

Impacts of global warming on New Zealand freshwater organisms: a preview and review

Patrick A. Ryan^{1,3} and Alan P. Ryan^{2,4}

¹Johnson & Wales University, 7150 Montview Boulevard, Denver, CO 80220, USA

²1 Featherstone Avenue, Kairaki Beach, Kaiapoi, New Zealand

³Author's email: pryan@jwu.edu (biological aspects)

⁴Author's email: cumin@ihug.co.nz (meteorological aspects)

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Abstract

Global warming is a reality and there is evidence that some New Zealand freshwaters have already increased by as much as 1.6 °C over a 17-year period. Temperature increases may cause a southwards retreat of vulnerable aquatic species in New Zealand as a 3 °C temperature increase will shift a derived degree day / latitude regression 670 km southward. Introduced salmonids, stream invertebrates and non-diadromous native fishes may be unable to make compensatory migrations and be extirpated from portions of their range. Diadromous galaxiids may be harmed by egg loss due to increased flood frequency. Existing evidence on genetic heterogeneity of stream insects is ambiguous but some species may have the genetic capacity to cope with increased temperatures. Maintenance or enhancement of riparian vegetation is likely to be important to keep adult stream insects within their temperature tolerance ranges. Higher CO₂ levels may result in reductions in nitrogen levels in leaves that fall into streams, thereby reducing food value to aquatic consumers. Higher temperatures may also produce faster growth rates but smaller adult size in some freshwater invertebrates. An increase in the frequency of extreme climatic events will have the capacity to alter aquatic community structure and higher temperatures may enhance the reproduction of parasites with consequent negative effects on their hosts. Furthermore, warmer stream temperatures could increase the possibility of aquarium escapees establishing in northern waters.

Keywords: Global warming – New Zealand – freshwaters – galaxiids – salmonids – stream invertebrates

Introduction

The idea that the atmosphere acts as a thermal blanket extending through its entire depth was first advanced formally

by Arrhenius (1896). The term 'global warming' is used in many different contexts, and for this reason is a frequent cause of confusion. In its most general sense, it refers to the influence of

greenhouse gases, mainly carbon dioxide, on the mean temperature of a planet. Without the greenhouse effect, the Earth's mean temperature would be about 35 °C colder than at present. As early as 1735 George Hadley (1735) realised that low latitudes were colder, and high latitudes warmer than expected, and that vertical and horizontal circulations effect the necessary transfers of latent and sensible heat. To account for these anomalies a series of ever more complex models of the ocean-atmosphere system has been developed (general circulation models - GCMs).

The general circulation of our planet is not immutable - its features change as planetary mean temperature varies. When temperatures are low, as in glaciations, the flow is generally zonal - that is, predominantly on an east-west axis. During warm periods, as at present, there are more meridional components.

Because the thermal capacity of the atmosphere is insignificant compared with that of the oceans, oceanic warming is essentially irreversible. Oceanic temperatures also affect the general circulation in other ways. The main one is the El Niño Southern Oscillation (ENSO), which affects weather over much of Earth and which has a cyclic but irregular fluctuation. El Niño occurs when the sea temperature is above normal off the coast of Peru, and La Niña occurs when it is below normal. El Niño and La Niña may persist for a few months to a few years, and they force large-scale changes in the global circulation. Global warming tends to lock ENSO in the El Niño mode, which results in mainly zonal flow with prevailing westerlies in New Zealand. In New Zealand these westerlies may bring with them increased rain on the west coasts. Other factors that may

affect the general circulation, include the Interdecadal Pacific Oscillation, which exists on a timescale of decades, and is independent of ENSO. Its effects are seen mainly in the distribution of precipitation.

The geographical distribution of global warming temperature change is not uniform and some places may even become cooler. Global warming deniers seize on this fact and attempt to use it out of context to support their arguments. Furthermore, an expected consequence of warming is an increase in the frequency of extreme events such as floods, droughts and temperature extremes, because of increased meridional flow components. Warming therefore helps to explain why events that have been regarded as very rare – ‘once in a century events’ – are now more commonplace. Projections of climate change in New Zealand by NIWA (cited in Ministry for the Environment 2004) indicate it will become drier in the east, and wetter in the west than at present. These changes, wetter in the west, drier in the east, higher temperatures, and more frequent extreme events will have impacts on our freshwaters. None of these impacts are precisely predictable but most will be perceived as negative. Mohseni *et al.* (2003) showed that there is a linear relationship between air temperature and stream temperature up to about 25 °C, but at higher air temperatures, stream water temperatures level off due to evaporative cooling. Scarsbrook (2006) found that New Zealand's coolest rivers (5th percentile water temperature) have shown a warming trend of 1.6 °C over the 17 years from 1989 to 2005. This appears to be the only medium-term study on New Zealand stream temperatures.

McDowall (1992), in his wide-ranging

discussion of potential consequences of global climate change on New Zealand freshwaters, made the very valid point that compared with other, more direct human impacts, its effects may be less than those induced over the past century by deforestation. He also noted that "we need to consider and understand impacts at the individual, population, species and community, and ecosystem levels". The remainder of this paper is devoted to discussing these impacts identified in the 14 years since publication of McDowall's (1992) paper.

