)		21.8	Waipahihi Stream	James 1985
	Orthoclaadiinae	L	41	Hurunui River Spring	Stark <i>et al.</i> 1976
	Tanypodinae	L	35	Hurunui River Spring	Stark <i>et al.</i> 1976
	Eriopterini (Tipulidae)	L	c.40	Ketetahi Springs, Tongariro (Mangatipua Stream)	Winterbourn 1968
	<i>Limonia</i> sp. (Tipulidae)		33.5	Waipahihi Stream	James 1985
	<i>Odontomyia</i> sp. (Stratiomyidae)	L	38.5	Waipahihi Stream, Taupo	Winterbourn 1968

	Stratiomyidae	L	47	Copland Springs,	Winterbourn 1973
	Stratiomyidae (Stratiomyinae)	L	47	Hurunui River Spring	Stark <i>et al.</i> 1976
	<i>Culex</i> sp. (Culicidae)	L, P	c.30	Tokaanu	Winterbourn 1968
	<i>Culex pervigilans</i> (Culicidae)	L, P	32	Copland Springs	Winterbourn 1973
	<i>Paradixa fuscinervis</i> (Dixidae)	L	31	Copland Springs	Winterbourn 1973
Hemiptera	<i>Anisops wakefieldi</i> (Notonectidae)	A	34	Lake Rotowhero	Winterbourn 1968
(Bugs)	<i>Anisops assimilis</i> (Notonectidae)		38	Copland Springs	Winterbourn 1973
	<i>Sigara arguta</i> (Coroxidae)	L	34	Waimangu Valley; Lake Rotowhero	Winterbourn 1968
Odonata	<i>Ischnura aurora</i> (Zygoptera)	L	34	Waipahihi Stream, Taupo	Winterbourn 1968
(Damselflies & Dragonflies)	<i>Xanthocnemis zealandica</i> (Zygoptera)		24.5	Waipahihi Stream	James 1985
	<i>Austrolestes colenisonis</i> (Anisoptera)		24.5	Waipahihi Stream	James 1985
Crustacea	<i>Cyprinotus incongruens</i> (Ostracoda)		35	Waimangu Valley	Winterbourn 1968
Mollusca	<i>Lymnaea tomentosa</i> (Pulmonata)		35	Waipahihi Stream, Taupo; Waipuwerawera Stream, Taupo; Waimangu Valley; Waiotapu Stream	Winterbourn 1968
(Snails)	<i>Lymnaea columella</i> (Pulmonata)		35	Waipahihi Stream	James 1985
	<i>Physa fontinalis</i> (Pulmonata)		34	Waipahihi Stream, Taupo; Waimangu Valley; Lake Rotomahana foreshore	Winterbourn 1968
	<i>Physa acuta</i> (Pulmonata)		24.5	Waipahihi Stream, Waipuwerawera Stream	James 1985
	<i>Planorbarius corneus</i>		24.5	Waipahihi Stream, Waipuwerawera Stream	James 1985
	<i>Potamopyrgus</i> sp. (Prosobranchia)		28	Waipuwerawera Stream, Taupo; Waimangu Valley; Lake Rotomahana foreshore; Waiotapu Stream, Copland Springs	Winterbourn 1968, Winterbourn 1973, James 1985
Acari	<i>Hydrozetes lemnae</i> (Hydrozetidae)	A	41	Hurunui River Spring	Stark <i>et al.</i> 1976
	<i>Trimalaconothrus novus</i> (Malaconothridae)		41	Hurunui River Spring	Stark <i>et al.</i> 1976
Annelida	Naiadidae (Oligochaeta)		33.5	Waipahihi Stream, Taupo	Winterbourn 1968
(Segmented worms)	<i>Nais variabilis</i> (Oligochaeta)		32	Copland Springs	Winterbourn 1973
	Lumbriculidae (Oligochaeta)		24	Waipuwerawera Stream, Taupo	Winterbourn 1968
	<i>Glossiphonia</i> sp. (Hirudinea)		22	Waipuwerawera Stream, Taupo	Winterbourn 1968
Platyhelminthes	<i>Dugesia</i> sp. (Tricladida)		28	Waimangu Valley	Winterbourn 1968
(Flatworms)					

As discussed in Section 2.2, fluctuating temperatures may result in lower thermal tolerance limits than constant temperature experiments. Cox & Rutherford (2000) found that the incipient lethal limits for *Deleatidium* and *Potamopyrgus antipodarum* were reduced by 2.5°C under fluctuating temperatures, where the fluctuating temperature treatment was characterised as the mean daily temperature. These results suggest that these invertebrate taxa were responding to a temperature between the mean and maximum daily temperature.

4.3.3 Field studies of thermal limits

The distribution of freshwater macroinvertebrates in several thermal waters in the Central Plateau of the North Island was described by Winterbourn (1968), while in a subsequent paper he described the distribution of freshwater macroinvertebrates in the Copland Springs (Westland, South Island – Winterbourn 1973) (Table 9).

The taxon found at the highest temperature was the shore fly *Ephydrella* spp., whose larvae were observed at up to 47°C (Table 9). The species *Ephydrella thermarum* which inhabits North Island thermal waters (Winterbourn et al. 2006). Other taxa found at temperatures in excess of 40°C include larvae of another shorefly (*Scatella*), the hydrophilid beetle *Enochrus*, the bloodworm *Chironomus* and the tipulid *Eriopterini* (Table 9). It is interesting to note that of these species, all except *Chironomus*, respire using atmospheric oxygen via spiracles that are projected through the surface film, which means that they would not be limited by the low dissolved oxygen concentrations present at such warm water temperatures. *Chironomus* on the other hand possesses myoglobin, an oxygen storing pigment that allows it to inhabit low-oxygen environments, such as geothermal streams.

In both of these field studies, *Potamopyrgus* was found at temperatures up to 28°C, yet the experiments of Quinn et al. (1994) gave a LT50 value of 32.4°C and Experiment 2 of Winterbourn (1969) yielded a CTM of 30°C (Table 8). The experiments of Winterbourn (1969) showed that snail activity reduced markedly from about 28°C and that this was predominantly driven by water temperature with dissolved oxygen playing a minor role.

In a study of the effects of environmental variables on macroinvertebrate communities in 88 New Zealand Rivers, Quinn & Hickey (1990a) found that stoneflies were largely restricted to rivers with a mean annual water temperature of less than 13°C and annual maximum temperature of less than 19°C (Quinn & Hickey 1990a). Similarly, mayflies were largely restricted to rivers with an annual maximum temperature of less than 21.5°C (Quinn & Hickey 1990a). Strong relationships between temperature and abundance were not evident for other macroinvertebrate families.

4.4 Macroinvertebrates – sub-lethal effects

4.4.1 Growth and development

Temperature affects the rate of both growth and development (progression through life-history stages) of macroinvertebrates (see Anderson & Cummins 1979 and Vannote & Sweeney 1980 for review). In addition to the direct effect of temperature on the growth of invertebrates, temperature interacts with both food quantity and quality to affect growth (Anderson & Cummins 1979; Vannote & Sweeney 1985).

Altered growth can have significant flow-on effects on development. For example, temperature affects the growth, moulting frequency, time to maturity and longevity of freshwater crayfish *Paraneohpops* spp. (Jones 1981; Whitmore & Huryn 1999; Parkyn et al. 2002). Temperatures of less than 10 °C limit crayfish growth (Whitmore & Huryn 1999; Parkyn et al. 2002), and the number of degree days >10 °C can be used to estimate the time to reproduction as well as longevity (Parkyn et al. 2002). Parkyn & Collier (2002) reported that whilst temperature affects moult frequency, both moult frequency and moult increment were affected by diet.

In experiments assessing the effects of temperature and salinity on mortality and growth of the zooplankton species *Daphnia carinata*, Hall & Burns (2002) found that juveniles had higher growth rates and matured earlier at 20 °C than 15 °C, but also observed higher mortality at 20 °C than 15 °C in the highest salinity treatment (600 mg L⁻¹ chloride).

4.4.2 Life history effects

Temperature can drive population structure as well as the timing of emergence (Briers et al. 2004; Hassall et al. 2007). Huryn (1996) found that water temperature was the single most significant factor affecting growth rates of larvae of the mayfly *Deleatidium* in experiments carried out in two high-country streams in Otago. He found that temperature controlled the duration of cohorts, with eggs deposited before mid-February likely to complete larval development and larvae emerge by the following May (minimum cohort duration ~three months). In contrast, eggs deposited after that time were unlikely to complete larval development until the following summer (maximum cohort duration ~11 months) owing to low growth rates in cold water over winter.

Reproduction

Temperature dependent growth affects adult body size of macroinvertebrates, which influences fecundity in many insect species (Sweeney & Vannote 1978; Vannote & Sweeney 1985; Honěk 1993). Body size may also affect the longevity of adult life-stages in species in which adults do not feed (Taylor et al. 1998), potentially affecting the ability of adults to find a mate in sparse populations. Such sub-lethal thermal effects on individuals may still have effects at the population level through reduced growth and fecundity (i.e., fitness effects). Given the interactions between temperature, the quality and quantity of food and the rate of growth and development, it is difficult to predict the effect of thermal alteration on macroinvertebrates.

Temperature is an important factor affecting the rate of egg development in aquatic insects (Gillooly & Dodson 2000). A review by Pritchard et al. (1996) found that, within the viable temperature range, the rate of egg development increased with increasing temperature in almost all dipteran (true fly), odonate (dragonflies and damselflies) and ephemeropteran (mayfly) taxa, (for a review of data for Australian mayfly species, see Parnrong & Campbell 2003). In contrast, they also found that, within the viable temperature range, the rate of egg development increased with decreasing temperature in many stoneflies (Pritchard et al. 1996). Temperature has been found to affect the rate of embryonic development in *Paratya australiensis* (28 d at 18°C versus 22 d at 21°C - Hancock 2008), an Australian species of *Paratya*, and it is likely that a similar relationship is present in *P. curvirostris*. There is also evidence for the rate of egg development of mysid shrimp being influenced by water temperature (Chapman & Lewis 1976).

Migration

Few native freshwater macroinvertebrates are known to undertake substantial longitudinal migrations. The exceptions to this are the freshwater shrimp *Paratya curvirostris* (Heller) (family Atyidae) and the mysid shrimps *Tenagomysis chiltoni* and *T. novaezealandiae* (Chapman & Lewis 1976; Sutherland & Closs 2001). A study of the life-history of *P. curvirostris* in three North Canterbury streams found evidence to support an amphidromous life history strategy (Carpenter 1983). Amphidromous shrimp produce large numbers of small eggs in freshwater habitats that hatch into larvae, which are washed downstream into estuarine areas where they undergo growth and development before migrating upstream. Upstream migration has also been reported for this species in the lower Waikato River (Shaw 1981) and is the ancestral condition in the Atyidae (Page et al. 2005).

4.5 Periphyton

4.5.1 Field studies in thermal waters

Several studies have investigated the distribution of periphyton in thermal springs and provide some indication of the thermal tolerance of some periphyton taxa. However, it should be noted that the absence of a taxon at a particular temperature may arise due to factors other than thermal tolerance. These include high salinity, sulphide concentrations, or the presence of toxicants.

Thermal algae are not generally found above about 65°C. Cyanobacteria are the most thermally-tolerant periphyton group and are often found in water from 30 to 65°C, and sometimes as high as 70°C (Cassie-Cooper 1996). Diatoms are often among the most abundant groups at temperatures up to 40°C, along with the green algae *Chlorella saccharophila* (Cassie-Cooper 1996).

