# How aquatic insects live in cold climates

**H.V. Danks**

Biological Survey of Canada (Terrestrial Arthropods), Canadian Museum of Nature,
P.O. Box 3443, Station D, Ottawa, Ontario, Canada K1P 6P4
(e-mail: hdanks@mus-nature.ca)

**Abstract**—In cold climates most aquatic habitats are frozen for many months. Nevertheless, even in such regions the conditions in different types of habitat, in different parts of one habitat, and from one year to the next can vary considerably; some water bodies even allow winter growth. Winter cold and ice provide challenges for aquatic insects, but so do high spring flows, short, cool summers, and unpredictable conditions. General adaptations to cope with these constraints, depending on species and habitat, include the use of widely available foods, increased food range, prolonged development (including development lasting more than one year per generation), programmed life cycles with diapause and other responses to environmental cues (often enforcing strict univoltinism), and staggered development. Winter conditions may be anticipated not only by diapause and related responses but also by movement for the winter to terrestrial habitats, to less severe aquatic habitats, or to different parts of the same habitat, and by construction of shelters. Winter itself is met by various types of cold hardiness, including tolerance of freezing in at least some species, especially chironomid midges, and supercooling even when surrounded by ice in others. Special cocoons provide protection in some species. A few species move during winter or resist anoxia beneath ice. Spring challenges of high flows and ice scour may be withstood or avoided by wintering in less severe habitats, penetrating the substrate, or delaying activity until after peak flow. However, where possible species emerge early in the spring to compensate for the shortness of the summer season, a trait enhanced (at least in some lentic habitats) by choosing overwintering sites that warm up first in spring. Relatively low summer temperatures are offset by development at low temperatures, by selection of warm habitats and microhabitats, and in adults by thermoregulation and modified mating activity. Notwithstanding the many abiotic constraints in cold climates, aquatic communities are relatively diverse, though dominated by taxa that combine traits such as cold adaptation with use of the habitats and foods that are most widely available and most favourable. Consequently, except in the most severe habitats, food chains and community structure are complex even at high latitudes and elevations, including many links between aquatic and terrestrial habitats. Despite the complex involvement of aquatic insects in these cold-climate ecosystems, we know relatively little about the physiological and biochemical basis of their cold hardiness and its relationship to habitat conditions, especially compared with information about terrestrial species from the same regions.

**Résumé**—Dans les climats froids, la plupart des habitats aquatiques sont recouverts de glace pendant plusieurs mois. Néanmoins, dans ces régions, la gamme des conditions dans les divers types d'habitats, dans les diverses parties d'un même habitat et d'une année à l'autre peut varier considérablement; certains milieux aquatiques permettent même de la croissance pendant l'hiver. Le froid et la glace de l'hiver posent des problèmes aux insectes aquatiques, mais c'est le cas aussi des forts débits du printemps, des étés courts et frais et des conditions imprévisibles. Les adaptations générales pour faire face à ces contraintes comprennent, selon l'espèce et l'habitat, l'utilisation de nourriture largement disponible, l'accroissement de l'éventail alimentaire, la prolongation du développement et en particulier, la durée de plus d'un an par génération, les cycles biologiques programmés avec présence de diapause ou d'autre réaction aux signaux environnementaux (maintenant souvent un univoltinisme strict) et un développement étalé. Les conditions hivernales peuvent être anticipées non seulement par la diapause et les autres réactions de même type, mais aussi par un déplacement vers les habitats terrestres pour l'hiver, vers des habitats aquatiques moins extrêmes ou vers des sections différentes du même habitat et par la construction de refuges. L'hiver lui-même est contré par divers types de résistance au froid, y compris la tolérance au gel au moins chez certaines espèces — particulièrement chez les moucherons chironomidés — et, chez d'autres, la surfusion même lorsqu'elles sont entourées de glace. Des

Received 6 December 2006. Accepted 20 February 2007.

Can. Entomol. **139**: 443–471 (2007)

cocons spéciaux fournissent une protection à certaines espèces. Quelques espèces se déplacent durant l'hiver ou résistent à l'anoxie sous la glace. Les problèmes du printemps, les forts débits et l'affouillement par la glace, peuvent être endurés ou évités par le passage de l'hiver dans des habitats moins rigoureux, l'enfouissement dans le substrat ou le report des activités après le débit maximal. Cependant, lorsque c'est possible, les espèces émergent tôt au printemps pour compenser la brièveté de la saison estivale, une caractéristique qui est favorisée (au moins dans certains habitats lénitiques) par le choix d'habitats d'hivernage qui se réchauffent les premiers au printemps. Les températures relativement basses de l'été sont compensées par un développement à basse température, par la sélection comportementale d'habitats et de microhabitats chauds et, chez les adultes, par la thermorégulation et la modification des activités reproductrices. En dépit des nombreuses contraintes abiotiques des climats froids, les communautés aquatiques y sont relativement diversifiées, bien que dominées par des taxons qui possèdent des combinaisons de caractères, tels que l'adaptation au froid et l'utilisation des habitats et des nourritures qui sont les plus disponibles et les plus avantageux. En conséquence, à l'exception des habitats les plus rigoureux, les chaînes alimentaires et la structure des communautés sont complexes même aux latitudes et aux altitudes élevées et elles comprennent de nombreux liens entre les habitats aquatiques et terrestres. Malgré le rôle complexe des insectes aquatiques dans ces écosystèmes de climat froid, on connaît relativement peu de choses sur les bases physiologiques et biochimiques de leur résistance au froid et de ses relations avec les conditions de l'habitat; cela est d'autant plus vrai si on fait des comparaisons avec ce qu'on sait des espèces terrestres des mêmes régions.