Response to global warming at the cellular level

Heat shock proteins and enzymes

Heat shock proteins (hsps) are part of a family of molecular chaperones that assist in the proper folding and, ultimately, maturation of other proteins. Compartmentalisation occurs when hsps attach to exposed sites on partially denatured proteins and prevent their aggregation while affording an opportunity for restoration to the original protein conformation (Somero & Hofman 1996). Partial or total denaturation can occur in response to stressors other than heat, such as oxygen deprivation, exposure to pesticides, heavy metals or osmotic stress. The interactions between these factors and possible synergistic effects are currently unknown. Increased environmental temperatures will reduce oxygen availability to some stream organisms and may also lead to an increase in hsp production.

Heat stress may lead to irreversible denaturation of proteins. To avoid build up of ineffective protein and to release amino acids for recycling, irreversibly denatured proteins are tagged with the

protein ubiquitin; this leads to proteolysis by non-lysosomal proteases. The accumulation of ubiquitinated proteins can provide an index of irreversibly denatured proteins (Somero & Hofman 1996). Either partial or complete denaturation may lead to high energy costs as protein synthesis accounts for 20-30% of cellular ATP usage in a cell at rest. In particular, the synthesis of hsps is costly and the refolding of a damaged protein may require hundreds of ATP equivalents (Parsell & Lindquist 1993).

An increase in environmental temperature beyond an organism's normal range can therefore invoke a substantial energy cost. Stenothermal organisms may be more at risk than eurythermal organisms, and because most freshwater organisms are typically subject to a smaller range of temperatures than many terrestrial organisms they may be more at risk. Increased energy costs are one consequence, denaturation of proteins is another.

By their very nature, enzymes are required to be both stable and flexible, however an increase in thermal stability may lead to a loss of flexibility and hence function. Powers *et al.* (1993) showed that differences in enzyme stability in killifish (*Fundulus heteroclitus*) from different latitudes were the result of a single amino acid substitution (serine for alanine in a 330 residue allozyme). Somero & Hofman (1996) argued that if such a small change is required to adapt to increased temperature then the rate of protein evolution in response to thermal stress could be rapid. However, they cautioned that eurytherms may be better able to adapt to global warming because they already possess isoenzymes with different thermal optima and have better ability to restructure membrane systems

when faced with temperature increases. At temperatures just above the physiological range, membranes become disordered, and may no longer possess barrier properties. Even moderate warming (2-4 °C) is likely to have an impact on membrane structure and function (Robertson & Hazel 1996). One membrane response to elevated temperature is to raise cholesterol levels (Crockett 1998) although other mechanisms may also be involved.

Response to global warming at the organism level

Sweeney *et al.* (1992) discussed the potential impact on aquatic insects of a predicted 4 °C increase in stream temperature in eastern North America. While 4 °C is undoubtedly too high to be applied to New Zealand in the short term, the conclusions drawn by the authors are relevant. In North America, a

4 °C temperature increase displaces the degree day regression 680 km northward. Plotting a similar scenario for New Zealand (a 3 °C stream temperature increase) shifts the degree day recession 670 km southward (Figure 1).

Direct responses by organisms to increases in temperature will depend upon a variety of factors, some of which may be currently unknown. Many, such as upper thermal limits and oxygen requirements, should be relatively easy to determine, but the speed of evolutionary response to global warming may not. Hutchinson's (1957) concept of the niche as a multidimensional hypervolume is useful here, since global warming will change the hypervolume. Thus, some current dimensions will protrude beyond the new space, whereas others will not reach it. Some species will have sufficient genetic plasticity, or a high enough rate of evolutionary change to cope with the changes. Others will not. Currently,

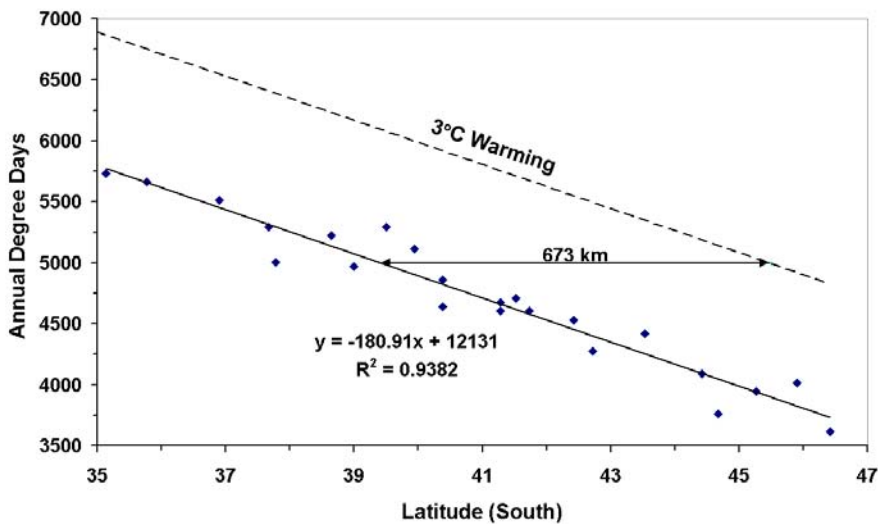


Figure 1. Linear regression between latitude of various New Zealand meteorological stations and their annual degree days (solid line). The dashed line shows the relationship if a 3 °C warming occurs. This degree of warming displaces the regression about 670 km southwards. Data were obtained from NIWA (<http://www.niwascience.co.nz/edu/resources/climate/meanairtemp/>). Sites above 125 m asl were excluded. Graph inspired by Fig 7.1 in Sweeney *et al.* (1992).

organisms occupy a realised niche, which in part is the result of inter-specific interactions, but their fundamental niches, the places they could inhabit in the absence of competition, are unknown. Sweeney *et al.* (1992) attempted to address the hypervolume concept two-dimensionally. Their representation postulates a set of environmental requirements each represented by a vector within a current "envelope of resources" (Figure 2). The broken curve in their figure represents the new envelope resulting from global warming, and where vectors puncture the new envelope, fitness may be reduced.