Winterbourn (1973) presented information on the distribution of periphyton in the Copland Springs which gives some indication of the thermal tolerance of some periphyton taxa. The dominant algae in channels receiving spring water was the cyanobacterium *Mastigocladus laminosus* and it was found in temperatures up to 50°C (Winterbourn

1973). Two other cyanobacteria, *Phormidium* and *Oscillatoria geminata*, were also found in this temperature range, while, *Synechocystis* (also a cyanobacterium) dominated areas with temperatures up to 45 °C (Winterbourn 1973). Other algae taxa were found in warm-water pools (27 °C), including dense growths of the filamentous green alga *Spirogyra* and some of the green alga *Cosmarium* (Winterbourn 1973).

Stark et al. (1976) surveyed algae in a hot-spring channel near the upper Hurunui River. The cyanobacteria *Phormidium* sp., *Lyngbya* sp., and *Mastigocladus laminosus* formed mats in the spring source where the effluent water temperature was 53-54 °C, while short filaments of *Oscillatoria geminata* were also evident around one of the spring sources (54 °C). The cyanobacterium *Calothrix* sp. dominated the periphyton at temperatures of 15-38 °C. In February, two species of *Synechococcus* were observed. One of these formed a bright pink layer at temperatures of 48-50 °C and resembled the cosmopolitan species *S. minervae*. The second species was found in *Phormidium*-dominated mats at 41 °C.

Table 10

Thermal limits of periphyton species observed in hydrothermal waters.

Division	Taxon	Maximum temperature observed (°C)	Location	Source
Cyanobacteria	<i>Lyngbya</i> sp.	53-54	Hurunui River springs	Stark <i>et al.</i> 1976
	<i>Mastigocladus laminosus</i>	50	Copland Springs	Winterbourn 1973
		54	Hurunui River springs	Stark <i>et al.</i> 1976
	<i>Oscillatoria geminata</i>	45	Copland Springs	Winterbourn 1973
		54	Hurunui River springs	Stark <i>et al.</i> 1976
	<i>Phormidium</i> spp.	45	Copland Springs	Winterbourn 1973
		53-54	Hurunui River springs	Stark <i>et al.</i> 1976
	<i>Synechocystis</i>	45	Copland Springs	Winterbourn 1973
	<i>Synechococcus</i> spp.	48-50	Hurunui River springs	Stark <i>et al.</i> 1976
Chloropyta	<i>Spirogyra</i>	27	Copland Springs	Winterbourn 1973
	<i>Cosmarium</i>	27	Copland Springs	Winterbourn 1973

5 Multiple stressors and cumulative effects

In natural systems, it is rare for a single variable to be acting in isolation on a population. In reality, biotic and abiotic variables can interact in many different ways to create the observed patterns in the distribution of taxa. This is the case for water temperature – water temperature directly affects some variables in a straight-forward way (e.g. dissolved oxygen concentrations, availability/toxicity of some toxicants), but affects others in a less clear-cut manner (e.g. prey composition and abundance) and may affect the tolerance of organisms to other factors (e.g. stressors). This section presents a general review of the literature on how temperature may interact with other factors (biotic and abiotic).

In general, organisms living under conditions close to their environmental tolerance limits appear to be more vulnerable to additional chemical stressors. In most cases, increasing temperatures coupled with decreasing food or nutrient level raise toxicity of contaminants. (Heugens et al. 2001). Therefore, increasing temperature associated with climate change will enhance the toxicity of contaminants (Noyes et al. 2009).

5.1 Interactions with environmental factors

5.1.1 Water density

The most fundamental influence of temperature on aquatic environments is on the physical characteristics of the water itself (such as density and viscosity). Water is unusual in that it is most dense at 4 °C (1,000 kg/m³) and becomes less dense when it is heated above, or cooled below this point. This affects many aspects of the physical environment, including the fact that ice floats and the thermal stratification observed in many lakes. Changes in water viscosity can affect locomotion, especially in small fish larvae (Fuiman & Batty 1997; von Herbing 2002) and invertebrates (Linley 1986; Larsen et al. 2008) by altering the balance of forces (viscous, inertial and drag forces) acting on them.

5.1.2 Dissolved oxygen

Temperature and the solubility of oxygen in water are inextricably linked; with oxygen solubility declining with increasing water temperature. This poses a problem for aquatic invertebrates and fish because as temperature increases, metabolic rate, and associated oxygen demand, increases. In aquatic poikilotherms, the onset of thermal limitation is characterised by a decrease in aerobic performance due to limitations of the circulatory and ventilatory systems to satisfy oxygen demands (Portner & Knust 2007). Such limitations occur at both the upper and lower limits of the thermal envelope.

5.1.3 Salinity

As with fish, the salinity tolerance of aquatic invertebrates is temperature dependent. For example, Hall & Burns (2002) found that adults of the zooplankter *Daphnia carinata* exhibited lower survival at 20 °C than at 10 °C for all salinities over 400 mg L⁻¹ chloride.

5.1.4 Ultraviolet (UV) radiation

Temperature has been shown to affect the response of aquatic systems to UV radiation. Much of the research to date has focussed on the effects of UV on planktonic systems, particularly in alpine and high-latitude lakes. In phytoplankton, UV has been found to depress growth at low temperatures under all nutrient treatments, but not at higher temperatures under ambient nutrient conditions, while under increased nutrient concentrations, UV did depress growth of some taxa (Doyle et al. 2005). In zooplankton, the effect of UV exposure is generally reduced at higher temperatures (Cooke et al. 2006), although such effects depend on the mechanism of UV tolerance employed. Elevated temperature increased UV tolerance in two species of zooplankton that relied on photoenzymatic repair (PER), whereas it decreased UV tolerance in one that has less PER ability (Williamson et al. 2002). This outcome may result from the temperature-dependence of enzyme-based DNA repair systems, which should be less effective at low temperatures. In experiments conducted on the cladoceran *Daphnia pulicaria*, Macfayden et al. (2004) found that, whilst total DNA damage increased with increasing temperature, the net DNA damage (total DNA damage – DNA repair) was higher at low temperatures, due to greater rate of repair at higher temperatures. On the basis of these results, Macfayden et al. (2004) concluded that photoprotection (e.g. melanin) is likely to be more effective in low temperature systems).

Ultraviolet radiation is of greatest concern in aquatic ecosystems at high altitudes and latitudes, particularly in clear-water systems, with little dissolved organic material to reduce UV penetration into water. Consequently, interactions between temperature and UV should be paid particular regard in these systems.

5.1.5 Toxicants

Toxicants is a rather broad category, but is used here to refer to chemicals that, when encountered in waterways, are generally from a human source. Consequently, this section is particularly relevant to urban waterways where modifications resulting from urbanisation (such as channelisation, riparian vegetation removal) may lead to thermal impairment. Since they flow through residential, commercial and industrial areas, urban streams are also likely to receive inputs of toxicants. Therefore there is potential for interaction between toxicity and temperature.

Temperature may affect the ability of organisms to respond to other stressors by disrupting defensive mechanisms, such as the production and activity of oxidative enzymes. Temperature affects expression of the cytochrome P4501A1 (CYP1A) gene (Kloepper-Sams & Stegeman 1992). In fish, expression of this gene is related to the production of enzymes that oxidise compounds that originate both within and outside of the body. Expression can be induced by exposure to many contaminants including

polychlorinated biphenyls (PCBs), dioxins, furans, and polycyclic aromatic hydrocarbons (PAHs) (Adams 2002).

Ammonia

Ionised ammonia (NH_4^+), and un-ionised ammonia (NH_3) exist in equilibrium with each other depending on pH, temperature, and salinity (ANZECC & ARMCANZ 2000). Reduction in temperature and pH favours ionised ammonia over un-ionised ammonia (Figure 5). High levels of un-ionised ammonia (NH_3) can be toxic to aquatic life. Acutely toxic concentrations of ammonia may cause loss of equilibrium, hyper-excitability, increased breathing, cardiac output and oxygen uptake; and in extreme circumstances, convulsions, coma and death in fish (ANZECC & ARMCANZ 2000). Sub-lethal concentrations of ammonia may reduce hatching success, growth rate and morphological development, and result in pathological changes in tissues of gills, liver and kidneys (ANZECC & ARMCANZ 2000).

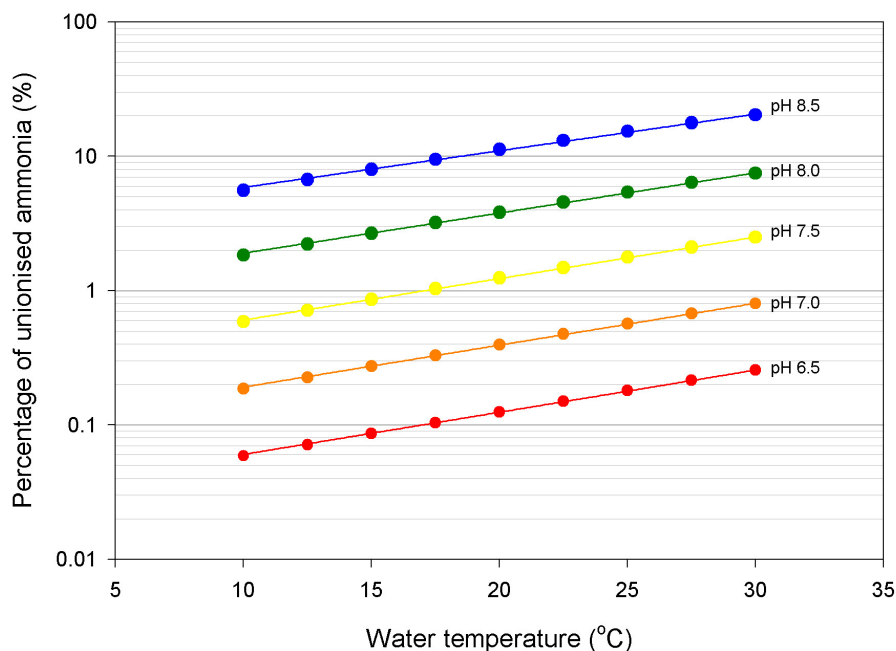


Figure 5

Relationship between unionised ammonia (NH_3) as a percentage of total ammonia ($\text{NH}_3 + \text{NH}_4^+$) and temperature at five different pH values. Sourced from Table 8.3.6 of ANZECC & ARMCANZ 2000.

USEPA (1999) reported that water temperature was a significant factor affecting the acute and chronic response to ammonia in freshwater fish and the acute response of freshwater invertebrates. The toxicity of ammonia to nine native freshwater invertebrate species was studied by Hickey & Vickers (1994). Taxa studies included: two mayflies (*Deleatidium*, *Zephlebia*), one stonefly (*Zelandobius furcillatus*), one caddis fly (*Pycnocentria evecata*), two molluscs (the snail *Potamopyrgus antipodarum* and the

finger nail clam *Sphaerium novaezelandiae*), two crustaceans (the shrimp *Paratya curvirostris* and the amphipod *Paracalliope fluviatilis*) and one oligochaete worm (*Lumbriculus variegatus*). The invertebrate taxa tested were more sensitive to ammonia than inanga (Richardson 1991), but temperature did not significantly affect the acute toxicity of un-ionised ammonia (Hickey & Vickers 1994).

