Tolerances to Diurnally Varying Temperature for Three Species of Adult Aquatic Insects from New Zealand

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ABSTRACT Adult survival is thought to be an important factor regulating the size of aquatic insect populations, yet very little is known about the factors that cause mortality during the adult stage. Percentage mortalities over varying time intervals and 96-h lethal temperature values (96-h_{dmax} LT_{50}) were calculated for the adults of the common New Zealand caddisfly *Hydrobiosis parumbripennis* McFarlane (Hydrobiosidae) and stonefly *Zelandoperla decorata* Tillyard (Gripopterygidae), and 48-h_{dmax} LT_{50} values were calculated for the leptophlebiid mayfly *Acanthophlebia cruentata* (Hudson) using an amplitude of diurnally varying temperature regimens within and outside the insect's normal environmental range. Maxima ranged from 18 to 40°C and amplitude varied from 6 to 18°C. Mortality of adult mayflies and caddisflies were consistently higher than that of stoneflies for all comparable diurnal temperature trials. Daily temperature maxima were more important than the diurnal range in regulating mortality, with a rapidly increasing mortality as temperature maxima exceeded 24 (*Acanthophlebia*) or 30°C (*H. parumbripennis* and *Z. decorata*). Interpolated LT_{50} values for diurnally varying air temperature regimens were ~31–33°C for adult *H. parumbripennis* and *Z. decorata* and ~28–29°C for *Acanthophlebia* adults. The LT_{50} value for *Z. decorata* based on diurnally varying air temperature regimens was ≈10°C higher than that for constant temperature regimens. These findings have potential implications for managing riparian zones alongside streams and also for predicting the impacts of global warming on aquatic insect distributions.

KEY WORDS thermoperiod, lethal temperature, adult aquatic insects, riparian, global warming

SURVIVAL DURING THE ADULT phase (both subimago and imago) of aquatic insects is influenced by biotic factors such as predation (e.g., by birds, spiders, and insects orders such as Odonata) and abiotic factors such as climate and terrestrial habitat quality (Werneke and Zwick 1992). Most adult aquatic insects remain close to the stream after emergence, but a few individuals can range more widely, and they potentially play an important role in the exchange of genetic material with neighboring populations and in recolonization after disturbance (Collier and Smith 1998; Griffith et al. 1998; Briers et al. 2002). Mayflies are often reputed as having a short life span of only 1–2 d and have been characterized as the quintessence of a short-lived organism (Carey 2001), whereas many stonefly and caddisfly adults are relatively long-lived (up to 2–3 mo in laboratory conditions; Collier and Scarsbrook 2000; unpublished data). The extended flight periods of several groups (e.g., caddisflies, Crichton 1959, Smith et al. 2002) and the longevity of many species suggest that conditions experienced in the terrestrial environment are potentially important in regulating survival during the adult stage. Zwick (1989) emphasized the possible importance of adult aquatic insect longevity in population dynamics, suggesting that even small changes in the percentage mortality of adults could have a significant effect on the abundance of the next generation. However, Brittain (1990) suggested that short longevity coupled with high abundances could serve as an adaptation to minimizing exposure to predation. Adult survival may be critical at the population level as the number of females successfully ovipositing can regulate the size of subsequent aquatic larval populations (Enders and Wagner 1996), although recent genetic studies have suggested that larval populations can be derived from only a few matings (Hughes et al. 2003).

Microclimate has been implicated as an important factor influencing the longevity and development of insects that spend their entire lives in the terrestrial environment (Fleishman et al. 1990, Chandler and Wright 1991, Erelli et al. 1998), but few studies have examined its significance for the survival of adult aquatic insects (however, see Collier and Smith 2000). However, several workers have documented effects of weather conditions on activity and flight periodicity (Brindle 1957, Anderson 1978, Waringer 1991, Briers et al. 2003). Microclimate conditions, particularly air temperature and humidity, tend to be more severe during summer in open environments, such as those found in agricultural settings or after forest harvesting

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Table 1. Microclimate data for three air temperature treatments applied to *A. cruentata*, *H. parumbripennis*, and *Z. decorata*

	Treatments									
	1	2				3				
Temperature range (°C)	16	12–18	18–24[a]	24–30	30–36	12–18	12–25	12–30	12–35	12–40
Mean daily temperature (°C)	16	13.6	20.2	26.4	32.7	13.6	17.9	18.5	19.1	22.4

[a] No data for *Z. decorata.*

(Brosofske et al. 1997, Davies-Colley et al. 2000). Retention or restoration of forested strips alongside streams has been suggested as a means of mitigating land-clearance impacts, as well as having beneficial effects for stream temperature, shade, and terrestrial biota (Quinn et al. 1993, Naiman and Dechamps 1997). Even narrow riparian buffers may be sufficient to achieve desired air temperature conditions in sheltered environments (Meleason and Quinn 2004), although this is not always the case, especially where sites are exposed (Dong et al. 1998, Davies-Colley et al. 2000). However, little information exists on the desirable microclimate targets required to sustain temperature-sensitive adult aquatic insects in riparian areas.