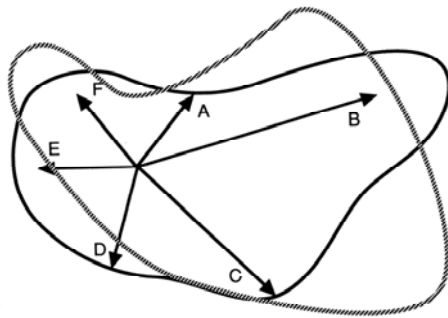


Figure 2. The hypothetical relationships between environmental requirement vectors (A-F) and the envelope of resources currently available (solid perimeter) and following global warming (shaded perimeter). From Sweeney *et al.* (1992).

While this theoretical construct is easy to grasp, research elucidating actual interactions is not. Sweeney *et al.* (1992) analysed the life histories and geographical distributions of six species of univoltine mayflies from streams in the deciduous forest biome of eastern North America and found that genetic diversity in four of the species decreased with an increase in latitude. The authors speculated that as temperature increases, some species may

not have the requisite genes to cope. However, average temperature over the 60 day period of maximum larval growth prior to adult emergence of one species, *Ephemerella septentrionalis*, varied very little regardless of geographic location (Figure 3), and adults appeared when stream temperature averaged 14-16 °C. If a rather specific average temperature is required during the 60 days prior to emergence, warming will interfere with this, and if extrapolated to New Zealand would shift many species' distributions southwards.

Dissolved oxygen concentration decreases as water temperature rises, but at the same time an organism's metabolic demands increase. Some stream insects are able to increase oxygen uptake through behavioural mechanisms of various kinds (Eriksen *et al.* 1984) such as ventilatory movements, but this also increases metabolic rate, which necessitates more oxygen. Species living close to their dissolved oxygen limits may seek more highly oxygenated water, but if they are unable to do so they will be eliminated. Meyer & Pulliam (1992) also suggested that changes in riparian inundation patterns would affect biogeochemical processes alongside streams and rivers and alter the exchange of elements between them and their flood plains. If flood plains become drier, saturated zones next to the channel and in the hyporheic zone may become depleted in oxygen as the movement of water through them slows with consequent negative impacts on aerobic organisms. Such a scenario could apply to streams and rivers in the east of New Zealand as the climate warms.

In an innovative study, Hogg & Williams (1996) divided the 60 m long channel of a stream in southern Ontario

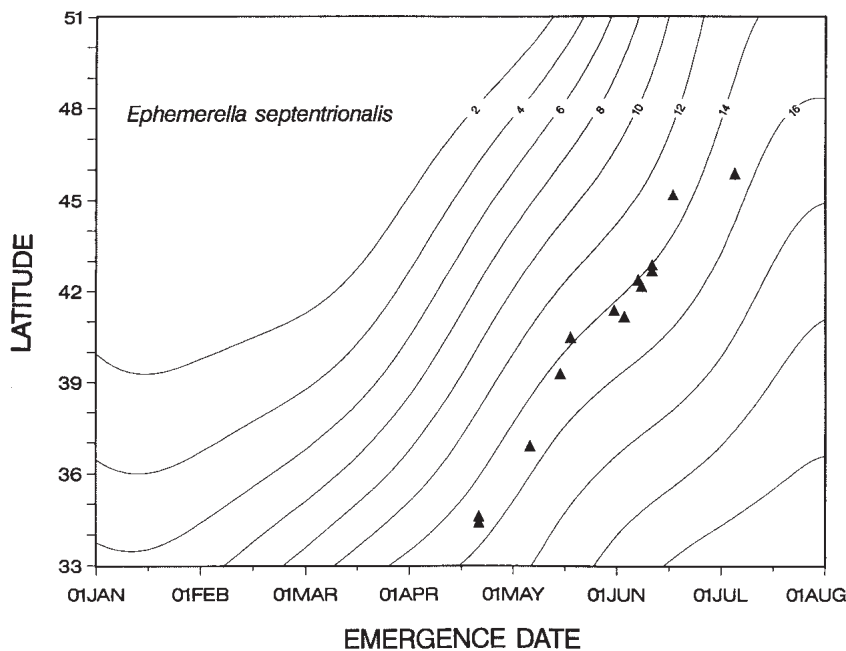


Figure 3. Date of first adult emergence (triangles) for various geographic populations of *Ephemera septentrionalis* superimposed on isothermal lines showing the date that a given temperature is reached in streams throughout its geographic range. Isotherms created from 50 sites in the eastern United States. From Sweeney *et al.* 1992).

with a galvanized metal strip set 15 cm into the substrate and rising 6 cm above the water surface. A propane water heater was used to increase the temperature in one half of the channel by 2 °C in spring, summer and autumn and by 3.5 °C in winter. The authors collected data for one year prior to manipulation and for two years during the manipulation. Their results revealed a reduction in total animal density in the warmer channel, as well as reduced size at maturity and faster development of their three main study species, an amphipod, a caddisfly and a stonefly. Hogg & Williams (1996) cautioned that “changes in life history parameters such as size at maturity, timing of emergence, and adult sex ratio are likely to be more sensitive indicators of small, gradual shifts in environmental temperature (e.g., global warming) than

are changes in taxon composition, species richness, community biomass, or densities of individual taxa”.