Metal toxicity

Elevated temperature interacts with trace metal toxicity; organisms exposed to high temperatures are more sensitive to metal toxicity and, conversely, exposure to metals can decrease the thermal tolerance of animals (Sokolova & Lannig 2008). Temperature and metal exposure can synergistically affect energy supply at the cellular ATP production sites. Trace metals strongly affect mitochondrial function by reducing activity of the electron transport chain and ATP production, decreasing mitochondrial efficiency leading to increased reactive oxygen species levels (Sokolova & Lannig 2008).

5.2 Effects on ecosystem function

Temperature is a key driver of carbon and nutrient processes in freshwater ecosystems. Strong seasonal patterns in ecosystem metabolism of rivers and streams (Roberts et al. 2007; Clapcott & Barmuta 2010) and water mixing (and nutrient exchange) in lakes (Rutherford 2010) illustrate how changes of temperature of a few degrees that dramatically alter the functioning of whole ecosystems.

Freshwater ecosystems naturally function over a range of temperatures. Low levels of bacterial activity have been observed at 0.4 °C in Antarctic lakes (Laybourn-Parry et al. 2004) and low rates of metabolism observed at 8 °C in headwater streams (Clapcott & Barmuta 2010). In contrast, accelerated organic matter breakdown has been observed at 20 °C in lowland streams (Clapcott et al. 2010) and high rates of bacterial activity observed up to 72 °C in geothermal springs (Dillon et al. 2007).

According to the metabolic theory of ecology the primary factor that causes differing rates of metabolism between ecosystems is temperature (Brown et al. 2004); the caveat here is 'all else being equal'. In theory, metabolic activity increases logarithmically in response to increasing temperature until inhibiting temperatures are reached. Ecosystem respiration (ER) is more temperature dependent than productivity (gross primary productivity, GPP); hence respiration will increase faster than productivity in response to increasing temperature. This means that at higher temperatures there could be a greater disparity between productivity and respiration (P/R ratio) leading to low P/R ratios. In these systems, where much more carbon and nutrients are consumed than produced, there are more metabolic byproducts, e.g. more ER means more CO₂ is released into the atmosphere. This is a subject of increasing research interest regarding climate change effects on freshwaters (e.g. Williamson et al. 2008).

In practice, few studies have shown a strong link between temperature and ecosystem metabolism, probably because the latter is dependent on other factors too, such as light and nutrient/substrate availability. In rivers, flow has been shown to shape patterns in ecosystem metabolism (Acuña et al. 2004). Similarly, placement in the river continuum (and hence ecosystem size, flow, and resource availability) determines the dominance of

autotrophic (productivity-dominated) or heterotrophic (respiration-dominated) ecosystems (Vannote et al. 1980; Battin et al. 2008). At an ecosystem scale, mainly weak relationships have been reported between variation in temperature and river GPP (Mulholland et al. 2001), suggesting the strong predictive relationships developed from laboratory studies (Phinney & McIntire 1965) are not transferable to the field.

Stronger relationships have been reported between variation in temperature and river ER (Bott et al. 1985; Roberts et al. 2007), probably due to the dominant contribution of microbial processes to ecosystem respiration, i.e. microbial metabolism is temperature-dependent. Similarly, there is a strong link between temperature and organic matter decomposition dominated by microbial processes, with higher rates of breakdown observed at higher temperatures (Benfield et al. 2001).

Recent technological advancements (e.g. continuous dissolved oxygen loggers) mean that theoretical and small-scale predictions of the effects of temperature change can now be readily tested at an ecosystem scale. However, a recent application in the Waikato River demonstrated how current models used to estimate ecosystem metabolism are violated by artificial diurnal fluctuations in temperature, i.e. due to the discharge of heated water from power generation (Clapcott & Young 2009). Clearly, further research is required to incorporate the effects of large variations in temperature in estimates of ecosystem metabolism.

5.3 Effects on biotic factors

5.3.1 Community-level effects

Water temperature has the potential to directly or indirectly affect the structure of aquatic communities. Changes in water temperature may directly affect the abundance or distribution of taxa since this is a fundamental factor influencing habitats suitability. Section 5.1 outlines some of the other environmental factors that are affected by water temperature and that can, in turn, affect the suitability of habitats for various aquatic taxa. In addition to changes that may be driven by abiotic factors, water temperature may also influence biotic interactions which can result in community-level effects. The possible nature of such effects is explored in more detail below (Sections 5.3.2, 5.3.3, 5.3.4, 5.3.5).

The community-level consequences of thermal alteration are difficult to predict and are unlikely to reflect differences in the thermal tolerance of individual taxa alone. This is particularly the case for our native taxa, given the limited thermal tolerance data currently available. Thermal alteration could result in the loss or reduction in the population size of important species (in particular keystone species – *sensu* Mills et al. 1993; Paine 1995) or may enable invasion by species that may have significant implications for the structure of the community, and even ecosystem.

5.3.2 Food availability and foraging

Temperature affects locomotion (Bannon 2006; Lyon et al. 2007) and feeding behaviours (e.g. Fraser et al. 1993) which can affect a species foraging efficiency and success. Maximum sustained swimming speed rises with increasing water temperature to reach a maximum at a point several degrees below the upper thermal limit, then declines rapidly as temperatures approach the upper thermal limit (Bannon 2006). Consequently, altered temperature may affect the maximum water velocity that fish will be able to hold in and may affect foraging efficiency and the net rate of energy intake of fish.

Periphyton

Periphyton is an important food source for many invertebrates. Water temperature is among the most important factors affecting the rate of accrual of periphyton biomass, although the response also depends on the availability of nutrients (nitrogen, phosphorus and carbon) and light (Biggs 2000). The rate of biomass accrual increases with increases in temperature. The consequences of such increases in periphyton accrual are difficult to predict. Following flow disturbance, high rates of accrual will result in more rapid recovery by periphyton but periphyton proliferation may affect habitat quality for macroinvertebrates (Townes 1981; Quinn & Hickey 1990b; Quinn et al. 1997; Biggs 2000). In addition, high water temperatures may reduce the abundance of some macroinvertebrate taxa (see Section 4.3), which may reduce grazing pressure on periphyton with flow-on effects for biomass accrual and periphyton composition.

5.3.3 Competition

Temperature has been found to mediate competitive interactions between fish (e.g. Baltz et al. 1982; Persson 1986; Reeves et al. 1987; Taniguchi et al. 1998; Taniguchi & Nakano 2000; Reese & Harvey 2002), rotifers (e.g. Stelzer 1998) and algae (e.g. Tilman et al. 1981). As discussed in Sections 4.2 and 4.4, water temperature is a primary factor determining the activity rate, growth potential and consumption rate for fish and invertebrates. Such an effect can have ramifications for the competitive ability of individual taxa.

Temperature has been shown to affect the foraging ability (capture probability, handling time, capture rate, instantaneous search rate, swimming speed) of roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) in a laboratory study, with perch having superior foraging abilities at temperatures below 17-19°C while higher temperatures favoured roach (Persson 1986). In addition, the distributions of these two species in stratified lakes were consistent with the findings of these laboratory results (Persson 1986).

Exotic species

Given the pervasive effect of temperature in the ecology of poikilotherms, it is likely to affect the probability of successful invasion of aquatic environments by non-native species (Lennon et al. 2001). There is often more extensive information on the thermal tolerance of exotic species than for natives, either from studies conducted within their native range or because of their studies conducted when they have invaded other areas.

Such information can be used by managers to inform predictions of the invasion risk for different environments.

Information available for carp (*Cyprinus caprio*), and mosquito fish (*Gambusia affinis*) indicate that both of these species are more tolerant of high temperatures than most native fish and are more likely to be limited by low water temperatures than by high temperatures. Common carp (of which koi carp are thought to be a variety), have wide thermal tolerance limits, with a lower lethal limit of less than 5°C (see review in Paterson & Baker 2011). However, experimental work suggests that adult carp become stressed at temperatures below 15°C, while the temperature range for egg development is 16-26°C (Elliott, 1981). These data suggest that carp are unlikely to be abundant in environments that fall below 15°C for extended periods of time. Thermal preference data for common carp suggest that carp thrive at temperatures of 24-35°C (see review in Paterson & Baker 2011). Similarly, mosquito fish has a broad thermal tolerance, with an upper lethal temperature as high as 43°C (see review in Paterson & Baker 2011), greatest feeding activity at 24-30°C and no growth at temperatures below 10°C (Wurtsbaugh, 1983). These data indicate that mosquitofish will do very well in very warm waterways.

It is beyond the scope of this review to summarise such information for non-native species present in New Zealand's waterways but the following publications do provide some such information: Simons (1984) presents data for mosquito fish (*Gambusia affinis*) in addition to data on native species; Elliott (1994) summarises data for several salmonids, including brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*), and for three cyprinids (Roach, *Rutilus rutilus*, Goldfish *Carassius auratus*, and carp *Cyprinus caprio*) (Figure 4.2, 4.3 and Table 4.1 in Elliott 1994); Paterson & Baker (Paterson & Baker 2011) reviews information for brown bullhead catfish, grass carp, goldfish, koi carp, tench, rudd, *Gambusia*, European perch, and brown and rainbow trout.

5.3.4 Predation

The rate of natural mortality (i.e. mortality not caused by fishing) in fish stocks is correlated with water temperature, with temperature-mediation of predation risk being one suggested mechanism (Pauly 1980). Within the thermal growth zone of a species, higher temperatures will drive higher metabolic rates, thereby increasing energy requirements. For predatory species, this will result in an increase in the rate of prey consumption. For prey species, it may increase predation risk by increasing the length of time spent exposed to predation risk whilst feeding, or it may drive a change in foraging behaviour resulting in greater risk of predation (such as greater forays into the water column by benthic fish). Low temperatures or high temperatures that exceed the upper growth limit may suppress feeding in predator and prey species.

As already mentioned, temperature also affects swimming performance (Bannon 2006; Lyon et al. 2007), although the consequences of such an effect are not easily predicted and are likely to vary depending on circumstances including the behaviours of predator and prey species. Increased water temperature may result in hyperactivity which may increase exposure to predation risk or, conversely, it may increase the likelihood of escape by reducing reaction times and increasing burst swimming capacity. Conversely, reduced levels of activity may reduce the exposure to predation risk or it may also increase reaction times or burst escape swimming performance resulting in a lower

chance of escaping predators (Johnson & Bennett 1995). The outcome of changes in temperature on the risk of predation will be determined by the relative differences in temperature dependent activity between predator and prey.

Water temperature can indirectly affect the risk of predation as a result of its effects on the growth rate of either the prey or predator. Faster growth may mean that prey are able to grow large more quickly, thereby becoming less vulnerable to predation (Anderson et al. 2001). Alternatively, rapid growth by predatory species may enable them to capture species that are not available to smaller predators.

5.3.5 Parasites and disease

The correlation between the rate of natural mortality in fish stocks and water temperature noted by Pauly (Pauly 1980), may also be a consequence of an increase in parasitism and disease. Water temperature is the most important abiotic variable influencing parasites, affecting growth rates, time to maturation, mortality rates, the number of generations possible per year, and the duration of the growing and transmission season (Marcogliese 2001). Higher temperatures accelerate production of cercariae of trematodes within the snail host, which may reduce the longevity of the host and the mortality rate in the next host (either intermediate or definitive) (Poulin 2006). Such changes may have significant implications for host populations.