[Traduit par la Rédaction]

## Table of contents

## Introduction

Cold and seasonal climates have very cold winters with ice and snow, cold summers with limited resources of food and heat for development, and other constraints on aquatic life. Nevertheless, many species of aquatic insects live in such regions. Climates have been formally classified in different ways, such as cold, Arctic, boreal, sub-Arctic, cool-temperate, humid-continental, and so on, but for the purpose of this review I regard climates as "cold" if mean air temperatures are below 0 °C for at least several months and most aquatic habitats remain frozen for a similar period. Thus included are various Arctic, Antarctic, boreal, cold-temperate, and alpine regions. However, relatively few aquatic species live in such climates in the Antarctic region: the only insect species in the most severe Antarctic sites is the chironomid *Belgica antarctica* Jacobs, which lives in terrestrial habitats (Convey and Block 1996); the less severe habitats of the sub-Antarctic, although cool all summer, are not especially cold in winter (Danks 1999).

Although large areas of the earth's surface have cold climates, there is much more information on terrestrial species than on aquatic ones from these regions. Biological studies of aquatic insects in boreal and polar regions are limited too, compared with the amount of limnological and hydrological information, and even when insect communities have been characterized there may be little information about modes of adaptation to the cold. Recent work has emphasized only a few kinds of habitat, notably alpine streams, and only a few features such as river-ice breakup in spring. Moreover, many recent studies have focused on diversity, functional groups, or specific hypotheses, often at the expense of detailed biological information. Therefore, I cite not only recent papers when available but also a variety of older studies that have not been superseded. Part of the shortfall of information also stems from the difficulty of work in cold aquatic habitats, which may be remote at high latitudes, challenging to sample because they are deeply frozen or snow-covered in winter, or dangerous, like large rivers during ice breakup and high spring flows. Consequently, detailed information on how aquatic insects live in these habitats is relatively sparse and scattered. To fully exploit the material that is available, I synthesize information here from a broader perspective than most earlier reviews (*e.g.*, Harper 1981; Oswood *et al.* 1991; Irons *et al.* 1993; Frisbie and Lee 1997; Lencioni 2004) and include many elements in addition to the effects of ice.

## Cold habitats for aquatic insects

Aquatic insects live in a very wide range of habitats, which are affected in different ways in cold climates. The main differences depend on whether habitats are lentic or lotic, on their size and permanence, on the stability of the channel (*e.g.*, Milner *et al.* 2006), on how water is supplied to them, and on other features including the chemical characteristics of the substrate (*e.g.*, Füreder *et al.* 2006), pH (Heino 2005), salinity, and modification by external influences such as beavers (for a sample classification see Milner *et al.* 1997). In general, large, permanent habitats are less affected by cold than small or temporary ones because the volume of water buffers temperature changes and water is retained even during seasonal low levels or freezing. However, major seasonal stresses in lotic waters are caused by spates (see Spring challenges below), and hydrological variables are especially important for understanding these habitats and their seasonal changes and stability. Hydrological features in both lotic and lentic habitats are influenced by such characteristics as vegetation type (*e.g.*, Snyder *et al.* 2002), relief of the catchment, and lake morphology (Blenckner 2005).

Unlike large, permanent habitats, small or temporary water bodies may lose water or freeze entirely and then have temperature profiles that are similar to those of terrestrial habitats. For example, typical temporary pools are frozen solid in winter, whether or not they hold water before freeze-up (*e.g.*, Wiggins *et al.* 1980; Winchester *et al.* 1993).

Alpine regions differ from high-latitude ones in having a greater supply of wind-borne allochthonous food and greater and more even annual insolation. Alpine streams have been studied in some detail (*e.g.*, Milner and Petts 1994; Ward 1994; Füreder 1999; Gíslason *et al.* 2001; Brittain and Milner 2001; Füreder *et al.* 2001, 2005; Lods-Crozet *et al.* 2001; Robinson *et al.* 2001; Hieber *et al.* 2003, 2005; Brown *et al.* 2003, 2006; Milner *et al.* 2006). They differ most strikingly according to the water source and such features as altitude, slope, suspended sediment load, and so on, but there are also differences among habitats in many other factors such as bed stability (Friberg *et al.* 2001) or fungi that break down leaves (Robinson *et al.* 1998).

Alpine streams derived from glacial meltwater usually have high turbidity (from glacial rock flour), low temperatures, and high flow in summer rather than in spring. Key species of the headwaters, *Diamesa* midges, cope with these summer disturbances; most other species develop in winter lower in the channel and so avoid the disturbances of summer (Schütz *et al.* 2001). Alpine streams fed by snowmelt and rainfall are warmer and much less turbid than those fed by glaciers, with peak flows in spring. They contain diverse insect species according to the distance downstream, although the many temporary streams in alpine areas are less well characterized. Streams fed or influenced by groundwater tend to have more constant temperature and flow, and chemical characteristics that depend on the water sources (*e.g.*, Gíslason *et al.* 2000). Alpine streams that serve as lake outlets are another distinct set of habitats, with different regimes of temperature and other factors and a different fauna (Hieber *et al.* 2002).