In the upper Rhône River, France, water temperature rose on average by 1.5 °C between 1979 and 1999 and several changes in faunal distribution patterns were noted by Daufresne *et al.* (2003). Thus, both thermophilic fish and invertebrate taxa that were found initially downstream, progressively replaced more northern species of cold-water fish and invertebrates upstream. However, confounding factors included the building of several dams and a nuclear power plant!

Like streams, lakes may also face increases in temperature and have been found already in Loch Leven (Scotland) where a 1 °C increase in annual mean temperature was reported in the 34 years up to 2001 (Carvalho & Kirika 2003).

The major impacts of global warming on lakes appear to be associated with either eutrophication or oxygen depletion in the hypolimnion (Kumagai *et al.* 2003). Schindler (2001) recorded an increase in evaporation of 30% in lakes of the Experimental Lakes Area in north-western Ontario when average annual air temperature increased from 14 °C to 16 °C. He also noted that some permanent first order streams might become ephemeral, and result in a reduction in inflows to lakes even if precipitation remained the same. Microcosm studies by Moss *et al.* (2003) showed that warming had a smaller impact on phytoplankton populations than either eutrophication or the addition of sticklebacks (*Gasterosteus aculeatus*), but a predicted shift towards cyanophytes at the expense of macrophytes did not occur, perhaps because their small (2 m diameter) experimental microcosms reduced the ability of wind to bring sediment into suspension. Finally, Briand *et al.* (2004) suggested that the invasion of temperate European lakes by a toxic, bloom-forming cyanobacterium *Cylindrospermopsis raciborskii* stemmed from its ability to tolerate a wide range of climatic conditions and from global warming, which is resulting in more favourable conditions for its growth.

New Zealand

Few freshwater research projects have aimed specifically at understanding the effects of global warming in New Zealand, although the Ministry for the Environment (2004) has been highly proactive in other global warming areas. Typically, freshwater research has explored environmental factors other than global warming and alluded to the latter only in

passing. Therefore, many of McDowall's (1992) concerns about the extent of our knowledge remain.

Fittingly, McDowall (2004) took up at least one of the challenges by examining the threats posed by introduced aquarium fish to our freshwater ecosystems. He noted that the Ministry of Agriculture and Fisheries (MAF), which is responsible for the control of the importation of aquarium fish, had approved around 280 names; 178 of which were genera, one, *Barbus* containing over 820 species! Until now, releases of aquarium fish from captivity have involved species that can only survive in geothermal waters. This may not be the case in the future if our freshwaters warm up by several degrees. In its home environment, the realized niche of a species is strongly restricted by predators, pathogens and parasites, but once released in a new place it may be free to realise more of its fundamental niche. A species may also bring new diseases. For example, McDowall (2004) noted that grass carp (*Ctenopharyngodon idella*) brought six diseases to New Zealand and required careful quarantine to ensure they did not become established. It is unlikely that the aquarium trade would be so scrupulous.

In a review of experimental studies Poulin (2006) found that by increasing water temperature by 10 °C, the output of trematode cercariae from snails increased almost eight fold; an increase much greater than that typically found over this temperature range (2-3 times) for physiological processes. He also noted that the small increases in air and water temperatures forecast by climate models may influence the geographic distribution of some diseases and could promote the proliferation of their infective stages in many ecosystems.

Invertebrates

Smith & Collier (2005) investigated the effects of temperature on the adult stages of three aquatic insect species under controlled laboratory conditions and found that contrary to conventional wisdom the stonefly they examined (*Zelandoperla decorata*) was able to withstand considerably higher temperatures than either a caddisfly (*Hydrobiosis parumbripennis*), or a mayfly (*Acanthophlebia cruentata*). Smith & Collier (2005) concluded that flight times and microclimate were important factors determining the air temperature that flying adults could tolerate. *Zelandoperla decorata* typically flew during the afternoon when air temperatures were highest, whereas *A. cruentata* experienced high mortality as temperature rose above 24 °C. Davies-Colley *et al.* (2000) suggested that New Zealand stream and riparian biota may have evolved in contiguous native forest, and that subsequent habitat alteration by Polynesian and European colonisers may have reduced the extent of riparian zones and changed their microclimates. Smith & Collier (2005) therefore recommended planting or controlling streamside vegetation to manage microclimates for adult aquatic insects. The implications of this scenario for dispersal beyond local forested catchments are clear.