Temperature may also affect the virulence of pathogens and, consequently, the mortality rate associated with a pathogen (Fish & Rucker 1945; Gilad et al. 2003; Jiravanichpaisal et al. 2004; You et al. 2010) and stress responses as a result of thermal stress may affect the susceptibility of fish to parasites and disease (Pickering & Pottinger 1989).

6 Application of temperature criteria

6.1 Scale, magnitude and types of thermal impacts

Given that this review is intended to inform the management of water temperature to protect native aquatic life, it is worthwhile establishing the range of activities that may influence water temperature in water bodies and how the effects of these changes may vary. The scale of the effects of such activities range from small-scale, point-source discharges (such as the discharge of cooling water from a thermal power station) to the diffuse effects of activities that may affect entire catchments (e.g. vegetation clearance or urbanisation). Similarly, the consequences of different discharges will differ – some inputs will raise water temperatures (thermal power plant effluents), others may cause cooling (hypolimnetic discharges from a reservoir), while others will influence the daily variation in water temperature but may or may not affect the mean daily temperature. Clearly, a single 'one-size-fits-all' approach will not adequately address all activities that may influence water temperature.

A wide range of factors act in concert to determine the water temperature at a point in time and space. Such factors include heat transport from upstream, heat flux between the water and its surroundings (air, riverbed, banks), solar radiation, shading, meteorological conditions (e.g. relative humidity, air temperature, wind) and channel geometry (Figure 6 - reviewed in Theurer et al. 1984). The ecological implications of different types of thermal impact are likely to vary markedly. When setting thermal criteria for a particular activity, it is important to understand the specific thermal implications of that activity and how these might impact biota of interest, the scale of such impacts and to set thermal criteria accordingly.

The scale and magnitude of effect of a point-source thermal discharge will depend on the volume and conditions (including temperature) within the discharge and the receiving waterbody as well as the environmental conditions (meteorological conditions). Processes such as evaporative cooling, conduction and convection can rapidly ameliorate any thermal effects resulting in a relatively limited downstream extent of impacts of the discharge and management responses could be undertaken at a local scale to maximize the rate of such processes to reduce the extent of the impact of the discharge.

On the other hand, activities such as vegetation clearance and urbanisation can cause large-scale effects. For example, following clear-cut logging in the catchments of some small streams, the summer mean daily temperatures increased by 2-3.8°C and summer maxima increased by 4-7.3°C (Quinn & Wright-Stow 2008).

Urbanisation can also lead to large-scale alteration of thermal regimes by altering riparian vegetation, changing the flow regime and through changes to a stream's hydraulic geometry (Galli 1990; LeBlanc et al. 1997). Water quality monitoring in Hawke's Bay found that urban streams regularly exceed 25°C. Summer rainfall can result in peaks in water temperature, as rainfall falling on heated impermeable surfaces (e.g. bitumen, concrete, asphalt) runs off into waterways (Galli 1990). In addition to such thermal effects, many urban streams flow through residential, commercial and industrial areas and are likely to receive inputs of toxicants (Paul & Meyer 2001), meaning that the

potential interaction between toxicity and temperature is of particular relevance (but not limited to) to this type of waterway.

Much of the focus of thermal management of waterways focuses on activities that raise water temperature, but cool water discharges can also have significant ecological effects. The most common source of inputs of cool water is hypolimnetic discharges from reservoirs (e.g. Waitaki Dam, Waipapa Dam), but may also occur as a result of discharges of groundwater to surface waters (such as in some aquaculture facilities). Such discharges may have positive effects for species if the receiving body of water is warmer than is optimum for that species. Alternatively, it may have negative consequences for some species by retarding growth and development (see Sections 4.2 and 4.4).

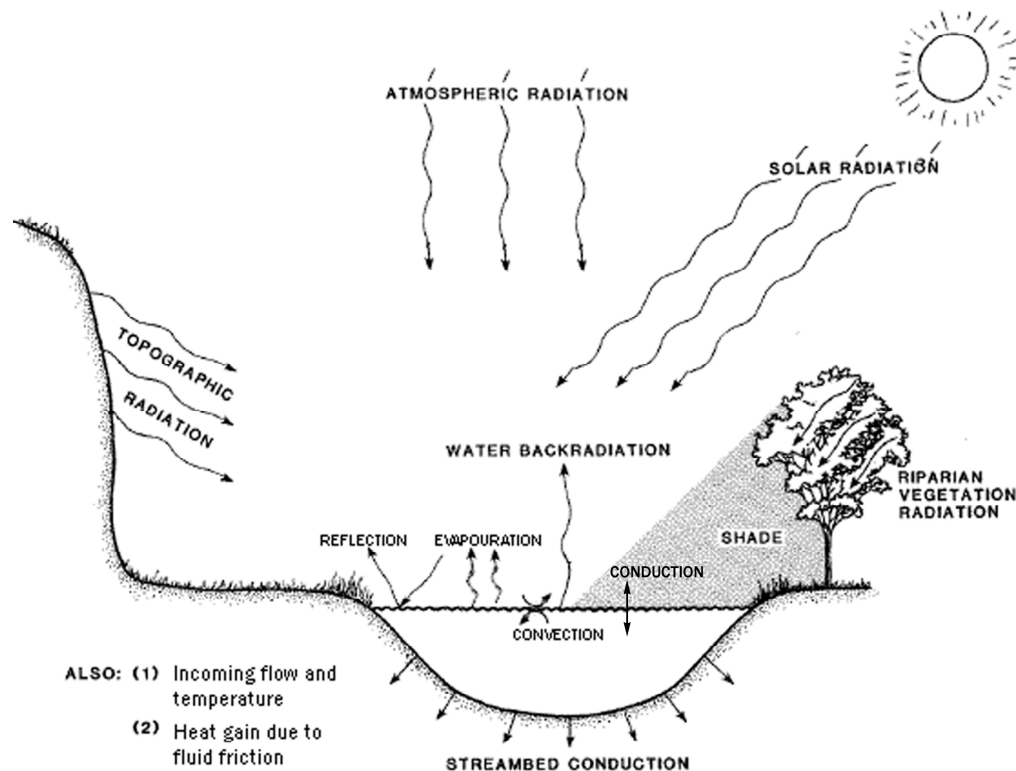


Figure 6

Sources of heat flux between a stream and its surroundings. Modified from Theurer et al. 1984.

6.2 Management objectives and thermal criteria

The management objectives for thermal effects of different activities will depend on the significance and nature (resident or migratory) of the values present as well as the potential scale and magnitude of the effects of the activity. Where the thermal effects of an activity are localised (such as in the case of a small discharge), it may be that some reduction in the suitability of habitat in the vicinity of this discharge would be acceptable, especially if no high-value species occurred in the affected area. In such a situation, the management objectives should focus on acute criteria that provide temperatures that provide for ongoing survival of target species. If large-scale thermal effects are expected

or the values present are high, the objectives of management should shift to more restrictive chronic criteria that avoid sub-lethal effects on growth or fitness. Management objectives may include the maintenance of diversity (i.e. taxonomic richness), population size and productivity, growth potential of particular species.

Setting thermal criteria relies on judgements on the significance of the values concerned and the extent of effects.

Table 11

Decision matrix for resident populations with management objectives and possible thermal criteria (italicised) across a range of in-stream values and scale and magnitude of potential thermal impacts. Colours denote the balance of acute/chronic criteria: Green = acute criteria, yellow = acute and chronic criteria, orange = acute and chronic criteria with greater restrictions on chronic effects than yellow, red = chronic criteria. Interim acute criteria are outlined in Table 14 and interim chronic criteria are outlined in Table 15.

		Scale and/or magnitude of effects		
		Low	Moderate	High
Values	Low	Ensure survival of resident species	Ensure survival of, and limit effects on, growth of resident species	Ensure survival of, and limit effects on, growth of resident species
		<i>Acute criteria</i>	<i>Acute criteria and some limits on duration of temperatures outside growth range of significant resident species</i>	<i>Acute criteria and some limits on duration of temperatures outside growth range of significant resident species</i>
	Moderate	Maintain reduced population, limit effects on growth and fitness	Maintain reduced population, limit effects on growth and fitness	Maintain population size, limit effects on growth and fitness
		<i>Acute criteria and more restrictive limits on duration of temperatures outside growth range of significant resident species</i>	<i>Acute criteria and more restrictive limits on duration of temperatures outside growth range of significant resident species</i>	<i>Chronic criteria for most sensitive target species</i>
	High	Maintain reduced population, limit effects on growth and fitness	Maintain population size, no effect on growth and fitness	Maintain population size, no effect on growth and fitness
		<i>Acute criteria and more restrictive limits on duration of temperatures outside growth range of significant resident species</i>	<i>Chronic criteria for most sensitive target species</i>	<i>Chronic criteria for most sensitive target species</i> <i>Growth modelling</i>

Table 12

Decision matrix for migratory populations with management objectives and possible thermal criteria (italicised) across a range of in-stream values and scale and magnitude of potential thermal impacts. Colours denote the balance of acute/chronic criteria and follow the same coding as Table 11.

		Scale and/or magnitude of effects		
		Low	Moderate	High
Values	Low	Ensure passage is possible for migratory species for a limited portion of the likely migration season	Ensure passage is possible for migratory species for a limited portion of the likely migration season	Ensure passage is possible for migratory species for a limited portion of the likely migration season
		Acute criteria	Acute criteria	Acute criteria
	Moderate	Maintain passage for migratory species but potentially at reduced abundance	Maintain passage for migratory species but potentially at reduced abundance	Maintain passage for and abundance of migratory species
		Chronic criteria	Chronic criteria	Chronic criteria for most sensitive target species
	High	Maintain passage for and abundance of migratory species	Maintain passage for and abundance of migratory species	Maintain passage for and abundance of migratory species
		Chronic criteria	Chronic criteria for most sensitive target species	Growth modelling or chronic criteria for most sensitive target species

6.3 Approach to setting thermal criteria

The approach to setting thermal criteria described here follows that of Todd et al. (2008), who outlined methods to set thermal criteria to protect cold-water fisheries in Colorado. The appeal of Todd et al.'s approach is that it offers several options for calculating acute and thermal criteria depending on the type of thermal tolerance data available. Given the ranges of ways to measuring thermal tolerance that have been employed in New Zealand, such an approach is advantageous.

6.3.1 Acute criteria – following Todd et al. (2008)

The objective of acute criteria is to protect species from the lethal effects of short-lived high temperatures and are expressed as the daily maximum temperature (DM – defined as the highest two-hour average water temperature measured within any given 24-h period - Todd et al. 2008). As such, their intention is to delineate the point at which thermal stress occurs after short-term exposure and substantial mortality is likely to be observed if those temperatures persist. Criteria such as the incipient lethal temperature and CTM are relevant when defining this point. However, to avoid the risk of significant mortality, upper acute thermal criteria should occur at a point between the incipient lethal temperature and the growth optimum for the species considered.

Todd et al. (2008) described several approaches to calculating acute criteria depending on the available information on the thermal tolerance of the species in question. For

species where an ultimate upper incipient lethal temperature (UUILT) has been identified, this was used to determine the acute criteria for that species (using either equations A1 or A3 in Table 13). The UUILT is defined as the point at which the upper incipient lethal temperature no longer increases with acclimation (see Figure 1). In the absence of a UUILT value, the upper incipient lethal temperature (UILT) at acclimation temperatures representing 'summer conditions' ('summer' UILT) can be substituted (using either equations A2 or A4 in Table 13). While there are no regional data on summer stream temperatures currently available, air temperature is the single best predictor of stream temperature (Bartholow 1989).