The effects of temperature and humidity on stonefly longevity have been documented by Collier and Smith (2000); however, those experiments were run using constant temperatures that do not accurately mimic natural diurnal fluctuations that are typically higher in mid-afternoon and lower early in the morning. These thermoperiods can have profound effects on the life history traits of insects that are not reflected by constant temperature conditions (Brakefield and Kesbeke 1997). To address this issue, we examined the effects of microclimate conditions using 24-h, diurnally varying temperature cycles on the survival of adults of the gripopterygid stonefly, *Zelandoperla decorata* Tillyard, and the monotypic leptophlebiid mayfly, *Acanthophlebia cruentata* (Hudson), both which are characteristic of native forested catchments, and the hydrobiosid caddisfly, *Hydrobiosis parumbripennis* McFarlane, which has a cosmopolitan distribution.

Materials and Methods

Final-instar nymphs (indicated by fully developed wingpads) of *Z. decorata* were collected from Wairere Stream (37°44′45″ S, 175°52′10″ E) in the greater Waikato region of New Zealand's North Island from September 2000 to December 2000 (see Collier and Smith 2000 for further site details). *H. parumbripennis* pupae were collected from September 2001 to April 2002 at the confluence of two Waikato hill-country streams (37°48′00″ S, 175°04′30″ E; PW2 and PW3 in Quinn et al. 1997 and Collier et al. 1997), and *A. cruentata* from the Whakakai Stm (37°46′45″ S, 175°04′13″ E), ≈30 km west of Hamilton from February 2004 to April 2004.

A total of 113 *Z. decorata*, 100 *H. parumbripennis*, and 89 *A. cruentata* were used in the temperature treatments, and of these, 66, 59, and 41%, respectively, were females. Nymphs and pupae were reared to emergence at a constant 16°C in an aerated bucket with a mesh lid. Nymphs were fed microbially conditioned leaves and epilithon on stones from their donor streams. Emergent nymphs, subimagos, and caddisflies were provided with protruding sticks or stones on which to emerge. Once emerged, a single adult was placed into a 500-ml clear plastic container with a modified mesh lid with freely available water. Water was made available to imagos of *A. cruentata* even though their mouthparts are vestigial, because Harker (1999) noted that a mayfly with vestigial mouthparts and incapable of feeding could take very small amounts of fluid into the gut. Adult *H. parumbripennis* and *Z. decorata* were fed a 5% sucrose solution, and sooty mold fungi was also fed to *Z. decorata*, based on analysis of gut contents by Smith and Collier (2000).

Diurnal temperatures were controlled and regulated by two purpose-built microclimate chambers, each controlled by a Genesis II Digital Control System (Innotech, Australia), and run from independent PCs. Each microclimate chamber consisted of a 1.2-m^3 aluminum reinforced plastic outer and inner shell with a 50-mm-thick polystyrene core. Day lighting was provided by twin 18-W/840 Triphosphor fluorescent lights (Philips, Thailand) on a 12:12-h light-dark cycle. Three temperature regimens within and outside the insect's normal environmental range were run (Table 1). Treatment 1 used a constant temperature of 16°C. Treatment 2 maintained a regular diurnal temperature range of 6°C with maxima of 18, 24, 30, and 36°C for *H. parumbripennis* and *A. cruentata*, and 18, 30, and 36°C for *Z. decorata* (Fig. 1). Treatment 3 involved a minimum baseline temperature of 12°C to represent cooler morning and evening temperatures commonly experienced during Waikato summers, followed by a steady increase over a 5- to 6-h period to reach maxima of 18, 25, 30, 35, or 40°C, before declining to the 12°C minima 18–19 h later (Fig. 1). This treatment gave diurnal ranges of 6, 13, 18, 23, and 28°C, respectively. Temperature maxima were used to calculate the 96-h lethal temperature values (96-h_{dmax} LT_{50}) for *H. parumbripennis* and *Z. decorata.* Because of the reduced longevity of *A. cruentata*, 48-h_{dmax} LT_{50} were calculated.