The genetic structure of aquatic insect populations, and by implication their potential to adjust to climatic change, has also been considered by a number of New Zealand biologists. Hogg *et al.* (2002) examined allozyme variation in populations of *Archichauliodes diversus* (Megaloptera) and *Coloburiscus humeralis* (Ephemeroptera), and although they found little differentiation in the latter,

three genetically distinct groups were identified in *A. diversus*. These findings were interpreted to mean that *C. humeralis* is a strong disperser, but that *A. diversus* is not. Alternatively, the lack of differentiation amongst *C. humeralis* populations may be a lingering effect of small founder populations (Boileau *et al.* 1992), and the very low heterozygosity of its northern populations suggested that facultative parthenogenesis may occur at the periphery of its range (Hogg *et al.* 2002). This low genetic diversity may put these populations at risk if they lack genes to cope with the increased temperatures that characterise global warming. Research on the genetic diversity of a stream-dwelling caddisfly *Orthopsyche fimbriata* (Smith *et al.* 2006a) and a mayfly, *Acanthophlebia cruentata* (Smith *et al.* 2006b) using mitochondrial DNA markers, also provided equivocal results. The caddisfly exhibited low haplotype diversity in Northland and none at some central North Island sites, whereas the mayfly had low diversity at some central sites and higher diversity elsewhere. Neither study enabled firm conclusions to be made regarding the isolation of populations, or the dispersal of adults. An important point made by the authors was that although the occurrence of significant genetic variation among populations may imply little or no contemporary gene flow, the converse, lack of genetic differentiation, does not necessarily imply extensive adult dispersal and gene flow.

Results of the above studies do not enable us to make firm predictions about the impact of global warming on dispersal of adult aquatic insects in New Zealand, or on the likelihood that their distributions will change in response to global warming. However, it is possible

that habitat loss may restrict winged adults from colonising streams that are not part of their immediate catchment and so limit long-range dispersal. Furthermore, as the stream insects studied so far had low heterozygosity in the far north, it is plausible that increasing stream and air temperatures could lead to a southward retraction of their ranges.

One of the predicted impacts of climate change on New Zealand is an increase in the frequency and severity of extreme climatic events that can be expected to affect aquatic communities. Long periods of low flow in the nutrient-enriched Waipara River, North Canterbury, led to successional changes in periphyton composition over summer (from diatoms and cyanobacteria to filamentous green algae; Suren *et al.* 2003a), and also changes to the invertebrate community that reflected the increase in filamentous green algae and were strongly correlated with the number of days at low flow (Suren *et al.* 2003b). The authors cautioned that further abstraction of water from already enriched streams may lead to management problems, and that changes to aquatic populations on the east of the country and in other areas of low precipitation may be related more strongly to reductions in flow rate than to temperature increases *per se*.

Floods can also be consequences of extreme climatic events and although their effects on stream and river faunas are well known (e.g., Scrimgeour & Winterbourn 1989; Scarsbrook 2002), an increase in their frequency and severity could lead to a simplification of communities. Thus, Collier & Quinn (2003) found that numbers of taxa and invertebrate densities in small Waikato streams took 5-7 months to recover to pre-flood levels after a 1 in 28 year flood. Suren & Jowett

(2006) also found that invertebrate density decreased more commonly after floods than after low flows in the Waipara River, and that the degree of faunal change was proportional to flood magnitude.

Other studies outside New Zealand have shown that increasing atmospheric carbon dioxide levels can bring about a reduction in the amount of nitrogen in tree leaves (Fajer *et al.* 1989; Berryman *et al.* 1993) and consequently reduced growth rates of their insect herbivores (Fajer *et al.* 1989). The dead leaves that fall into streams are important food resources for many stream invertebrates and their quality as measured by nitrogen or protein content and other chemical factors can be expected to affect their growth (Anderson & Cargill 1987). Sweeney *et al.* (1992) compared growth and survivorship of the mayfly *Leptophlebia cupida* fed leaves of three native and three introduced plant species and found that although growth rate was not related to the geographic origin of the plants, survivorship of larvae was much greater when fed the three native species. If the composition of riparian vegetation changes as a result of different flow regimes or an increase in temperature, leaf inputs may be altered in both quality and quantity with implications for the fauna, including possible local extinction through sub-lethal changes in life history traits (Sweeney *et al.* 1992).

Fish

Very few studies have considered the impacts of global warming on New Zealand freshwater fish communities. McDowall (1992) noted that an “[u]nderstanding of what controls the distribution and abundance of New Zealand freshwater fish species, of the composition and interactions of species

within freshwater communities and ecosystems and of the way ecosystems function is very limited.”

Nevertheless, there is an increasingly large literature on the thermal niches of fishes (Magnuson & Destasio 1996), especially in countries where freshwater fish represent a huge recreational and food resource. In Japan, Nakano *et al.* (1996) hypothesised that an 80% range reduction in Dolly Varden (*Salvelinus malma*) and a 34% range reduction in white-spotted charr (*S. leucomaenis*) would be the result of a 3 °C increase in mean annual air temperature. Similarly, in the United States several studies have predicted substantial range changes in cold-water fishes. For example, Keleher & Rahel (1996) predicted a 59.8% reduction in salmonid habitat with a 3 °C increase in mean July air temperature. More ambitiously, Mohseni *et al.* (2003) modelled the impacts of a doubling of atmospheric carbon dioxide on the habitats of 57 fish species in the contiguous United States based on records from 764 stream gauging stations. Their study expanded on an earlier one by Eaton & Scheller (1996) but used different stream temperature / air temperature relationship assumptions and concluded that suitable habitat for cold water fishes would decrease by 36% and that for cool water fishes by 15%. In contrast, habitat for warm water fishes was predicted to increase by 31%. The authors stressed that actual distributions of particular fish species are highly dependent on both their minimum and maximum temperature tolerances and because these are not all known the predicted changes must be accepted, cautiously.