If neither a UUILT nor UILT was available, Todd et al. (2008) used the CTM minus a conversion factor (equation A5 in Table 13), where such conversion factors were able to be obtained from the literature. In all cases, the acute criteria were determined by subtracting a safety margin from the critical temperature (UUILT, UILT or converted CTM). Where possible, this safety margin was calculated as 1/5th of the difference between the UUILT (or 'summer' UILT) and the thermal growth optimum (referred to as the 1/5th rule) (as in equations A1 and A2 in Table 13). Where an estimate of T_{opt} was not available, a 2°C safety margin was subtracted from the critical temperature (equations A3, A4 and A5 in Table 13). The purpose of this safety margin was to adjust the acute criteria to a level where low mortality rates would be expected, since setting the acute criteria at the UILT would be expected to result in c.50% mortality.

The reliability of acute criteria depends on the equation used and whether the values used in the calculation of acute criteria were experimentally-based, or indirectly derived from experimental values (as for the estimates of T_{opt} in Table 5). The equations used to calculate acute criteria presented in Table 13 are listed in decreasing order of reliability (i.e. A1 = highest reliability, A5 = lowest).

Table 13

Methods of calculating acute and chronic thermal criteria following the methods of Todd et al. (2008). For both acute and chronic criteria, the methods are listed in order of preference, with the first row representing the preferred approach. UUILT = upper ultimate incipient lethal temperature, 'summer' UILT = upper incipient lethal temperature for individuals acclimated at 'summertime temperatures', T_{opt} = thermal growth optimum, T_{pref} = thermal preference, CTM = critical thermal maximum.

Criteria	Available information	Equation	#
Acute	UUILT, T_{opt}	$UUILT - 0.2 * (UUILT - T_{opt})$	A1
	'summer' UILT, T_{opt}	'summer' UILT - 0.2 * ('summer' UILT - T_{opt})	A2
	UUILT	$UUILT - 2^{\circ}\text{C}$	A3
	'summer' UILT	'summer' UILT - 2°C	A4
	CTM, conversion factor to approx. UILT	$CTM * \text{conversion factor} - 2^{\circ}\text{C}$	A5
Chronic	Upper T_{opt}	Upper T_{opt}	C1
	T_{opt} , UUILT	$T_{opt} + 0.33 * (UUILT - T_{opt})$	C2
	T_{pref} , CTM	$T_{pref} + 0.33 * (CTM - T_{pref})$	C3

6.3.2 Chronic criteria – following Todd et al. (2008)

The intent of chronic criteria is to protect species from sub-lethal effects of elevated temperatures. Chronic criteria are expressed as the maximum weekly average temperature (MWAT - calculated as the seven-day mean of consecutive daily mean temperatures, where daily means are calculated from multiple, equally spaced values per day). Such effects are reviewed in Section 4. Generally, the approach to determining chronic criteria is to maintain or enhance conditions for the growth and reproduction of target species. To achieve this, criteria should take account of thermal limits and optimum temperature for growth.

Todd et al. (2008) described several approaches for calculating chronic criteria depending on the thermal tolerance information available. Where an estimate of the upper thermal optimum (upper T_{opt} – see Figure 7) was available, this was used as the chronic criteria (equation C1 in Table 13). If no upper T_{opt} value was available, the thermal optimum (equation C2) or thermal preference (equation C3) of the species could be used to approximate the upper T_{opt} using the equations presented in Table 13.

As for acute criteria, the reliability of chronic criteria depends on the equation used and whether the values used in the calculation of acute criteria were experimentally-based, or indirectly derived from experimental values (as for the estimates of T_{opt} in Table 5). The equations used to calculate chronic criteria presented in Table 13 are listed in decreasing order of reliability (i.e. C1 = highest reliability, C3 = lowest).

6.3.3 Growth modelling

Where sufficient information is available, it is possible to model the growth potential of individual fish species under different thermal regimes. This is regularly done for brown trout using the model of Hayes (2000). Fish growth is usually modelled as a power function of temperature, commonly using the Von Bertalanffy growth equation:

$$L_t = L_{\infty} (1 - e^{-k(t-t_0)})$$

where:

L_{∞} = asymptotic length (maximum length of fish in population),

L_t = is length at age t ,

t_0 = age at which the length is theoretically equal to zero.

k = the growth coefficient.

The growth coefficient (k) is of most interest, since this is the factor that is temperature-dependent. Typically, k increases with increasing temperature to an optimum, then steeply declines (Figure 7). This curve can be estimated on the basis of four parameters (Mallet et al. 1999):

$$k = k_{opt} \frac{(T - T_{min})(T - T_{max})}{(T - T_{min})(T - T_{max}) - (T - T_{opt})^2}$$

where:

k = growth coefficient

k_{opt} = growth coefficient at thermal optimum,

T = Temperature at which growth is being modelled,

T_{min} = Minimum temperature at which growth ceases,

T_{opt} = Temperature at which optimal growth occurs,

T_{max} = Maximum temperature at which growth ceases.

When an estimate of k_{opt} (which requires substantial research effort) is not available, k_{opt} can be set to 1, which means equation 3 will predict growth (k) relative to the maximum rate of growth (i.e., it is a dimensionless variable).

Growth modelling can be used to compare the effects of different thermal regimes on the growth potential of the species of concern. For example, assessing effects of an existing activity where pre- and post-activity temperature records are available, or assessing potential effects of a proposed activity based on temperature modelling. This approach is often the only practical way to determine what the net effect of a change in thermal regime will be on the growth of an individual species.

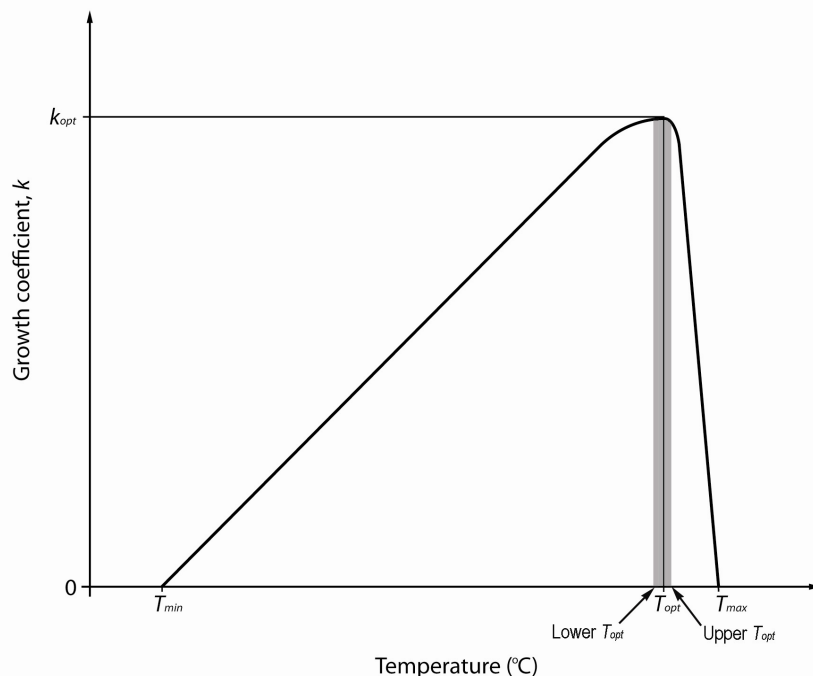


Figure 7

Relationship between the growth coefficient, k and water temperature. T_{min} = minimum temperature at which growth ceases, T_{max} = maximum temperature at which growth ceases, T_{opt} = temperature at which the growth coefficient is optimal (K_{opt}).

6.3.4 Species sensitivity distributions

All of the approaches outlined are based on the thermal requirements of individual taxa. Often this means that thermal criteria for waterways are applied based on the most sensitive species present. An alternative approach is to develop a species sensitivity distribution (SSD) for the waterway based on the thermal sensitivity of organisms present (lethal temperature) (De Vries et al. 2008). De Vries et al. (2008) outline the way in which SSDs are calculated. SSDs are cumulative distribution curves of the thermal tolerances of a subset of the species present in the waterway of concern, usually at a given acclimation temperature. Each SSD can be used to determine the percentage of the species that would be protected at a given temperature, or, conversely, the temperature at which a particular percentage of the community will be protected (rather like the different levels of protection (90, 95 and 99%) used in existing ANZECC guidelines, e.g. ANZECC & ARMCANZ 2000).

Such an approach avoids the criticism that thermal criteria and growth modelling are usually applied to single species and does not represent community-level effects of thermal alteration. However, the thermal tolerance data available for native taxa are currently insufficient to develop robust SSDs.

7 Information needs for setting temperature criteria

Most of the thermal tolerance data for native freshwater fish are CTM or short-term (10 minute exposure time) LT50 data. Such data really only provides an estimate of the upper ultimate lethal temperature, and are of relatively limited value to those who wish to manage water temperatures for the protection of native values. This section outlines the areas where additional data are required to facilitate the development of robust thermal criteria to protect against the acute and chronic effects of the thermal alteration of waterways.

7.1 Setting upper thermal criteria following Todd et al. (2008)

For both acute and chronic effects of high temperatures, the most reliable approach to calculating criteria uses the UUILT and T_{opt} (equation A1 in Table 13). To obtain an estimate of the UUILT would require a concerted experimental effort, with specimens exposed to a range of acclimation temperatures held at various temperatures for up to 7 days to calculate the LT50 for each acclimation temperature (the UILT). The UUILT is then able to be estimated as the plateau on a plot of UILT against acclimation temperature.

An alternative approach would be to conduct a series of experiments, as outlined above, to estimate the UILT across the range of mean summer water temperatures expected in waterways for which the criteria are being developed. While this approach may save some experimental effort when the range of water temperatures in a region is limited, if criteria are to be developed for application at a national scale, or even within most regions, it is likely that the data collected would be sufficient to estimate the UUILT.

At present, UILT have been estimated for only four species of fish (Table 2). Of these, inanga and smelt are largely restricted to lowland waters, although smelt can also form lacustrine populations in upland lakes (e.g. Lake Taupo), while both eel species are widely distributed. This poses a problem for the management of water temperature in upland waterways – since the two eel species are among the most thermally tolerant native species present in New Zealand freshwaters. Species that are found in inland locations, such as koaro and dwarf galaxias, are likely to be substantially less tolerant of high water temperatures than eels so it would be useful if thermal criteria could be calculated for them. Based on CTM values, it appears that many native bully species have moderate tolerance to high water temperatures.

The UILT has been estimated for eleven common macroinvertebrate taxa (Table 7 and Table 8). In the majority of these experiments, experimental animals were collected from the field and were used in experiments without prior acclimation (see Quinn et al. 1994 for details). From these data it is possible to approximate UILT values for acclimation temperatures in the range from which the fish were collected (12-15°C in most cases).

The other variable needed to provide robust thermal criteria is an estimate of T_{opt} . There have been no experiments conducted to directly measure T_{opt} of a native New Zealand freshwater organism. Such experiments involve the measurement of growth over an

experimental period under controlled thermal conditions and are usually conducted with fish fed to satiation. Graynoth & Taylor (2000) report maximal food consumption rates of eels occur at 25°C (Table 5).