Results

Female and male caddisflies or mayflies lived similar lengths of time at a constant temperature of 16°C (15.7 and 17.1 d and 2.8 and 2.3 d, respectively), whereas female stoneflies lived much longer than males in this study (12.6 versus 6.7 d). For both sexes combined, adult *Z. decorata* and *H. parumbripennis* survived, on

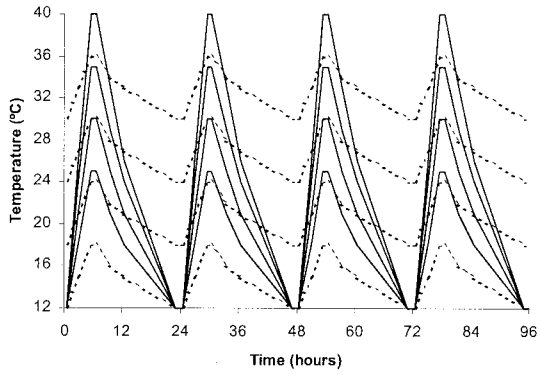

Fig. 1. Diurnally varying temperature cycles over 24, 48, and 96 h for treatment 2 (dotted lines; constant 6°C diurnal range with variable maxima) and treatment 3 (solid lines; constant 12°C minima with variable maxima) used to study thermal tolerances of *H. parumbripennis*, *Z. decorata*, and *A. cruentata*.

average, 11.6 and 16.5 d, respectively, compared with 4.8 d for *A. cruentata* at 16°C (Table 2). There was considerable variation in mortality for the three species in treatment 1 (16°C), with minimum longevity (subimago + imago) of 1.5 d and a maximum of 9 d for *A. cruentata*, whereas *H. parumbripennis* and *Z. decorata* had a minimum longevity of 5–6 d and maximum longevity of 42–53 d. Under both diurnally varying treatments, *Z. decorata* longevity was greater at equivalent temperatures than *H. parumbripennis*, and the tendency for greater female longevity in *Z. decorata* generally persisted until maximum temperatures exceeded 30°C. There was also substantial individual variation in both diurnally varying treatments for the three species, but this variation declined as temperature maxima increased (Table 2).

Mean days alive declined for all species (both sexes combined) with increasing air temperature in treatments 2 and 3 (Table 2; Fig. 2). For the longer-lived *H. parumbripennis* and *Z. decorata*, longevity at comparable maximum temperatures was similar in both treatments (Table 2). There was a sharp decline in longevity for *H. parumbripennis* and *Z. decorata* when temperature maxima increased above 30°C (mean longevity < 1.3 d), and a rapid decrease in the longevity of *A. cruentata* when the daily maxima exceeded 24°C (mean longevity < 3.9 d; Table 2) for treatments 2 and 3, indicating that temperature maximum rather than the diurnal range was the key thermal cue inducing mortality (Fig. 2). There was a gradual increase in percentage dead after 96 h for *H. parumbripennis* and *Z. decorata* as the daily maxima approached 30°C, and beyond this temperature, mortality jumped to 100%, with treatments 2 and 3 showing the same pattern of mortality (Fig. 2A and B). The interpolated 96-h_{dmax} LT_{50} value for *Z. decorata* was ~33°C (Fig. 2B) compared with 31–32°C for *H. parumbripennis* (Fig. 2A). Figure 2C shows a gradual increase in percentage dead of *A. cruentata* after 48 h when the daily maxima exceeded 24°C. The interpolated 48-h_{dmax} LT_{50} value for *A. cruentata* was somewhat lower at 26–27°C than the 96-h_{dmax} LT_{50} value for the other two species (Fig. 2C).

When mortalities were compared for diurnally varying temperature treatments with similar maxima (within 2°C), but different diurnal ranges over 24, 48, and 96 h, it was evident that, in the absence of thermal refugia, significant mortality could occur within 1 d if temperature maxima exceeded 24°C for *A. cruentata* and 30°C for *H. parumbripennis* and *Z. decorata* (Fig. 3). Although, mayfly mortality was highly variable (20–100% at a daily maximum >24°C, regardless of the length of exposure; Fig. 3C), our data suggest that *A. cruentata* mortality could be around 10% if daily temperature maxima remained <25°C for <3 consecutive days. However, mayfly mortality rapidly increased to 50% when the diurnal temperature maxima reached 25°C within a 24-h period, with mortality rising to 70% at this temperature over 2 consecutive

Table 2. Longevity data for three air temperature treatments applied to *A. cruentata*, *H. parumbripennis*, and *Z. decorata*