At high latitudes, differences among water bodies, even those of the same general type, are equally striking. For example, permafrost influences both the catchment and the individual water body (and thus the macroinvertebrates) through its effects on hydrology, water temperature, and surrounding vegetation (Smidt and Oswood 2002). Steep-sided ponds warm up in spring much more slowly than shallow saucer-shaped ones (Oliver and Corbet 1966). The temperature of sun-warmed shallow ponds can exceed 20 °C all summer even in the high Arctic (*e.g.*, DeBruyn and Ring 1999), while deep lakes there sometimes remain ice-covered all year (Oliver 1964). Different streams and different habitats within streams differ in hydrology, especially the major spring peak from melting ice and snow, but they also differ in warming and cooling rates as well as heat accumulations (Irons and Oswood 1992). Tundra streams tend to be warmer than boreal ones because they are not shaded from solar heating by vegetation and because daylight is continuous above the Arctic Circle in summer.

In cold-climate habitats, key climatic elements influencing the fauna stem from seasonality and variability. Food supply is also important. Insect responses to these factors are outlined in Table 1 and considered in the next three sections.

## Food resources

Overall productivity is reduced in cold regions; this is one of the major themes in aquatic habitats, according to Oswood (1997). Indeed, all of the normal sources of food for aquatic insects tend to be reduced. First, terrestrial vegetation surrounding aquatic habitats is less rich and diverse in cold climates, limiting allochthonous inputs of litter. In particular, trees are absent in Arctic and alpine zones, reducing the autumn pulse of deciduous leaves that is characteristic of many temperate habitats and supplies the coarse particulate organic matter (CPOM) on which many lotic communities depend. Boreal regions are dominated by coniferous trees, which have needles that decay slowly and are unpalatable to many aquatic insects. Second, other organisms that serve as prey for consumers are reduced in cold and unproductive habitats. Third, cold conditions slow the growth of periphyton in streams, thereby limiting autochthonous food (*cf.* Oswood 1997). Seasonally variable flow further lowers production (Aagaard *et al.* 1997). Plankton growth in many lakes is likewise inhibited by low temperatures and low nutrient levels. Indeed, Hershey *et al.* (2006) showed that benthic methanotrophic bacteria and dissolved organic carbon (rather than primary productivity in the pelagic zone) are important food sources for benthic chironomids in northern oligotrophic lakes. Adding nitrogen or phosphorus fertilizers to Arctic streams may increase periphyton production (and also habitat complexity by stimulating moss growth, for example), which changes insect communities and increases species abundance (*e.g.*, Hershey *et al.* 1988; Peterson *et al.* 1993; Harvey *et al.* 1998; Lee and Hershey 2000; Benstead *et al.* 2005), but similar effects are known from more southern habitats. Nevertheless, nutrient supply is one element dictating habitat type in Arctic streams (Huryn *et al.* 2005). Moreover, food and temperature interact in governing insect growth and development, especially as temperatures become limiting in northern habitats (*cf.* Giberson and Rosenberg 1992*a*).

The limitation of certain kinds of food does reduce several taxa in cold climates, and aquatic insects that persist typically use the resources that are available. Many aquatic as well as terrestrial species are broadly saprophagous in the Arctic (Danks 1990) and depend on detritus, although its patchy and temporally limited supply influences faunal patterns (Cowan and Oswood 1984). Many of the species from an Arctic river use fine rather than coarse particulate organic matter (Hershey *et al.* 1995, 1997). Most species are not narrowly specialized (Ulfstrand 1967) and some species eat a wider range of foods than is typical elsewhere. For example, some northern caddisflies can eat leaves that have not been conditioned by the microflora (Irons 1988 for *Hydatophylax variabilis* (Martynov)). Larvae of the black fly *Prosimulium ursinum* (Edwards) are partly predaceous when other food is limited (Currie and Craig 1988).

Not all aquatic habitats in cold regions are oligotrophic. Shallow ponds not only are warm in summer (and see below) but also even in tundra areas are well supplied with detritus swept in from surrounding areas by snowmelt, so they contain species feeding on that detritus and the microflora it supports. For example, many species of chironomids are found in shallow pools, mosquitoes are characteristic of snowmelt pools even in the high Arctic (*e.g.*, Corbet and Danks 1973), dytiscid beetles are very well represented in the vernal pools of northern habitats (*e.g.*, Larson 1997), and limnephilid caddisflies are relatively well represented in tundra pools (Wiggins and Parker 1997).