7.2 Lower thermal criteria

While much of the emphasis of thermal studies is on the upper thermal tolerances of species, low water temperatures can also directly influence survival and growth of poikilotherms. It is likely that most native species can tolerate short-term exposure to low water temperatures, so chronic lower thermal criteria are probably more relevant than acute criteria. Low water temperatures can retard growth – as has been reported for eels below 8.6-9.6°C (Graynoth & Taylor 2000). This is the only estimate of the lower growth limit (T_{min}) found during this review. Determining the lower thermal tolerance of a species is also required if growth modelling is to be conducted (see Section 7.3)

7.3 Growth modelling

Growth modelling represents a powerful tool for investigating the consequences of thermal modification of waterways on the growth potential of an individual species. As outlined in Section 6.3.3, a simple growth model that estimates growth at a temperature as a proportion of maximum potential growth at that temperature can be constructed with only three parameters: T_{opt} , T_{min} and T_{max} . These parameters can be estimated by growth experiments involving the measurement of growth over an experimental period under controlled thermal conditions. Usually such experiments are conducted with fish fed to satiation. Graynoth & Taylor (2000) present growth models for shortfin and longfin eels and use these to estimate growth in the wild relative to maximum growth observed under experimental conditions. When no experimental estimate of T_{opt} is available, this can be estimated using the equations of Jobling (1981) presented in Table 4.

8 Interim thermal criteria for native biota

In this section, we have used available data on the thermal tolerance of native biota to determine acute and chronic thermal criteria for the protection of individual species following the approach of Todd et al. (2008). The reliability of these thermal criteria depends on what thermal tolerance data are available for each species.

It should be kept in mind that trout are present in many rivers and lakes in New Zealand and that Part II, Section 7h of the Resource Management Act specifies that trout (and salmon) habitat be recognised and provided for. There is a wealth of information on the thermal requirements of trout (and salmon) and thermal criteria have been developed for their protection (e.g. Todd et al. 2008). Moreover, a brown trout growth model is available and has been tested on a New Zealand river (Hayes 2000; Hayes et al. 2000) and applied to several other rivers and lakes (e.g., Stark & Hayes 1997; Young et al. 2000; Hayes et al. 2007). Available data (including that reviewed in Section 4) suggests that brown trout are more sensitive to high water temperatures than most, if not all, of our native fish species. Therefore, in waterways where significant trout fisheries are present, thermal criteria to protect trout from high water temperatures will provide appropriate thermal protections for most native fish. This does not apply to coldwater discharges, since most native fish have higher upper temperature tolerances than trout and there probably have higher lower temperature tolerances Graynoth & Talyor (2000) confirmed this for the lower growth limit of eels.

8.1 Interim acute thermal criteria

The most defensible method of establishing acute criteria following Todd et al. (2008) is to use the UUILT and the thermal growth optimum (T_{opt}) (using Equation A1 from Table 13). Establishing the UUILT for a species requires substantial experimental effort – medium-long-term tests conducted on specimens acclimated at a range of different temperatures. Such data are not currently available for any native species.

The next choice is to use the UUILT at an acclimation temperature that reflects the natural mean summer temperatures of the system of interest (using Equation A3 or A4 from Table 13 depending on whether an estimate of T_{opt} is available). There are currently limited UUILT data available for New Zealand fish and the data available are across a limited range of acclimation temperatures (Table 6). Consequently, interim acute criteria have been calculated for two acclimation temperatures: 15°C for upland waterways and 20°C for lowland waterways. The choice of these acclimation temperatures was driven primarily by the paucity of data already discussed, but available river water temperature data suggests that these criteria are still likely to be widely applicable across much of the North Island.

Figure 8 presents the predicted mean January air temperature for the North Island based on the Freshwater Ecosystems of New Zealand (FENZ) geo-database (Leathwick et al. 2008; Leathwick et al. 2011). Clearly, there is likely to be substantial variation in mean summer water temperature within the Waikato and Hawkes Bay regions, and to a lesser extent in the Auckland region, as there is in air temperature (Figure 8). Water temperature data for sites in the Auckland, Hawkes Bay and Waikato regions (from

Mosley 1982 and National River Water Quality Network sites downloaded from the Water Quality Information System, <https://secure.niwa.co.nz/wqis/index.do>) show that average summer temperatures at many lowland sites are close to 20 °C, while many rivers at higher elevations or sourced from ranges have average summer temperatures of close to 16 °C (Appendix 2). There will, of course be situations where the two acclimation temperatures will not be appropriate. Many northern lakes experience summer temperatures in excess of 20 °C, while spring-fed streams may have low summertime temperatures, even in lowland areas. In such situations, further experimental work (at appropriate acclimation temperatures) will be necessary in order to develop reliable thermal criteria for individual taxa of interest.

Each of the acute interim thermal criteria presented in Table 14 are assigned with a level of confidence. The level of confidence is based on the equation used to calculate the criteria and whether the data used to calculate the criteria were based directly on experimental data or were derived indirectly from experimental data (as in Table 5). The level of confidence in acute criteria calculated using equation A1 would be high, A2 moderate-high, A3 moderate and so-on (to A5 = low). If equation A2 was used, but the summer UILT was derived, rather than directly experimentally-derived, this would reduce the confidence by half a category to moderate. If the T_{opt} value was estimated rather than calculated, the confidence was reduced by half a category again (to low-moderate).

The interim acute criteria with the highest confidence was that for lowland systems for common smelt (moderate), which was calculated using equation A2 using an UILT from the experimental work of Richardson & West (1998) and a estimated T_{opt} from (Table 5). Interim acute criteria for glass eels (moderate level of confidence) were derived using equation A4 and an UILT from Jellyman (1974). All other criteria were rated as being of low to moderate confidence.

It is important to keep in mind that most of the values presented in Table 14 are based on UILT values from constant-temperature experiments. Under daily-varying temperatures, the LT50 temperature can be expressed as the mean daily temperature or daily maximum (e.g. Cox & Rutherford 2000). Because the acute criteria outlined above are expressed as the daily maximum temperature (see Section 6.3.1), the UILT used in the calculation should also be expressed as the daily maximum temperature. In the experiments of Cox & Rutherford (2000), the constant 96-h LT50 for *Deleatidium* was 24.2 °C, compared with 21.9 °C for the mean temperature under the time-varying temperature treatment and 26.9 °C for the maximum in the time-varying temperature treatment. Thus, based on equation A4, the acute criteria would be 22.2 °C based on the constant-temperature experiment or 24.9 °C based on the LT50 calculated from the daily maximum temperature under the time-varying treatment. These results suggest that acute criteria calculated based on constant-temperature experiments may be more conservative (by 3 °C based on the results of Cox & Rutherford for *Deleatidium* and *Potamopyrgus*).

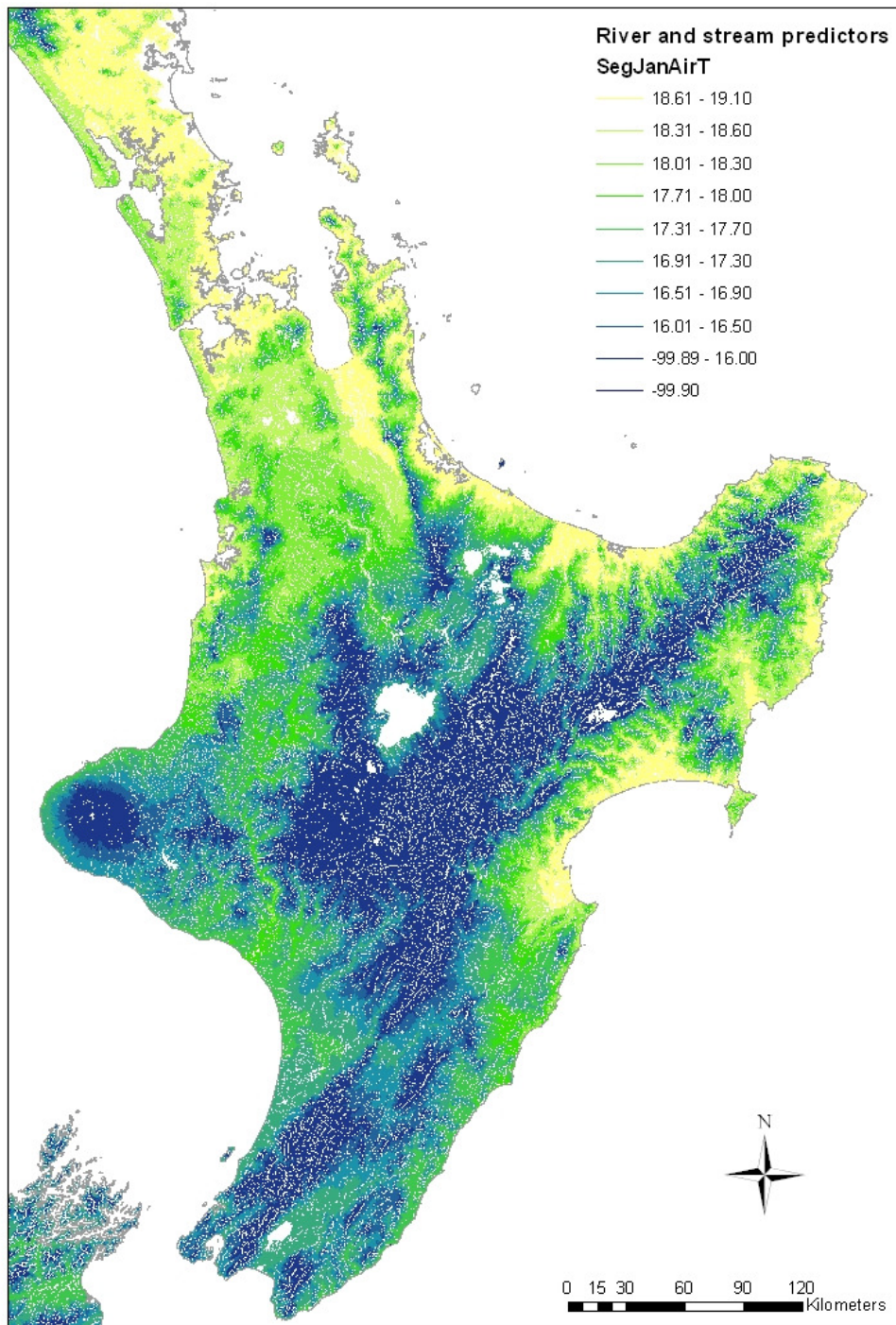


Figure 8
Predicted mean summer (January) air temperatures for North Island river segments (SegJanAirT) from the FENZ geo-database (Leathwick et al. 2008; Leathwick et al. 2011).

Table 14

Interim acute thermal criteria for native fish and macroinvertebrate species estimated using the approach of Todd et al. (2008). Acute thermal criteria are expressed as the daily maximum temperature (calculated as the highest two-hour average water temperature measured within any given 24-h period). UILT = upper incipient lethal temperature, T_{opt} = thermal growth optimum.