	Treatments									
	1	2				3				
Maximum air temperature (°C)	16	18	24	30	36	18	25	30	35	40
H. parumbripennis										
Mean days alive	16.5	11.5	9.8	5.0	0.5	11.5	7.2	6.0	0.5	0.5
Median days alive	13.0	9.0	8.0	4.0	0.5	9.0	7.0	6.0	0.5	0.5
Range (days alive)	6–42	3–35	2–29	2–11	0.5	3–35	4–10	1–12	0.5	0
n	20	17	10	11	5	17	11	11	10	5
Z. decorata										
Mean days alive	11.6	15.5	ND	5.6	1.0	15.5	10.2	7.4	1.2	0.5
Median days alive	9	13.5	ND	5.0	1.0	13.5	9.5	7.5	1.0	1.0
Range (days alive)	5–53	4–41	ND	2–11	1	4–41	4–23	3–11	0.5–2	0.5
n	18	24	ND	11	5	24	16	8	20	11
A. cruentata										
Mean days alive	4.8	5.7	5.0	1.2	0.6	5.7	2.1	3.8	1.4	0.5
Median days alive	4.0	4.5	5.0	1.0	0.5	4.5	1.5	3.0	1.0	0.5
Range (days alive)	1.5–9	1–17	1–8	0.5–3	0.5–1.0	1–17	1–5	1–7	0.5–2.5	0
n	11	10	10	10	10	10	10	10	10	8

See Materials and Methods for details.
ND, no data.

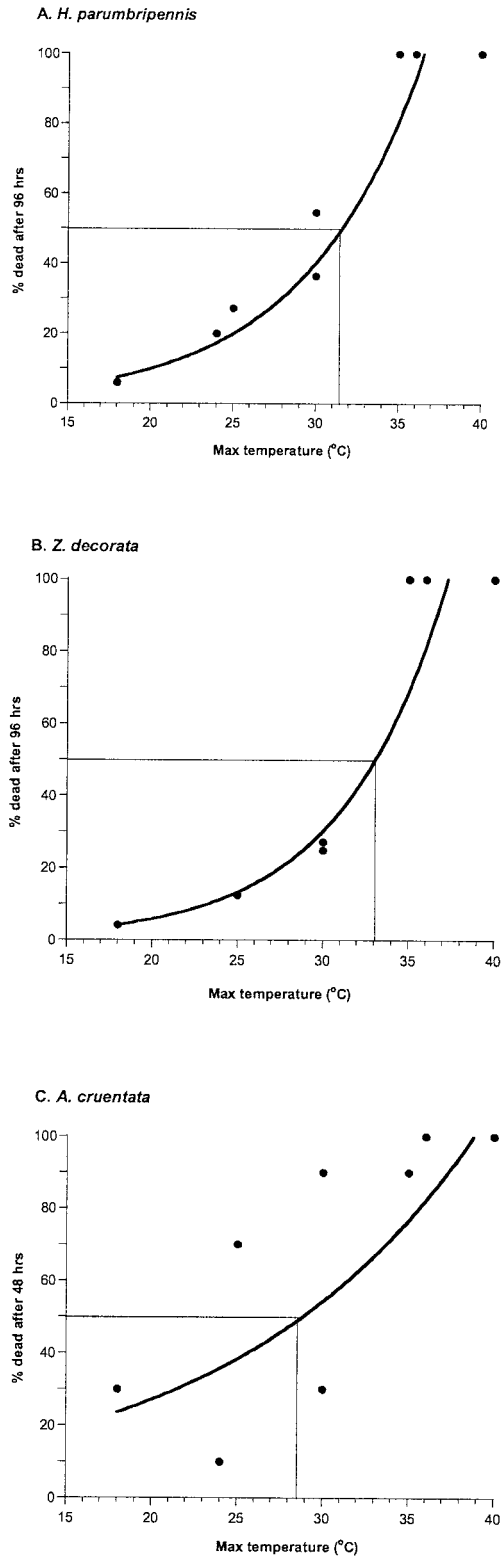

Fig. 2. Adult mortality at 96 h using maxima of two diurnally varying temperature treatments for (A) *H. parumbripennis* and (B) *Z. decorata* and (C) at 48 h for *A. cruentata*.