A second reflection of low productivity in cold climates is lower availability of the food used by adult biting flies for egg development, which has led to the prevalence of autogeny in Arctic biting flies. These species do not feed on blood as adults, unlike many of their temperate relatives, but instead develop eggs from reserves carried through from the aquatic larval stage. This trait is correlated with the scarcity of vertebrate hosts available to provide blood meals in the Arctic. Most tundra black flies are autogenous (Danks 1981). Fully one quarter of Yukon black flies are obligately autogenous, compared with only 2.4% of black flies as a whole (Currie 1997). High-Arctic mosquitoes show finely tuned responses to the unreliability of potential hosts, with both obligate and facultative autogeny in the first gonotrophic cycle (Corbet 1964, 1967). In *Aedes impiger* (Walker), for example, some females develop eggs immediately after emergence without

**Table 1.** Sample responses of aquatic insects to food limitation, seasonality, and variability in cold climates (for examples and references see text).

| Constraint or threat | Sample response |
|---|---|
| **Food limitation** | |
| Larval foods reduced | Use generally available detritus<br>Use dissolved organic carbon (DOC) or fine particulate organic matter (FPOM) rather than coarse particulate organic matter (CPOM)<br>Use wider food range |
| Adult foods reduced | Autogeny, increased range of hosts for feeding on blood |
| **Seasonality** (see also Tables 2–5) | |
| Low water temperatures | More than one year per generation, or univoltine<br>Voltinism different according to temperature<br>Development at low temperatures |
| Cold terrestrial conditions | Univoltinism, spring emergence |
| Summer disturbance but less disturbed winters | Winter growth in some alpine habitats and larger lakes and rivers |
| Long, cold winters | Diapause |
| Differences from year to year | Different voltinism, cohort splitting, photoperiodic control of growth, ongoing adjustment of dormancy or diapause |
| **Variability** | |
| Unpredictable seasons | Staggered development, skewed hatch or emergence, deferred emergence at low temperatures |
| Year-to-year variations | Prolonged diapause, parthenogenesis, reduced mating exposure (and see Table 5) |

feeding (obligate autogeny); others delay egg development for a period and then either develop eggs from host blood if they feed successfully (anautogeny) or develop far fewer eggs if they fail to find a host (delayed facultative autogeny). As might be expected, these species accept a relatively wide range of hosts, including both birds and mammals (Corbet and Downe 1966).

## Seasonality and insect life cycles

Cold climates are characterized by seasonality, with periods of the year that are too cold for activity by most species in most aquatic habitats. Other elements of cold climates that influence insect habitats (Danks 1999) include severity (persistent conditions that limit life, including low summer temperatures as well as cold winters), unpredictability (short-term perturbations that, especially where temperatures are cool to start with, may limit activity on a daily time frame), and variability (changes from year to year in summer temperatures and other features).

The larger aquatic habitats, as well as habitats fed by ground waters, are buffered against the worst conditions. Deep lakes do not freeze to the bottom, even in the Arctic. Rivers with adequate flow remain unfrozen beneath the ice. Also, some geothermally influenced habitats are relatively warm in winter as well as summer. Nevertheless, the life cycles of most insects, even in buffered or protected aquatic habitats, have to take account of local seasonality because most adults emerge into the much more seasonal terrestrial environment to carry out reproductive activities that tend to be especially sensitive to ambient conditions. Successful life cycles therefore accord with adaptive annual programmes that optimize the use of seasonal windows of opportunity. As might be expected, such seasonal regulation is prominent in aquatic insects at high latitudes.

Relevant variables in these seasonal life cycles are voltinism (duration of a generation), the timing of active stages including seasonal positions of immature development, the timing of dormancy in immature stages, and emergence of adults and reproductive activity. Dormant stages may be especially resistant to adverse conditions (see later sections) but here I focus on temporal aspects of the response.

Where climates are cold, rapid development is difficult and species with several generations per year are unusual. Indeed, many Arctic and alpine species have life cycles lasting more than one year. Sample durations are 2 years in dytiscids (Dolmen and Solem 2002) and some caddisflies (Solem 1985), 2 or 3 years in tanytarsine chironomids (Butler *et al.* 1981; Butler 2000), 3 years in a caddisfly (Hershey *et al.* 1997), up to 3 or 4 years in some other chironomids (Hershey 1985*a*), 5 years in some stoneflies (Townsend and Pritchard 1998; Zwick and Teslenko 2002) and dragonflies (Cannings and Cannings 1997), and as many as 7 years in two *Chironomus* species from Arctic tundra ponds (Butler *et al.* 1981; Butler 1982*a*). For many other specific examples see Danks (1981, p. 281; 1992, Tables 2 and 3). The longest life cycles tend to belong to the largest species (Danks 1992). Nevertheless, in alpine habitats ameliorated and stabilized by groundwater flow, multivoltine life cycles are possible in cool-adapted species such as the chironomid *Diamesa incallida* (Walker) (Nolte and Hoffmann 1992).

In several species with wide geographical ranges, life-cycle duration varies with latitude or elevation, for example from 1 year or less in warmer zones to 2 years or more in colder regions, or from 1 or 2 years in the southern part of the range to 3 or 4 years farther north. Data of this sort are available for alpine stoneflies, caddisflies, mayflies, and chironomids as well as for boreal and Arctic chironomids and dragonflies (for specific references see Danks 1981, 1992). A few species even have 1-year and 2-year life cycles within a single cohort in the same place (*e.g.*, Ulfstrand 1968; and see below).