In New Zealand, Boubee *et al.* (1991) studied the impact of acclimation temperature and preferred temperature in

a laboratory study of the inanga (*Galaxias maculatus*) and found that fish acclimated to 15 °C exhibited total avoidance of 29.5 °C water. In contrast, fish acclimated to 20 °C showed total avoidance of 31.5 °C water, just below the upper thermal maximum of around 33 °C (Simons, 1986). More recently, Bannon (2006) subjected rainbow trout parr and inanga of different life stages to elevated temperatures and reduced oxygen saturation while they were swimming. He demonstrated significant thermal sensitivity (as measured by swimming speed) as fish underwent metamorphosis from larvae to juveniles and suggested that elevated water temperature could significantly limit fish migration. The optimal upstream migration temperature for glass eels of both shortfin eels (*Anguilla australis*) and longfin eels (*A. dieffenbachii*) in the Tukituki River, Hawkes Bay was only 16.5 °C and when water temperature reached 22 °C, migration was almost completely suppressed (August & Hicks in press).

The distributions of salmonids in New Zealand may also be affected by temperature and McDowall (1992) suggested that the northern limits of trout may be reduced because of their low upper temperature tolerances for both spawning and egg development in winter. Thus, the northern limits for brown trout (*Salmo trutta*), could shift south to the Nelson area, whereas those for rainbow trout (*Oncorhynchus mykiss*) might be around Palmerston North (Glova 1990: cited in McDowall 1992). If so, the world-renowned Rotorua-Taupo fishery would be eliminated, good news perhaps for native fish species, which may be less affected.

New Zealand freshwater fish species are generally more eurythermal than trout and

their behavioural responses to warming may include moving to higher elevations and seeking cold refuges such as springs, ground water and forest streams (McDowall 1992). In some instances, warming might bring about a southward shift of distributions as in the salmonid species, but for non-diadromous species this could be difficult as the general east-west flow of New Zealand river systems may restrict fish to particular catchments (McDowall 1992).

Other impacts of global warming on New Zealand freshwater fish will include exposure to more extreme events. Increased flooding may scour out benthos and remove food sources for stream insects fed on by fish, and increased turbidity will reduce the field of vision for predatory fish that rely on vision to capture prey. In reviewing the impacts of suspended sediments on New Zealand stream biota Ryan (1991) noted that most of their impacts were negative. Richardson *et al.* (2001) showed that migrating juvenile kokopu (*Galaxias fasciatus*) avoid streams with turbidity higher than 25 NTU and Charteris *et al.* (2003) suggested that changes in the timing, frequency and magnitude of floods as a result of global warming may threaten the reproductive cues used by those diadromous galaxiid fishes that deposit eggs at stream margins during flood events. One consequence could be that more frequent flooding will remove eggs before their development is complete. Reduced rainfall on the eastern side of the country will also bring potential difficulties for native fish. Because dissolved oxygen decreases as temperature increases, fish could die from hypoxia, and the already threatened Canterbury mudfish (*Neochanna burrowsius*) is likely to lose more habitat as wetlands dry out (McDowall 1992).

Political Climate

New Zealand produces more than its fair share of greenhouse gases and seems little inclined to address the problem. It appears likely that global warming will have an impact on our climate with a flow on effect (pun unintended) on our freshwaters. At a time when the Government is running record surpluses, little is being put back into basic research. The attitude seems to be that because New Zealand is so small and produces so few anthropogenic greenhouse gases, there is no cause for concern. For the country that was the first to give women the vote, and declared itself nuclear free, this is appalling. New Zealand has a low population density and potentially an abundance of clean power. Instead of adopting a "wait and see" attitude, New Zealand should be aggressively researching and addressing the situation.

Conclusions

Regardless of the magnitude of climate change in New Zealand there will be impacts on our freshwater organisms and ecosystems. Under best-case scenarios the changes may be almost undetectable when compared with other more direct river and stream modifications. However, if climate change is at the upper end predicted by various models, changes in streams could be profound. Organisms unable to disperse to cooler areas or adapt to higher temperatures will be extirpated from parts of their current range. The requirement for enzymes to be both flexible and heat resistant may make heat adaptation difficult. For some animals, such as introduced salmonids, there may be a substantial shrinkage in their current range. Extreme weather events will occur

with increasing frequency and will increase stress on stream communities. Both drought and flood may change community composition.

Other impacts could include higher parasite loads, allochthonous plant material with lower nutritional values, increases in the metabolic rates of animals, earlier maturity of stream invertebrates at a smaller size, and a reduction in genetic diversity as populations become more isolated from each other. Some galaxiid fishes may face problems with egg security due to increased flood frequency. Others may encounter stream temperatures too high for successful upstream migration, a problem also faced by young glass eels. Furthermore, higher water temperatures will increase metabolic rates and lower concentrations of dissolved oxygen. To better understand this complex and increasingly pertinent subject, much more focussed research is required. If New Zealand is to research its own unique problems, increased government funding will be needed urgently.