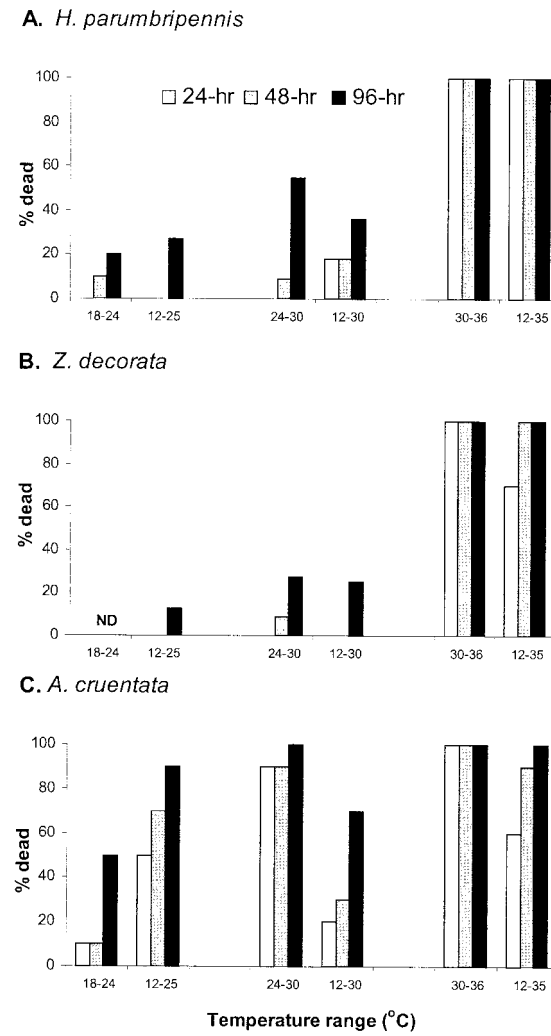

Fig. 3. Comparison of mortality of adult *H. parumbripennis*, *Z. decorata*, and *A. cruentata* over 24, 48, and 96 h subjected to similar diurnal temperature maxima (24–25, 30, and 35–36°C) but different diurnal ranges. (A) *H. parumbripennis*. (B) *Z. decorata*. (C) *A. cruentata*. ND, no data.

days (Fig. 3C). If temperature maxima were above 23°C over 4 consecutive days irrespective of the diurnal range, >20% of *H. parumbripennis* adults could die (Fig. 3A). Unlike *H. parumbripennis*, however, maxima of 30°C over 4 consecutive days were required to induce 20% mortality in *Z. decorata*, and >70% mortality was recorded within 24 h when temperature maxima exceeded 35°C, regardless of the diurnal range (Fig. 3B).

Discussion

The adults of the longer-lived *H. parumbripennis* and *Z. decorata* showed a similar pattern of thermal tolerance, with mortality rapidly increasing as temperatures exceeded 30°C, whereas mortality for the

shorter-lived *A. cruentata* gradually increased as the daily temperature maxima exceeded 24°C. We expected *A. cruentata* to be sensitive to increasing temperature because it is largely confined to native forested catchments (Quinn et al. 1997, Collier et al. 2004). *Acanthophlebia* adults are not restricted to crepuscular activity, with adults observed swarming up to 3 m above streams, at least on overcast and drizzly days (McLean 1967; B.J.S, unpublished data). Diurnal activity may be advantageous for short-lived species because it may maximize reproductive opportunities, potentially at the cost of temperature-induced mortality at open sites. *A. cruentata* also has extended emergence and recruitment periods (October–May), with adult numbers peaking around February–April (Collier et al. 2004). Extended emergence may provide a temporal refugium that helps populations persist through catastrophic pulse disturbances (e.g., Collier and Quinn 2003) and hot summers by ensuring that adults can oviposit most times of the of year.

In contrast to our findings, we expected adult stoneflies to be more sensitive to increasing air temperature than caddisflies because larval studies have indicated thermal sensitivity for stonefly nymphs (Quinn and Hickey 1990, Quinn et al. 1994). However, results indicated *H. parumbripennis* had greater mortality at lower maximum temperatures even though adults are common in pasture catchments and numbers peak during summer (Smith et al. 2002). However, *H. parumbripennis* limit flight to cooler evening periods and may use thermal refugia among riparian vegetation during the day.

Zelandoperla decorata is usually found in large, turbulent, stony streams draining native forested catchments, with most adults emerging in spring and early summer (McLellan 1975, 1999; unpublished data). They are typically active during the afternoon when air temperatures are highest and have been collected in direct sunlight and from the shaded sides of boulders in the middle and sides of the stream (unpublished data). Thermoregulatory behavior has yet to be recorded for southern hemisphere stoneflies, although adults of the northern hemisphere stoneflies *Zapada cinctipes* (Banks) (Nemouridae) and *Utacapnia trava* Nebeker and Gaufin (Capniidae) are known to thermoregulate body temperature by entering water (Tozer 1979, Dosdall and Lehmkuhl 1988). We did not observe adult *Z. decorata* entering the water (for both laboratory and field observations); however, it is possible that this species may thermoregulate its body temperature through abdominal contact with stone surfaces or through behavior by moving to the shaded cooler side of rocks and boulders.

The diurnally varying 96-h_{dmax} LT_{50} value for *Z. decorata* based on maximum temperatures (~33°C) was ~10°C higher than the constant temperature 96-h LT_{50} of 22–23°C for individuals collected from the same study stream (Collier and Smith 2000). This is considerably greater than the difference (2–3°C) measured by Cox and Rutherford (2000) for aquatic mayfly nymph and snail mortality under constant (20–35°C) and diurnally varying (10–40°C) temperature regimens and highlights the need to carry out species- and life-stage–specific analyses of thermal tolerances.