Common name	Life stage	UILT (°C)	T_{opt} (°C)	Acute criteria (°C)	Equation from Error! Reference source not found.	Confidence level
Lowland waterways (summer mean water temperature \approx 20 °C)						
Common smelt	Adult	26.8 ¹	23.8 ²	26	A2	Moderate
	Larvae	27.5 ³	23.8 ²	27	A2	Low-mod
Upland waterways (summer mean water temperature \approx 15 °C)						
Shortfin eel	Glass eel	28.0 ⁵	-	26	A4	Moderate
Longfin eel	Glass eel	25.0 ⁵	-	23	A4	Moderate
Common smelt	Adult	23.3 ⁶	19.2 ⁴	22	A2	Low-mod
<i>Deleatidium</i> spp.		22.6 ⁷	-	21	A4	Low-mod
<i>Deleatidium</i> spp.		26.9 ⁸		25	A4	Low-mod
<i>Zephlebia dentata</i>		23.6 ⁷	-	22	A4	Low-mod
<i>Aoteapsyche colonica</i>		25.9 ⁷	-	24	A4	Low-mod
<i>Pycnocentroides aureola</i>		32.4 ⁷	-	30	A4	Low-mod
<i>Pycnocentria evecta</i>		25.0 ⁷	-	23	A4	Low-mod
<i>Hydora</i> sp.		32.6 ⁷	-	31	A4	Low-mod
<i>Potamopyrgus antipodarum</i>		32.4 ⁷	-	30	A4	Low-mod
<i>Potamopyrgus antipodarum</i>		33.6 ⁷	-	32	A4	Low-mod
<i>Sphaerium novaezelandiae</i>		30.5 ⁷	-	29	A4	Low-mod
<i>Paratya curvirostris</i>		25.7 ⁷	-	24	A4	Low-mod
<i>Paracalliope fluviatilis</i>		24.1 ⁷	-	22	A4	Low-mod
<i>Lumbriculus variegatus</i>		26.7 ⁷	-	25	A4	Low-mod

¹ = From Richardson & West (1998): 5-d LT_{50} , acclimation temperature = 20 °C

² = Calculated from the CTM for fish acclimated to 20 °C using the equations of Jobling (1981) presented in Table 4.

³ = Interpolated from 24 h LT_{50} values at acclimation temperatures of 18 °C and 22 °C of Simons 1986b

⁴ = From Table 5.

⁵ = From Jellyman (1974): 14-d LT_{50} , acclimation temperature = 15 °C

⁶ = Estimated as short-term $LT_{50, 15^{\circ}\text{C}-5^{\circ}\text{C}}$, since short-term $LT_{50, 20^{\circ}\text{C}}$ -long-term $LT_{50, 20^{\circ}\text{C}}=31.9-26.8=5.1^{\circ}\text{C}$

⁷ = From Quinn *et al.* (1994): 96 h LT_{50} , acclimation temperature \sim 12-16 °C

⁸ = From Cox & Rutherford (2000): 96 h LT_{50} expressed as daily maximum temperature, 5 °C diel variation in water temperature, acclimation temperature \sim 12-16 °C

8.2 Interim chronic thermal criteria

The most defensible method of establishing chronic criteria following the methods of Todd et al. (2008) is to set them at the upper thermal growth optimum (upper T_{opt}) (using Equation C1 from Table 13). Doing so ensures that increases in temperature that stay within the chronic criteria will not limit growth. The upper T_{opt} has not been established for any native species to date, most likely because of the substantial experimental effort involved, although the best estimate available is for eels (~25 °C).

The second approach is to estimate the upper T_{opt} using Equation C2, which uses T_{opt} and the UUILT (Table 13). No direct measurements of T_{opt} are available for native New Zealand biota, although it can be estimated from upper lethal and preferred temperatures (as in Table 5).

The approach taken to calculate the chronic criteria presented in Table 15 used the third equation in Table 13 (Equation C3), which was calculated from the CTM and thermal preference data for each species. Because measurements of T_{pref} were available for only an acclimation temperature of 15 °C (from Richardson et al. 1994), T_{pref} values for lowland streams (at an acclimation temperature of 20 °C) were estimated from CTM or short-term LT50 values calculated using the equation of Jobling (1981) presented in Table 4. This was also the case for adult eels (both shortfin and longfin). Consequently the level of confidence in these interim criteria is low. The remaining chronic criteria were calculated on the basis of CTM values for fish acclimated at 15 °C and T_{pref} values from Richardson et al. (1994); the level of confidence in these values is low-moderate.

Given the low level of confidence in most of the chronic criteria listed in Table 15, they should be applied cautiously. It should be noted that using the approach outlined above resulted in chronic criterion for common smelt (in lowland systems) that is higher than the corresponding acute criteria. This is obviously erroneous and reflects the low level of confidence in these criteria. More reliable criteria could be developed if experimental work was conducted to establish the upper T_{opt} or T_{opt} and UUILT for native species.

Table 15

Interim chronic thermal criteria for native fish species estimated using the approach of Todd et al. (2008). Chronic criteria are expressed as the maximum weekly average temperature (MWAT - calculated as the seven-day mean of consecutive daily mean temperatures, where daily means are calculated from multiple, equally spaced values per day). CTM = critical thermal maximum, T_{pref} = thermal preference.

Common name	Life stage	CTM (°C)	T_{pref} (°C)	Chronic criteria (°C)	Equation from Error! Reference source not found.	Confidence
Lowland waterways (summer mean water temperature \approx 20°C)						
Short fin eel	Elver	35.9 ¹	29.2 ³	31	C3	Low
Cran's bully	Mixture	33.9 ²	27.4 ⁴	30	C3	Low
Common bully	Mixture	34.0 ¹	27.5 ⁴	30	C3	Low
Inanga	Whitebait	33.1 ²	26.3 ⁴	29	C3	Low
Banded kokopu	Adult	32.5 ²	25.4 ⁴	28	C3	Low
Common smelt	Adult	31.8 ¹	23.8 ⁴	26	C3	Low
Upland waterways (summer mean water temperature \approx 15°C)						
Short fin eel	Elver	35.7 ¹	26.9 ³	30	C3	Low-mod
Short fin eel	Adult	39.7 ²	35.4 ⁴	37	C3	Low
Longfin eel	Elver	34.8 ²	24.4 ³	28	C3	Low-mod
Longfin eel	Adult	37.3 ²	32.1 ⁴	34	C3	Low
Cran's bully	Mixture	30.9 ²	21.0 ³	24	C3	Low-mod
Common bully	Mixture	30.9 ²	20.2 ³	24	C3	Low-mod
Torrent fish	Adult	30.8 ²	21.8 ³	25	C3	Low-mod
Inanga	Adult	30.8 ²	18.1 ³	22	C3	Low-mod
Banded kokopu	Adult	28.5 ²	17.3 ³	21	C3	Low-mod
Common smelt	Adult	28.3 ²	16.1 ³	20	C3	Low-mod

¹ = CTM from Table 1.

² = Short-term LT_{50} from Table 1.

³ = Thermal preference from Table 1.

⁴ = Thermal preference estimated from CTM or short-term LT_{50} using equations of Jobling (1981) from Table 4.

9 Summary and conclusions

Water temperature influences all aspects of freshwater ecosystems, from primary producers through to fishes, resulting in effects ranging from mortality to sub-lethal effects, reproductive success and fitness.

A range of methods and approaches have been used to assess the thermal tolerance of aquatic organisms. The field distribution of species, particularly at temperature extremes (e.g. geothermal areas, glacial streams), can provide indications of the thermal tolerance of species, although distributions may be affected by other variables (e.g. salinity in geothermal springs) that co-vary with temperature. Physiological markers (e.g. heat shock proteins, reactive oxygen species) can also be used as indicators of thermal stress.

Controlled laboratory experiments provide the most defensible estimates of the thermal tolerance of aquatic species. In New Zealand, most laboratory studies have used the critical thermal maximum (CTM) method, which involves exposing acclimated experimental subjects to rising water temperature until behaviour indicates metabolic disruption or death occurs. The incipient lethal temperature method involves incubation of specimens across a range of temperatures and determining the temperature at which 50% mortality occurs over a set time period (usually between 24 h and 14 d). Both the CTM and incipient lethal temperature methods are designed to consider the lethal effects of temperature. The acclimated chronic exposure (ACE) method, in contrast, is intended to consider the lethal and sub-lethal effects of temperature. In the ACE method, after acclimation, the water temperature in the test tank is gradually increased until the test temperature is attained. Once the test temperature is reached, it is maintained for 60 days or until the death of the experimental subject.

A literature review yielded laboratory thermal tolerance data for twelve native fish and twelve native macroinvertebrates (Figure 9). Published estimates of the critical thermal maxima are available for: shortfin and longfin eels; Crans, common and upland bullies; torrentfish; inanga; giant kokopu, shortjaw kokopu, and banded kokopu; koaro and common smelt (Figure 9). Published incipient lethal temperatures were available for glass eels (shortfin and longfin eels), inanga whitebait and common smelt (larvae and adults) (Figure 9). Water temperature may also affect the behaviour (e.g. schooling), development, migration, spawning and growth of native fish (see Figure 9 for examples for native fish). Thermal growth optima were estimated for all twelve fish species using the published equations of Jobling (1981).

Critical thermal maxima were available for three macroinvertebrates: the mudsnail *Potamopyrgus antipodarum*, the shrimp *Paratya curvirostris* and koura *Paranephrops planifrons* (Figure 9). Incipient lethal temperatures were available for eleven species of macroinvertebrate: mayflies (*Deleatidium*, *Zephlebia dentata*), caddis flies (*Aoteapsyche colonica*, *Pycnocentroides aureola*, *Pycnocentria evecta*), the beetle *Hydora*, snails (*P. antipodarum*, *Sphaerium novaezelandia*), the crustaceans (*P. curvirostris*, *Paracalliope fluviatilis*) and an oligochaete worm (*Lumbriculus variegatus*) (Figure 9).

A review of studies of geothermal springs yielded data on the maximum thermal limits for six beetles (Coleoptera), 15 true flies (Diptera), three bugs (Hemiptera), two damselflies (Zygoptera), one dragonfly (Anisoptera), one crustacean, six snails (Mollusca), two mites

(Acari), four worms (Annelida), one flatworm (Platyhelminthes), six blue-green algae (Cyanobacteria) and two green alga (Chlorophyta).

Water temperature interacts with a range of environmental factors, or influences the response of organisms to environmental factors. This includes effects on the density of water, dissolved oxygen, salinity, ultra-violet radiation and toxicants (ammonia, metals, PAHs). In addition, water temperature affects ecosystem functions and may have community-level effects. The latter may result from temperature effects on food availability, foraging efficiency, competitive interactions, predatory interactions, parasites and disease.

Managing the impacts of the thermal alteration of waterways requires a clear understanding of the scale, magnitude and nature of potential thermal impacts and the ecological values that the waterway supports. Management objectives may be based on acute or chronic thermal criteria, growth modelling, or species sensitivity distributions (SSDs) depending on the management objectives (biodiversity, population productivity, growth potential of individual species).

Acute (Table 14) and chronic (Table 15) thermal criteria were developed following the approach of Todd et al. (2008). It should be emphasised that these criteria are interim values based on the limited information currently available on the thermal tolerance of native species. The level of confidence in most of the values presented is low to moderate, particularly for chronic criteria as most thermal tolerance data collected in New Zealand has focused on the short-term lethal effects of high temperatures.

Based on these criteria, maximum temperatures in upland streams that are less than 20°C should protect even the most sensitive native taxa. In comparison, the most sensitive native taxa in lowland streams should be protected as long as maximum temperatures are less than 25°C.