Notwithstanding the existence of multi-year life cycles, many cold-climate aquatic species are univoltine except in extreme habitats. Most chironomid species in an Arctic Alaskan river (Hershey *et al.* 1997), caddisflies from Alaskan rivers and streams (Irons 1988), many Yukon black flies (Currie 1997), mayflies from higher latitudes (Arnekleiv 1996), Arctic mosquitoes (see below), and an alpine blepharicerid (Frutiger and Buergisser 2002) always have only one generation per year. The fact that so many species are univoltine suggests that life cycles are constrained by strictly seasonal programs of development (*cf.* Danks 1987, 1991*b*), and such an expectation is consistent with the annual need of most species to reproduce in terrestrial environments. Nevertheless, univoltine and semivoltine species have several different kinds of life cycle, depending especially on the roles of dormancy in structuring the patterns of development.

Life cycles in which development is slow but more or less continuous are possible in stable habitats such as deep lakes and some species even grow during winter. Winter-developing species are known from alpine zones as well as northern areas. They include some caddisflies (*e.g.*, Ulfstrand 1968), winter stoneflies (Ulfstrand 1968; Brittain 1983), and mayflies (Brittain 1980). Some of the species active in winter are dormant in summer. Conversely, typical species are dormant during the coldest part of the year, but many of them start or continue this dormancy during unsuitable conditions other than the winter, a program that again tends to enforce a strictly 1- or 2-year development. For example, northern *Aedes* mosquitoes overwinter as drying- and freezing-resistant eggs and even in the high Arctic complete a generation each year (Corbet and Danks 1973). Depending on species, northern black flies emerge in spring from dormant eggs or larvae (*e.g.*, Currie 1997). Egg diapause in an alpine blepharicerid lasts 4 months, from late summer through winter (Frutiger and Buergisser 2002). The semivoltine alpine stonefly *Megarcys signata* (Hagen) has an egg diapause lasting almost a full year in natural habitats (Taylor *et al.* 1999). Other stoneflies such as *Pteronarcys dorsata* (Say) spend 10–11 months in diapause in the egg stage and take 3 or 4 years to develop (*e.g.*, Barton 1980).

There is less information for aquatic species than for terrestrial species about how such winter dormancies are controlled. Although eggs of the stonefly *Dinocras cephalotes* (Curtis) remain in a simple temperature-controlled quiescence for up to a year (Lillehammer 1987), many general observations confirm the existence of diapause in other species. Diapause programmes arrest development and not only anticipate the adverse season, ensuring that appropriate preparations are made in advance, but also require a period of diapause development: particular photoperiod or temperature exposures are required before individuals are competent to resume development when conditions become favourable again, thereby preventing inappropriate responses to short-term ameliorations in fall. Many aquatic species from cold climates have a true diapause induced by photoperiod and temperature (see Danks 1987 for a general review; Goddeeris 2004). For example, cold exposure (*e.g.*, –2 °C) of some duration is needed for hatch of eggs of the mayfly *Ephoron album* (Say) (Giberson and Galloway 1985), suggesting temperature-controlled diapause development. Diapause eggs of the mayfly *Hexagenia limbata* (Serville) hatch only after exposure to cold (Giberson and Rosenberg 1992*b*). Diapause development in eggs of the stonefly *Isoperla obscura* (Zetterstedt) is fastest at 0–1 °C (Økland 1991). Preliminary results for the midge *Diamesa mendotae* Muttkowski hint at increased pupation rates in larvae exposed to temperatures below the supercooling point, as opposed to above it (Bouchard *et al.* 2006*b*). Diapause in eggs of the stonefly *Arcynopteryx compacta* (McLachland) is completed more rapidly when they are dehydrated in ice (Gehrken and Sømme 1987; Lillehammer 1987; Gehrken 1989). Species of chironomids from high-Arctic ponds have a clear-cut diapause so that only species fully fed by winter will emerge the following year (Danks and Oliver 1972*a*), and thus those that are almost but not quite fully fed remain in diapause for nearly the whole of the subsequent summer (see Spring challenges below). Such diapause responses assist the synchrony of spring emergence (*e.g.*, Sawchyn and Gillott 1974*b*).

Control of development can also be achieved through adjustments of growth rate, not just by the complete cessation of development through diapause. In the dragonfly *Lestes congener* Hagen, larvae respond to seasonal "time stress" (as indicated by short photoperiods, for example) by accelerating activity and developmental rate (Johansson and Rowe 1999; Johansson *et al.* 2001). Similar responses to photoperiod are shown by alpine caddisflies (Shama and Robinson 2006).

In northern dragonflies such as *Coenagrion hastulatum* (Charpentier), *Leucorrhinia dubia* (Vander Linden), and *Aeshna juncea* (Linn.) (Norling 1976, 1984*a*, 1984*b*, 1984*c*), a diapause induced by long days in summer — which prevents emergence before the adverse season — is followed by a winter diapause induced by short days. This diapause is followed in turn by rapid development induced by long days in larvae large enough to emerge the same year, accelerating and synchronizing emergence in summer. These arrests and adjustments of development (which are modified also by temperature thresholds, direct temperature effects, and differences among instars in the occurrence and intensity of the responses) permit several different developmental options, such as 3-year or 4-year development.