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References

- Anderson, N.H. & Cargill, A.S. (1987). Nutritional ecology of aquatic detritivorous insects. In *Nutritional Ecology of Insects, Mites, and Spiders* (eds. Slansky, F. & Rodriguez, J.G.), pp 903-925, John Wiley, New York.
- Arrhenius, S. (1896). On the influence of carbonic acid in the air upon the temperature of the ground. *The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science* 41: 237-275.
- August, S.M. & Hicks, B.J. (in press). Water temperature and upstream migration of glass eels in New Zealand: implications of climate change. *Environmental Biology of Fishes*.
- Bannon, H.J. (2006). Effects of water quality parameters on prolonged swimming ability of freshwater fishes. Unpublished Ph.D. thesis, University of Waikato.
- Berryman, C.A., Eamus, D. & Duff, G.A. (1993). The Influence of CO₂ enrichment on growth, nutrient content and biomass allocation of *Maranthus corymbosa*. *Australian Journal of Botany* 41: 195-209.
- Boileau, M.G., Hebert, P. D. N. & Schwartz, S.S. (1992). Non-equilibrium gene frequency divergence: persistent founder effects in natural populations. *Journal of Evolutionary Biology* 5: 25-29.
- Boubee, J.A., Schicker, K.P. & Stancliff, A.G. (1991). Thermal avoidance in inanga, *Galaxias maculatus* (Jenyns), from the Waikato River, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 25: 111-180.
- Briand, J.F., Leboulanger, C., Humbert, J., Bernard, C. & Dufour, P. (2004). *Cylindrospermopsis raciborskii*

- (Cyanobacteria) invasion at mid-latitudes: selection, wide physiological tolerance, or global warming? *Journal of Phycology* 40: 231-238.
- Carvalho, L. & Kirika, A. (2003). Changes in shallow lake functioning: response to climate change and nutrient reduction. *Hydrobiologia* 506: 789-796.
- Charteris, S.C., Allibone, R.M. & Death, R.G. (2003). Spawning site selection, egg development, and larval drift of *Galaxias postvectis* and *G. fasciatus* in a New Zealand stream. *New Zealand Journal of Marine and Freshwater Research* 37: 493-505.
- Collier, K.J. & Quinn, J.M. (2003). Land-use influences macroinvertebrate community response following a pulse disturbance. *Freshwater Biology* 48: 1462-1481.
- Crockett, E.L. (1998). Cholesterol function in plasma membranes from ectotherms: membrane-specific roles in adaptation to temperature. *American Zoologist* 38: 291-304.
- Daufresne, M., Roger, M.C., Capra, H., & Lamouroux, N. (2003). Long-term changes within the invertebrate and fish communities of the Upper Rhône River: effects of climatic factors. *Global Change Biology* 10: 124-140.
- Davies-Colley, R.J., Payne, G.W. & van Elswijk, M. (2000). Microclimate gradients across a forest edge. *New Zealand Journal of Ecology* 24: 111-121.
- Eaton, J.G., & Scheller, R.M. (1996). Effects of climate warming on fish thermal habitat in streams of the United States. *Limnology and Oceanography* 41: 1109-1115.
- Eriksen, C.H., Resh, V.H., Balling, S.S. & Lamberti, G.A. (1984). Aquatic insect respiration. In *An Introduction to the Aquatic Insects of North America* (eds. Merritt, R.W. & Cummins, K.W.), pp 27-37, Kendall/Hunt, Dubuque.
- Fajer, E.D., Bowers, M.D. & Bazzaz, F.A. (1989). The effects of enriched carbon dioxide atmospheres on plant-insect herbivore interactions. *Science* 243: 1198-1200.
- Glova, G.J. (1990). Freshwater fisheries. In *Climate Change: Impacts on New Zealand - Implications for the Environment, Economy and Society*, pp 78-80, Ministry for the Environment, Wellington.
- Hadley, G. (1735). Concerning the cause of the general trade-winds," *Philosophical Transactions of the Royal Society of London* 39: 58-62.
- Hogg, I.D. & Williams, D.D. (1996). Response of stream invertebrates to a global-warming thermal regime: an ecosystem-level manipulation. *Ecology* 77: 395-407.
- Hogg, I.D., Willman-Huerner, P. & Stevens, M.I. (2002). Population genetic structures of two New Zealand stream insects: *Archichauliodes diversus* (Megaloptera) and *Coloburiscus humeralis* (Ephemeroptera). *New Zealand Journal of Marine and Freshwater Research* 36: 491-501.
- Hutchinson, G.E. (1957). Concluding remarks. *Cold Spring Harbour Symposium on Quantitative Biology* 22: 415-427.
- Keleher, C.J. & Rahel, F.J. (1996). Thermal limits to salmonid distributions in the Rocky Mountain region and potential habitat loss due to global warming: a Geographic Information System (GIS) approach. *Transactions of the American Fisheries Society* 125: 1-13.
- Kumagai, M, Ishikawa, K. & Ishiguro, N. (2003). Impacts of global warming