More reliable thermal criteria could be calculated if estimates of UILT at a range of acclimation temperatures and T_{opt} were available for key species. There is also a need to explore ways of developing thermal criteria to protect aquatic communities (e.g. species sensitivity distributions) and ecosystems in addition to the use of single-species thermal criteria.

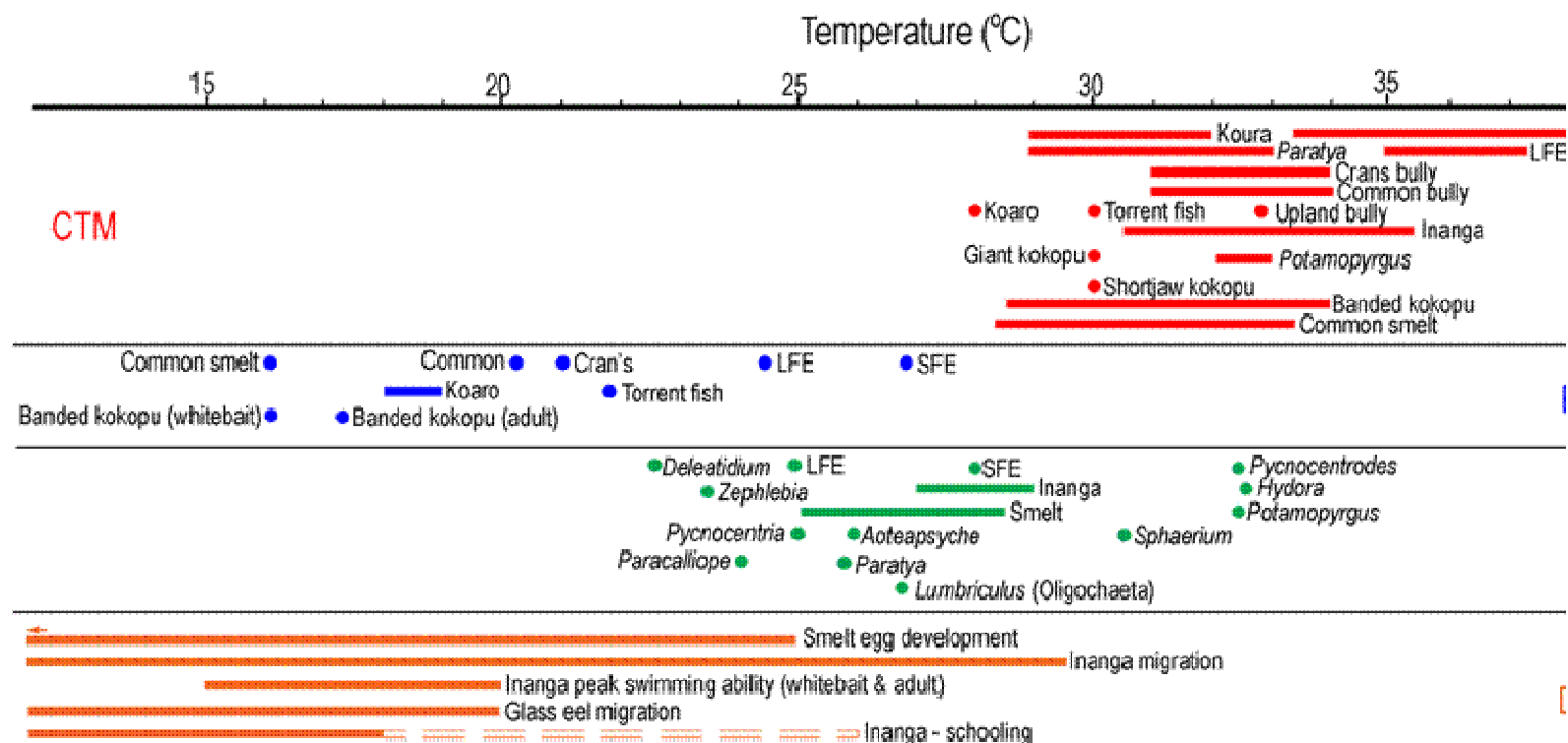


Figure 9

Summary of thermal tolerance of native fish and macroinvertebrates as expressed by critical thermal maxima (CTM - red), thermal preferences (blue), upper incipient lethal temperature (UILT – green) and behavioural and developmental effects (orange). Where CTM or UILT have been determined for multiple acclimation temperatures, the range is shown as a bar. Behavioural and developmental effects are shown as bars representing the range of temperatures when normal behaviour/development is apparent. Inanga schooling is dependent on acclimation temperature (for details see Table 3).

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10 Appendix 1 Glossary.

Term	Definition
Acclimation	A response by an animal that enables it to tolerate a change in a single variable (<i>e.g.</i> temperature). Commonly applied to animals held under laboratory conditions.
Acclimatisation	A reversible, adaptive response that enables an animal to tolerate environmental change involving changes in several variables
Behavioural thermoregulation	Control of an animal's body temperature by modifying the way in which it acts or where it resides.
Ectotherm	An animal that maintains its body temperature within fairly narrow limits by behavioural means (basking, seeking shade).
Eurytherm	A species with a wide range of thermal tolerance. Compare with the term, Stenotherm.
Final preferendum	The temperature at which acclimation and preferred temperature are equal.
Growth zone	The temperature range over which positive net growth occurs.
Growth maximum (T_{\max})	The maximum temperature at which positive net growth is observed.
Growth minimum (T_{\min})	The minimum temperature at which positive net growth is observed.
Growth optimum (T_{opt})	The temperature at which maximum growth is observed.
Incipient lethal temperature (ILT)	The incipient lethal temperature is usually defined as the temperature at which 50% mortality occurs in experiments conducted over a set period of time (usually seven days). Can be an upper (UILT) or lower incipient lethal temperature (LILT).
LILT	Lower incipient lethal temperature.
Poikilotherm	An animal whose body temperature varies according to the temperature of its surroundings.
Stenotherm	A species with a narrow range of thermal tolerance.
Stress zone	The temperature range over which thermal stress occurs and will ultimately kill the animal and the time until death is a function of exposure time to the thermal stress.
Tolerance zone	The thermal range over which the animal will survive for significant periods of time. The upper and lower limits of the tolerance zone are defined by the upper and lower incipient lethal temperatures.
T_{opt}	Temperature for optimal growth. This may be a range of temperatures where growth is maximal, in which case the upper limit of this range is the upper T_{opt} and the lower limit is the lower T_{opt} .
UILT	Upper incipient lethal temperature.
Ultimate lethal temperature	The temperature that results in the death of an organism within a short time period.
Ultimate upper incipient lethal temperature (UUILT)	The point at which the upper incipient lethal temperature no longer increases with acclimation temperature.
UUILT	Ultimate upper incipient lethal temperature.

11 Appendix 2 Temperature data

Table 16

Maximum monthly mean and minimum monthly mean water temperatures in rivers in Auckland, Waikato and Hawkes Bay Regions. NRWQN data sourced from the Water Quality Information System (WQIS) administered by NIWA (<https://secure.niwa.co.nz/wqis/index.do>). Data from Mosley (1982) were calculated from values in Appendix 2, summer maximum monthly mean was calculated as $T_{bar} + A$ and winter monthly minimum was calculated as $T_{bar} - A$.

Region	Site	Site name	Summer maximum	Winter minimum	Source
Auckland	AK1	Hoteo, Gubbs	21	10	NRWQN
Auckland	AK2	Rangitopuni R.	20	10	NRWQN
Waikato	HM1	Waipa, Otewa	18	9	NRWQN
Waikato	HM2	Waipa, Whatawhata	21	10	NRWQN
Waikato	HM3	Waikato, Hamilton	22	11	NRWQN
Waikato	HM4	Waikato, Rangiriri	22	11	NRWQN
Waikato	HM5	Waihou, Te Aroha	19	11	NRWQN
Waikato	HM6	Ohinemuri, Karangahake	21	10	NRWQN
Waikato	RO6	Waikato, Reids Farm	17	9	NRWQN
Waikato	TU2	Tongariro, Turangi	13	7	NRWQN
Hawkes Bay	HV1	Makaroro, Burnt Br.	16	6	NRWQN
Hawkes Bay	HV2	Tukituki, Red Bridge	22	10	NRWQN
Hawkes Bay	HV3	Ngaruroro, Chesterhope	22	9	NRWQN
Hawkes Bay	HV4	Ngaruroro, Chesterhope	17	5	NRWQN
Hawkes Bay	HV5	Mohaka, Ruapunga	21	8	NRWQN
Hawkes Bay	HV6	Mohaka, Glenfalls	17	6	NRWQN
Auckland	7811	Oteha, Days Bridge	20	10	Mosley (1982)
Auckland	43810	Maketu, Rimu Stand	22	11	Mosley (1982)
Auckland	45702	Waiwhiu, Dome Shadow	21	10	Mosley (1982)
Waikato	9228	Waiorongomai, Old Quarry	19	9	Mosley (1982)
Waikato	40703	Mangakowhai, Kaingapipi	16	12	Mosley (1982)
Waikato	43472	Waiotapu, Reporoa	23	13	Mosley (1982)
Waikato	1043428	Tahunaatara, Ohakuri Rd	17	9	Mosley (1982)
Waikato	1043434	Mangakara, Hirsts	17	10	Mosley (1982)
Waikato	1143444	Waikato, Reids Farm	19	11	Mosley (1982)
Waikato	1443434	Poutu, Dam Outlet	17	6	Mosley (1982)
Waikato	1043464	Poutu, footbridge	20	7	Mosley (1982)
Waikato	1043461	Tongariro, upper dam	14	5	Mosley (1982)
Waikato	1043466	Waihohonu, Desert Rd	10	6	Mosley (1982)
Hawkes Bay	21401	Wairoa, Marumaru	22	8	Mosley (1982)
Hawkes Bay	21409	Waiau, Otoi	19	7	Mosley (1982)
Hawkes Bay	21410	Waihi, Waihi	18	8	Mosley (1982)
Hawkes Bay	21601	Tahekenui, Glenstrae	24	8	Mosley (1982)
Hawkes Bay	21801	Mohaka, Raupunga	20	8	Mosley (1982)
Hawkes Bay	21803	Mohaka, Glenfalls	18	6	Mosley (1982)
Hawkes Bay	22501	Waikoau, Waikoau Rd	20	7	Mosley (1982)
Hawkes Bay	23001	Tutaekuri, Puketapu	22	11	Mosley (1982)
Hawkes Bay	23102	Ngaruroro, Fernhill	21	9	Mosley (1982)
Hawkes Bay	23103	Ngaruroro, Whana whana	19	8	Mosley (1982)

Region	Site	Site name	Summer maximum	Winter minimum	Source
Hawkes Bay	23104	Ngaruroro, Kuripapango	17	6	Mosley (1982)
Hawkes Bay	23106	Taruarau, Taihape Rd	17	6	Mosley (1982)
Hawkes Bay	23203	Tukituki, Red Bridge	23	9	Mosley (1982)
Hawkes Bay	23209	Otane, Glendon	21	8	Mosley (1982)
Hawkes Bay	23211	Waipawa, Waipawa	20	10	Mosley (1982)
Hawkes Bay	23219	Waipawa, Fletchers Crossing	19	7	Mosley (1982)
Hawkes Bay	23221	Mangatewai, SH50	20	7	Mosley (1982)
Hawkes Bay	23601	Waingongoro, Waimarama Rd	16	12	Mosley (1982)