In effect, development can be directed into alternative life-cycle pathways according to regional climates and their year-to-year variations, ensuring safe overwintering and appropriate seasonal coincidence of adults (Norling 1984*c*; Danks 1991*b*). A common annual pattern is rapid development in summer and long dormancy at other times, a typical response to seasonality. An added pattern as just noted is adjustment of seasonal timing through growth rate. Many other species vary the occurrence or duration of diapause, as discussed in the following section. Finally, life cycles may include not only timed adult emergence into terrestrial habitats but also timed movements among larval habitats, as discussed in later sections.

## Variability

Because conditions in cold climates may be close to the limits for insect life, unpredictability and variability are especially significant. For example, in high-Arctic regions summer temperatures are so low that the air temperature on a cold day is likely to fall below 0 °C: in a sample high-Arctic site there is a 90% chance that subfreezing temperatures will occur during July (Danks 1993*a*). A summer that is only a few degrees colder than usual may delay or prevent the thawing of ice on lakes, hindering insect emergence.

Although species from many zones show patterns of variation that seem designed to cope with unpredictability and variability (Danks 1983), alpine and northern aquatic insects provide some particularly clear examples. On shorter time frames, many species have staggered development that prevents the whole population from being synchronized in a vulnerable stage. The dormant eggs of many species are resistant to adverse temperatures and, unlike the larvae that hatch from them, do not depend upon the availability of food; staggered hatch of such eggs is relatively common in cold and variable habitats, though not confined to them (*e.g.*, Zwick 1996). For example, extended asynchronous hatch is characteristic of the alpine stonefly *Pteronarcys californica* (Newport) (Townsend and Pritchard 2000) as well as northern *Isogenoides* species (Sandberg and Stewart 2004) and some alpine mayflies (Knispel *et al.* 2006). In *Hexagenia* mayflies from northern habitats, half of the eggs hatch readily, but the rest enter diapause (Giberson and Rosenberg 1992*b*). Staggered hatch has been suggested, albeit for a temperate region, as a way to compensate for mortality from slush ice or spates (Wise 1980). Other potential adaptations to risk in aquatic insects from cold climates include scattered emergence, especially of females, after the main emergence period (Ulfstrand 1969).

On a longer time frame, high-Arctic chironomids defer pupation when a particular season is especially cold and thus likely not suitable for reproduction even if it allows larval development; they emerge instead only in the following year (Oliver 1968; Danks and Oliver 1972*a*). Likewise, diapause for more than one adverse season ("prolonged diapause") characterizes variable or unpredictable habitats. In most such cases a small proportion of individuals spend an extra year or more in diapause even though most of their siblings emerge (for discussion and references see Danks 2006*b*). Few examples are known in aquatic insects from cold climates, but this almost certainly reflects a lack of investigation, because there are many terrestrial examples (Chernov 1978; Danks 1981).

On a still longer time frame, the evolutionary role of parthenogenesis in buffering risk has been explored (*e.g.*, Downes 1962, 1965; Danks 1981). In variable environments, species that respond too rapidly to changing circumstances, such as an unusually warm polar summer, will be at a disadvantage when typical cool summers return. Such responses are constrained by obligate or predominant parthenogenesis, which prevents recombination and thus the rapid selection of variants in response to change. Parthenogenetic species of insects are indeed much more prevalent in the Arctic (and Antarctic) than in more equable climates. Parthenogenetic species among aquatic groups from cold climates include chironomids, caddisflies, mayflies, and black flies, including *Prosimulium ursinum* and species of the genus *Gymnopais* (review by Danks 1981, pp. 291–292; Currie 1997; Langton 1998). Of course, parthenogenetic species have the advantage too of not requiring mating activities that are difficult in cold aerial habitats (see Summer activity).

## Preparations for winter

As winter approaches, organisms must anticipate and prepare for its onset. The patterns of onset differ among aquatic habitats, but in the zones occupied by insects nearly all water bodies cool more slowly than terrestrial habitats in the same area because the high specific heat of water and the latent heat of freezing slow the rate at which temperatures fall. However, small water bodies cool more quickly than large ones. Except for spring-fed streams, watersheds freeze from the small, upper creeks to the large, high-order channels because of the much higher surface area to volume ratio of the former. This difference can be as much as one month in some regions. Also, alpine streams originate at elevations that are colder than the lowland rivers they supply. Shallow pools freeze before deeper ponds, which in turn freeze before large lakes.

A second relevant factor is the relationship of seasonal precipitation to the onset of cold weather. In many climates, ponds increase in depth following their summer minimum as temperatures cool, lowering evaporation, and as autumn rains begin. The result may be that much of the marginal area most susceptible to winter freezing is dry in summer and may not have been colonized by benthic organisms after the autumn rains (Danks 1971*a*).

In preparation for winter, insects may stay in their summer habitat, which may or may not freeze, or move to a different habitat with less severe conditions for the winter, either outside the summer water body or elsewhere within it. All of these strategies are used by one or another species in cold climates (Table 2).