As well as affecting longevity, air temperature may influence other aspects of adult aquatic insect biology, such as flight performance, metabolic rate, and egg development. These factors can have implications for population success and recolonization rates, although individual body weight and fecundity are not always linked to population success (Wagner 2002). Marden (1995) reported that adult maturation of flight muscle in the dragonfly *Libellula pulchella* is accompanied by striking changes in thermal physiology, with mature adults displaying a narrow thermal sensitivity range. Stewart et al. (1999) reported decreases in the number of eggs laid by a terrestrial beetle at higher temperatures (range, 15–30°C). We monitored ovarian development in female caddisflies and stoneflies in this study, but did not find any obvious patterns related to air temperature (unpublished data).

Before the arrival of humans (≈1,000 yr ago), New Zealand had ~80% forest cover compared with the present 30% cover (McGlone, 1983, Statistics NZ 2002). Davies-Colley et al. (2000) suggested that much of the New Zealand stream and riparian biota has probably evolved in once contiguous native forest where fluctuations in microclimate factors were less marked than in open areas. Measurements of temperature fluctuations in native forested riparian zones of New Zealand's central North Island have shown that diurnal temperature maxima are well below the estimated LT_{50} for the stonefly and caddisfly species we used (Collier and Smith 2000, Meleason and Quinn 2004; unpublished data). However temperature maxima recorded from native forest riparian buffers may exceed 24°C, apparently a critical threshold temperature for *A. cruentata*, although maxima of this magnitude are unlikely to occur over 4 consecutive days. It is known that even narrow riparian buffers can mitigate temperature increases in sheltered locations by 3°C (Meleason and Quinn 2004), and our findings support the practice of planting or protecting streamside vegetation to manage riparian microclimate conditions for adult aquatic insects.

Given that some New Zealand aquatic insect species have low genetic variability (e.g., Smith and Collier 2001, Hogg et al. 2002) and may be living close to the upper limit of their thermal tolerance as adults in some parts of New Zealand (this study), it seems plausible that, in the absence of spatial or temporal thermal refugia, marked changes in the distribution of sensitive species may occur with abrupt changes in air temperature regimens. Therefore, our study raises questions about the potential impacts of global warming on the future distribution of aquatic biota.

Global mean air temperatures have increased by 0.3–0.6°C over the past century in continental areas at high latitudes and are predicted to increase by 1–3.5°C by 2100 (Malmqvist and Rundle 2002). In addition, an increase is expected in thermal extremes that cause abrupt changes in ecosystem process rates or populations of key species (Carpenter et al. 1992). Studies of aquatic invertebrates have indicated that species

with limited genetic variability and/or low dispersal ability may be the most susceptible and suggest that global warming may alter the trajectories of species' evolution (Hogg et al. 1995, 1998, Hogg and Williams 1996).

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References Cited

Anderson, T. 1978. Influence of temperature on the sex ratio of Trichoptera in light-trap catches in western Norway. Nor. J. Entomol. 2: 149–151.

Brakefield, P. M., and F. Kesbeke. 1997. Geneotype-environment interactions for insect growth in constant and fluctuating temperature regimes. Proc. R. Soc. Lond. 26: 717–723.

Briers, R. A., H. M. Cariss, and J.R.H. Gee. 2002. Dispersal of adult stoneflies (Plecoptera) from upland streams draining catchment with contrasting land-use. Archiv. Fur. Hydrobiol. 155: 627–644.

Briers, R. A., H. M. Cariss, and J.R.H. Gee. 2003. Flight activity of adult stoneflies in relation to weather. Ecol. Entomol. 28: 31–40.

Brindle, A. 1957. The effect of temperature and humidity on the flight of Trichoptera. Entomol. Monogr. Mag. 93: 63–67.

Brittain, J. E. 1990. Life history strategies in Ephemeroptera and Plecoptera, pp. 1–12. *In* I. C. Campbell (ed.), Mayflies and stoneflies. Life histories and biology. Kluwer, Boston, MA.

Brosofske, K. D., J. Chen, R. J. Naiman, and J. F. Franklin. 1997. Harvesting effects on microclimate gradients from small streams to uplands in western Washington. Ecol. Appl. 7: 1188–1200.

Carey, J. R. 2001. Insect biodemography. Annu. Rev. Entomol. 46: 79–110.

Carpenter, S. R., S. G. Fisher, N. B. Grimm, and J. F. Kitchell. 1992. Global change and freshwater ecosystems. Annu. Rev. Ecol. Syst. 23: 119–139.