- on large lakes. In *Water Resources Systems - Water Availability and Global Change* (eds. Franks, S., Blöschl, G., Kumagai, M., Musiaka, K. & Rosbjerg, D.), pp 65-69, IAHS Publication 280.
- Magnuson, J.J. & Destasio, B.T. (1996). Thermal niche of fishes and global warming. In *Global Warming: Implications for Freshwater and Marine Fish* (eds. Wood, C.M. & McDonald, D.G.), pp 377-408, Society for Experimental Biology Seminar Series 61, Cambridge University Press, Cambridge.
- McDowall, R.M. (1992). Global climate change and fish and fisheries: what might happen in a temperate oceanic archipelago like New Zealand. *GeoJournal* 28: 29-37.
- McDowall, R.M. (2004). Shoot first and then ask questions: a look at aquarium fish imports and invasiveness in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 38: 503-510.
- Meyer, J.L. & Pulliam, W.M. (1992). Modification of terrestrial-aquatic interactions by a changing climate. In *Global Climate Change and Freshwater Ecosystems* (eds. Firth, P. & Fisher, S.G.), pp 177-191, Springer-Verlag, New York.
- Ministry for the Environment (2004). *Climate change effects and impacts assessment: a guidance manual for local government in New Zealand*. New Zealand Climate Change Office, Ministry for the Environment, Wellington.
- Mohseni, O., Stefan, H.G. & Eaton, J.G. (2003). Global warming and potential changes in fish habitat in U.S. streams. *Climatic Change* 59: 389-409.
- Moss, B., McKee, D., Atkinson, D., Collings, S.E., Eaton, J.W., Gill, A.B., Harvey, I., Hatton, K., Heyes, T. & Wilson, D. (2003). How important is climate? Effects of warming, nutrient addition and fish on phytoplankton in shallow lake microcosms. *Journal of Applied Ecology* 40: 782-792.
- Nakano, S., Kitano, E. & Maekawa, K. (1996). Potential fragmentation and loss of thermal habitats for charrs in the Japanese archipelago due to climatic warming. *Freshwater Biology* 36: 711-722.
- Parsell, D.A. & Lindquist, S. (1993). The function of heat-shock proteins in stress tolerance: degradation and reactivation of damaged proteins. *Annual Review of Genetics* 27: 437-496.
- Powers, D.A. Smith, M., Gonzalez-Villasenor, I. DiMichele, L., Crawford, D., Bernadi, G. & Lauerman, T. (1993). A multidisciplinary approach to the selection/neutralist controversy using the model teleost, *Fundulus heteroclitus*. In *Oxford Surveys in Evolutionary Biology* 19 (eds. Futuyma, D. & Antonovics, J.), pp 43-107, Oxford University Press, Oxford.
- Poulin, R. (2006). Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. *Parasitology* 132: 143-151.
- Richardson, J., Rowe, D.K. & Smith, J.P. (2001). Effects of turbidity on the migration of juvenile banded kokopu (*Galaxias fasciatus*) in a natural stream. *New Zealand Journal of Marine and Freshwater Research* 35: 191-196.
- Robertson, J.C. & Hazel, J.R. (1996). Membrane constraints to physiological function at different temperatures: does cholesterol stabilize membranes at elevated temperatures? In *Global Warming: Implications for Freshwater and Marine Fish* (eds. Wood, C.M. &

- McDonald, D.G.), pp 25-49, Society for Experimental Biology Seminar Series 61, Cambridge University Press, Cambridge.
- Ryan, P.A. (1991). Environmental effects of sediment on New Zealand streams: a review. *New Zealand Journal of Marine and Freshwater Research* 25: 207-221.
- Scarsbrook, M.R. (2002). Persistence and stability of lotic invertebrate communities in New Zealand. *Freshwater Biology* 47: 417-431.
- Scarsbrook, M.R. (2006). *State and trends in the national river water quality network (1989-2005)*. Ministry for the Environment, Wellington.
- Schindler, D.W. (2001). The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 18-29.
- Scrimgeour, G.J. & Winterbourn, M.J. (1989). Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. *Hydrobiologia* 171: 33-44.
- Simons, M.J. (1986). *Effects of elevated temperatures on three migratory fish from the Waikato River*. WaikatoValley Authority technical report 40.
- Smith, B.J. & Collier, K.J. (2005). Tolerances to diurnally varying temperature for three species of adult aquatic insects from New Zealand. *Environmental Entomology* 34: 748-754.
- Smith, P.J., McVeagh, S.M. & Collier, K.J. (2006a). Genetic diversity and historical population structure in the New Zealand mayfly *Acanthophlebia cruentata*. *Freshwater Biology* 51: 12-24.
- Smith, P.J., McVeagh, S.M. & Collier, K.J. (2006b). Population-genetic structure in the New Zealand caddisfly *Orthopsyche fimbriata* revealed with mitochondrial DNA. *New Zealand Journal of Marine and Freshwater Research* 40: 141-148.
- Somero, G.N. & Hofman, G. (1996). Temperature thresholds for protein adaptation: when does temperature change start to "hurt"? In *Global warming: Implications for Freshwater and Marine Fish* (eds. Wood, C.M. & McDonald, D.G), pp 1-24, Society for Experimental Biology Seminar Series 61, Cambridge University Press, Cambridge.
- Suren, A.M., Biggs, B.J.F., Kilroy, C. & Bergey, L. (2003a). Benthic community dynamics during summer low-flows in two rivers of contrasting enrichment 1. Periphyton. *New Zealand Journal of Marine and Freshwater Research* 37: 53-70.
- Suren, A.M., Biggs, B.J.F., Kilroy, C. & Bergey, L. (2003b). Benthic community dynamics during summer low-flows in two rivers of contrasting enrichment 2. Invertebrates. *New Zealand Journal of Marine and Freshwater Research* 37: 71-83.
- Suren, A.M. & Jowett, I.G. (2006). Effects of floods versus low flows on invertebrates in a New Zealand gravel-bed river. *Freshwater Biology* 51: 2207-2227.
- Sweeney, B.W., Jackson, J.K., Newbold, D.N. & Funk, D.H. (1992). Climate change and the life histories and biogeography of aquatic insects in eastern North America. In *Global Climate Change and Freshwater Ecosystems* (eds. Firth, P. & Fisher, S.G.), pp 143-176, Springer-Verlag, New York.