In large lakes at any latitude, characteristic species remain in central bottom sediments that do not freeze. Bottom temperature during the winter is 4 °C in typical temperate dimictic lakes but Arctic lakes cool below this temperature and may even remain below 4 °C all year, at least in some years (Oliver 1964; Milner *et al.* 1997). In the somewhat less severe climates of the cold-temperate zone, alternative habitats are available to insects moving from small bodies of water that may freeze. For example, gerrids and most other semi-aquatic bugs leave the summer habitat in the autumn and overwinter beneath litter and snow on land (Spence and Andersen 1994). Also overwintering on land are some northern caddisflies (Ellis 1978;

**Table 2.** Sample responses of aquatic insects that anticipate winter conditions in cold climates (for examples and references see text).

| Constraint or threat | Sample response |
|---|---|
| Increased water depth before winter | Avoidance of movement to newly submerged edges more likely to freeze |
| Likelihood of winter ice or freezing | Movement to terrestrial habitats, especially as adults |
| Likelihood of winter freezing | Movement to more central habitats |
| | Movement to deeper layers in substrate |
| | Construction of burrows or cocoons |
| | Development of cold hardiness (see Table 3) |
| Early onset of winter | Preparations for and entry into diapause well in advance of winter, at least for terrestrial adults |
| Long period of inactivity | Sequestering of energy supplies as fat |

Berté and Pritchard 1983), culicine mosquitoes (Danks 1981), and beetles such as dytiscids.

The aquatic stages of most stream species move within the habitat, colonizing central areas that will not freeze. Such species include some corixids, mayflies, caddisflies, stoneflies, and chironomids (Olsson 1982, 1983; Barton *et al.* 1987; Irons *et al.* 1993). Some lentic mayflies and caddisflies also move to deeper water in the autumn (*e.g.*, Wodsedalek 1912; Gibbs 1979; Tozer *et al.* 1981). Another set of species penetrates the substrate. For example, some of the species of chironomids in a shallow pond move deeper into the sediment in winter (Danks 1971*b*), although such movement may reflect only the seeking of additional protection during immobile dormancy, because penetration into sediments occurs in the same habitat in response to high water temperatures and anoxia in summer. Likewise, chironomid larvae occupying vegetation that dies back during winter leave it in fall to overwinter in the sediments (Danks and Jones 1978 for *Endochironomus nigricans* (Johannsen)). Nevertheless, deep penetration into the substrate, notably into the hyporheic zone of streams, is certainly one adaptation favouring the survival of stoneflies in northern regions (Stewart and Ricker 1997).

Finally, a small number of species remain in sites likely to freeze. Those known to do so include chironomids and empidids and a few mosquitoes, stoneflies, caddisflies, and dragonflies (see Surviving the winter).

The timing of preparations for winter therefore depends on habitat and life cycle, but at least some species make early preparations for diapause, especially those overwintering on land as adults. *Culex* mosquitoes that overwinter as adults enter diapause and then go into their overwintering habitats relatively early in the year, well before any likelihood of freezing temperatures (*e.g.*, Madder *et al.* 1983). Preparations for winter include the storage of energy in the form of fat that supports metabolism, albeit at a reduced rate, during the fall, winter, and spring, although in some species the trends are relatively weak (*cf.* Meier *et al.* 2000). However, Arctic gyrinid beetles, for example, like temperate ones, accumulate substantial fat reserves (Svensson 2005).

## Surviving the winter

Winter conditions in cold climates include low temperatures, ice formation, snow accumulation, and chemical changes in water sealed off beneath ice and overlying snow. Temperatures vary from 4 °C to about 0 °C in unfrozen habitats and from 0 °C to much colder in frozen ones. Moreover, conditions can differ among different zones of one habitat and also from one year to the next in the same habitat. Temperatures in the high-Arctic lake studied by Andrews and Rigler (1985) fell to –18 °C at 0.5 m depth but only –7.5 °C at 1.75 m. Irons *et al.* (1989) recorded bottom temperatures of –0.1 °C in one year and –12.8 °C in another year in an Alaskan stream. Sediments of a shallow pond in Alberta reached –8 °C during winter (Daborn and Clifford 1974). Freezing depends on temperature and snowfall but also on water supply. Ponds and streams in cold regions freeze to a greater depth whenever there is less snow for insulation and in dry years when winter water levels and flows are lower (Clifford 1969; Irons *et al.* 1989). Water levels may continue to fall in northern rivers throughout the winter (Olsson 1981).

Ice formation in the aquatic habitat can damage organisms mechanically and encourage freezing of their body fluids, but ice forms differently in different kinds of habitat. Lentic habitats, especially smaller ones that are not turbulent from wind action, typically are covered quite early in the winter by surface or sheet ice that overlies unfrozen water. Once all of the overlying water is frozen the substrate may freeze, the nature of the resulting winter habitat depending on the water content and particle size of the sediments. If air temperatures continue to fall these frozen substrates experience temperatures below –20 °C in Arctic habitats (Scholander *et al.* 1953). Surface ice also grows out from shore in sheltered areas over flowing water, but in turbulent flows surface ice formation is prevented. Instead, frazil ice forms where there is too much water movement to allow ice to consolidate, comprising suspended ice crystals that customarily lead to aggregations of ice or slush (review by Shen 2003). These crystals and aggregations may then coalesce and adhere to the bottom to form anchor ice. Anchor ice may even serve to seal off the streambed from further disturbances (Beltaos *et al.* 1993), although its subsequent release may then scour the bed downstream.