Chandler, L. D., and J. E. Wright. 1991. Longevity of the boll weevil (Coleoptera: Curculionidae) on cotton and alternate feeding sources under various temperature regimes in the laboratory. J. Econ. Import. 84: 1699–1704.

Collier, K. J., and B. J. Smith. 1998. Dispersal of adult caddisflies (Trichoptera) in forests alongside three New Zealand streams. Hydrobiologia. 361: 53–65.

Collier, K. J., and M. R. Scarsbrook. 2000. Riparian and hyporheic habitat use, pp. 179–206. *In* K. J. Collier and M. J. Winterbourn (eds.), New Zealand stream invertebrates: ecology and implications for management. The New Zealand Limnological Society, Caxton Press, Christchurch, New Zealand.

Collier, K. J., and B. J. Smith. 2000. Interactions of adult stoneflies (Plecoptera) with riparian zones I. Effects of air temperature and humidity on longevity. Aquat. Insects. 22: 275–284.

Collier, K. J., and J. M. Quinn. 2003. Landuse influences macroinvertebrate community response following a pulse disturbance. Freshwater Biol. 48: 1462–1481.

Collier, K. J., B. J. Smith, and B. R. Baillie. 1997. Summer light-trap catches of adult Trichoptera in hill-country catchments of contrasting land-use, Waikato, New Zealand. N.Z.J. Mar. Freshwater Res. 31: 623–634.

Collier, K. J., A. E. Wright-Stow, and B. J. Smith. 2004. Trophic basis of production for a mayfly in a North Island, New Zealand, forest stream: contributions of benthic versus hyporheic habitats and implications for restoration. N.Z.J. Mar. Freshwater Res. 38: 301–314.

Cox, T. J., and J. C. Rutherford. 2000. Thermal tolerances of two stream invertebrates exposed to diurnally varying temperature. N.Z.J. Mar. Freshwater Res. 34: 203–208.

Crichton, M. I. 1959. A study of captures of Trichoptera in a light trap near Reading, Berkshire. Trans. R. Entomol. Soc. Lond. 112: 319–344.

Davies-Colley, R. J., G. W. Payne, and M. van Elswijk. 2000. Microclimate gradients across a forest edge. N.Z.J. Ecol. 24: 111–121.

Dong, J., J. Chen, K. D. Brosofske, and R. J. Naiman. 1998. Modelling air temperature gradients across managed small streams in western Washington. J. Environ. Manage. 53: 309–321.

Dosdall, L. M., and D. M. Lehmkuhl. 1988. The nymph of *Utacapnia trava* (Nebeker and Gaufin) (Plecoptera: Capniidae). Pan-Pac. Entomol. 64: 353–357.

Enders, G., and R. Wagner. 1996. Mortality of *Apatania fimbriata* (Insecta: Trichoptera) during embryonic, larval and adult life stages. Freshwater Biol. 36: 93–104.

Erelli, M. C., P. A. Matthew, and G. K. Eaton. 1998. Altitudinal patterns in host suitability for forest. Oecologia (Berl.). 117: 133–142.

Fleishman, E., A. E. Launer, S. B. Weiss, J. M. Reed, C. L. Boggs, D. D. Murphy, and R. R. Finch. 1990. Longevity, senescence and the genome. University of Chicago Press, Chicago, IL.

Griffith, M. B., E. M. Barrows, and S. A. Perry. 1998. Lateral dispersal of adult aquatic insects (Plecoptera, Trichoptera) following emergence from headwater streams in forested Appalachian catchments. Ecol. Populat. Biol. 91: 195–201.

Harker, J. E. 1999. The structure of the foregut and midgut of nymphs, subimagos and imagos of *Cloeon dipterum* (Ephemeroptera) and the functions of the gut of adult mayflies. J. Zool. Lond. 248: 243–253.

Hogg, I. D., and D. D. Williams. 1996. Response of stream invertebrates to a global-warming thermal regime: an ecosystem-level manipulation. Ecology. 77: 395–407.

Hogg, I. D., D. D. Williams, J. M. Eadie, and S. A. Butt. 1995. The consequences of global warming from stream invertebrates: a field simulation. J. Therm. Biol. 20: 199–206.

Hogg, I. D., J. M. Eadie, and Y. De Lafontaine. 1998. Atmospheric change and the diversity of aquatic invertebrates: are we missing the boat? Environ. Manage. Monit. 49: 291–301.

Hogg, I. D., P. Willmann-Heurner, and M. I. Stevens. 2002. Population genetic structure of two New Zealand stream insects: *Archichauliodes diversus* (Megaloptera) and *Coloburiscus humeralis* (Ephemeroptera). N.Z.J. Mar. Freshwater Res. 36: 491–501.

Hughes, J. M., M. Hillyer, and S. E. Bunn. 2003. Small-scale patterns of genetic variation in the mayfly *Bungona narilla* (Ephemeroptera: Baetidae) in rainforest streams, southeast Queensland. Freshwater Biol. 48: 709–717.

Malmqvist, B., and S. Rundle. 2002. Threats to the running water ecosystems of the world. Environ. Conserv. 29: 134–153.

Marden, J. H. 1995. Large-scale changes in thermal sensitivity of flight performance during adult maturation in a dragonfly. J. Exp. Biol. 198: 2095–2102.

McGlone, M. S. 1983. Polynesian deforestations of New Zealand: a preliminary synthesis. Archaeol. Oceania. 18: 11–25.

McLean, J. A. 1967. Studies of Ephemeroptera in the Auckland area I. Light trapping in Cascade Kauri Park. Tane. 13: 99–105.

McLellan, I. D. 1975. The freshwater insects, pp. 537–559. *In* G. Kuschel (ed.), Biogeography and ecology in New Zealand. Dr W. Junk B. V. Publishers, The Hague.

McLellan, I. D. 1999. A revision of *Zelandoperla* Tillyard (Plecoptera: Gripopterygidae: Zelandoperlinae). N.Z.J. Zool. 26: 199–219.

Meleason, M. A., and J. M. Quinn. 2004. Influence of riparian buffer width on air temperature at Whangapoua forest. For. Ecol. Manage. 191: 365–371.

Naiman, R. J., and H. Dechamps. 1997. The ecology of interfaces: riparian zones. Annu. Rev. Ecol. Sys. 28: 621–658.

Quinn, J. M., and C. W. Hickey. 1990. Characterisation and classification of benthic invertebrate communities in 88 New Zealand rivers in relation to environmental factors. N.Z.J. Mar. Freshwater Res. 24: 387–409.

Quinn, J. M., A. B. Cooper, and B. Williamson. 1993. Riparian zones as buffer strips: a New Zealand perspective, pp. 53–87. *In* S. E. Bunn, B. J. Pusey, and P. Price (eds.), Ecology and management of riparian zones in Australia. Land and water research and development commission occasional series no. 05/93, LWRRDC, Canberra and CCISR, Griffith University, Brisbane.

Quinn, J. M., G. L. Steele, C. W. Hickey, and M. L. Vickers. 1994. Upper thermal tolerances of twelve New Zealand stream invertebrate species. N.Z.J. Mar. Freshwater Res. 28: 391–397.

Quinn, J. M., A. B. Cooper, R. J. Davies-Colley,. J. C. Rutherford, and R. B. Williamson. 1997. Land-use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand, hill-country streams. N.Z.J. Mar. Freshwater Res. 31: 579–598.

Smith, B. J., and K. J. Collier. 2000. Interactions of adult stoneflies (Plecoptera) with riparian zones II. Diet. Aquat. Insects 22: 285–296.

Smith, B. J., K. J. Collier, and N. J. Halliday. 2002. Flight periodicity of adult caddisflies in New Zealand hill-country catchments of contrasting land use. N.Z.J. Mar. Freshwater Res. 36: 836–878.

Smith, P. J., and K. J. Collier. 2001. Allozyme diversity and population structure of the caddisfly *Orthopsyche fimbriata* and the mayfly *Acanthophlebia cruentata* in New Zealand streams. Freshwater Biol. 46: 795–805.

Statistics NZ. 2002. New Zealand official yearbook 2002. Davis Bateman, Auckland.

Stewart, C. A., R. B. Chapman, A. M. Barington, and C.M.A. Frampton. 1999. Influence of temperature on adult longevity, oviposition and fertility of *Agasicles hygrophila* Selman and Vogt (Coleoptera: Crysomelidae). N.Z.J. Zool. 26: 191–197.

Tozer, W. 1979. Underwater behavioural thermoregulation in the adult stonefly, *Capada cinctipes.* Nature (Lond.). 281: 566–567.

Wagner, R. 2002. The influence of temperature and food on size and weight of adult *Chaetopteryx villosa* (Fabricius) (Insecta: Trichoptera) along a stream gradient. Arch. Hydrobiol. 154: 393–411.

Waringer, J. A. 1991. Phenology and the influence of meteorological parameters on the catching success of light-trapping for Trichoptera. Freshwater Biol. 25: 307–319.

Werneke, U., and P. Zwick. 1992. Mortality of the terrestrial adult and aquatic nymphal life stages of *Baetis vernus* and *Baetis rhodani* in the Breitenbach, Germany (Insecta: Ephemeroptera). Freshwater Biol. 28: 249–255.

Zwick, P. 1989. Upstream oviposition flights of Plecoptera, with notes on the adult phase as a possible control of stream insect populations. Hydrobiologia. 194: 207–223.

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