Snowfall influences habitat temperatures because air between the snow flakes makes snow a very good insulator, so that sediments beneath ice and snow are buffered from air temperatures. Therefore, these sediments reach equilibrium between the warm earth below them and the cold air above the snow. Consequently, aquatic habitats adjacent to the warm earth can warm up in midwinter when air temperatures ameliorate even though the air is still very cold (Danks 1971*a*). In the Arctic, however, habitats underlain by permafrost continue to cool (Andrews and Rigler 1985). The depth of snow that accumulates depends on weather and also on local distribution according to depressions, vegetation, wind, and so on, creating potentially large differences among habitats and subhabitats (Danks 1991*a*). Snowfall is relatively limited in the Arctic (although the strong winds there move it into substantial drifts) but relatively heavy in most alpine and boreal regions. Heavy snow may crack ice, releasing water that freezes as opaque ice below the snow and above the original clear ice.

At least in ponds, surface ice formation concentrates solutes in the unfrozen water below a continuous layer of surface ice. Surface ice also hinders oxygen exchange with the air. Although phytoplankton photosynthesis can occur in cold water, only a few centimetres of snow reduce the light penetrating lake ice to near zero, eliminating this source of oxygen (Schindler 1972; Reid *et al.* 1975; Sahlberg 1988). Cut off from the air by ice and shielded by snow, small and medium-sized lentic habitats regularly become virtually free of oxygen during winter, especially when sediments have a high biological oxygen demand, leading to winter kills of fish and even invertebrates (Danks 1971*a*; Nagell and Brittain 1977). Oxygen can also be reduced by surface ice even in rivers because of declines in turbulence and photosynthesis (Power *et al.* 1993).

Insects in winter therefore face several different challenges, and they respond in the many ways summarized in Table 3. Although conditions vary widely among the various aquatic habitats, the majority of insect species from cold climates are dormant during the coldest parts of the year, and many of them have to withstand very low or freezing temperatures. Their key requirement for cold hardiness is now considered in particular detail.

The elements of insect cold hardiness have been well established for terrestrial insects (for sample reviews and many additional references see Danks 1996, 2005, 2006*a*, 2007; Bale 2002). Insects can be injured by cold temperatures both above and below the freezing point. Injury occurs above freezing (“chilling injury”) when enzyme systems or membrane lipids are disrupted, for example. Many species also withstand temperatures below freezing. Typical insect species survive by supercooling (“freezing resistance”), when the body fluids remain unfrozen even at very low temperatures. Supercooling occurs because ice formation requires water molecules to adopt the hexagonal configuration of the ice crystal, and normally this is assisted by their aggregation around a nucleus that initiates freezing. In water bodies this would be a dust particle, for example. However, in very small volumes of clean water substantial supercooling is possible because in the absence of nucleators an appropriate aggregation of water molecules stable enough to initiate freezing will occur only if it is so cold that the molecules are moving very slowly. Droplets of pure water then supercool to the spontaneous or homogeneous freezing point, which is about –40 °C (Vali 1995). Insects can achieve similar or even lower supercooling points by avoiding, eliminating, or

**Table 3.** Sample responses of aquatic insects to winter conditions in cold climates (for examples and references see text).

| Constraint or threat | Sample response |
|---|---|
| **Low temperatures** | |
| Cold water | Chilling tolerance |
| Mild freezing, frazil or anchor ice | Freezing resistance (supercooling) at relatively high subfreezing temperatures above the body melting point<br>Presumed manufacture of cryoprotectants |
| Prolonged severe freezing | Freezing tolerance<br>Presumed manufacture of cryoprotectants |
| Mechanical damage from ice formation | Habitat and microhabitat choice<br>Penetration into substrate<br>Construction of cocoons |
| Progression of freezing in the microhabitat | Movement away from the ice front during winter |
| Severe cold in terrestrial overwintering habitats | Supercooling, resistance to inoculative freezing<br>Low activity thresholds for winter activity<br>Manufacture of cryoprotectants |
| **Chemical conditions** | |
| Concentration of solutes | Osmotic control and other adaptations |
| Oxygen low or absent | Dormancy<br>Resistance to anoxia |

masking nucleators. Ice itself is a very efficient nucleator, however, so contact with external ice would be expected to initiate inoculative freezing through the cuticle, especially in aquatic larvae that are not heavily sclerotized, and once a single internal ice crystal forms it initiates very rapid freezing in the remaining supercooled liquid.

Supercooling depends on the volume of liquid and so can also be enhanced by reducing the availability of water (*e.g.*, Zachariassen *et al.* 2004); most overwintering insects reduce the amount of freezable water by associating the water molecules with particular molecules or biological surfaces. Insects manufacture two main kinds of antifreeze molecules. First, small solutes such as glycerol (and other polyhydric alcohols, sugars, and some other substances: see tables in Lee 1991 and Ramløv 2000), separately or in combination, lower the true freezing point or melting point by colligative action, enhancing supercooling especially at the high concentrations often encountered. The solutes also specifically protect proteins and membranes (Storey and Storey 1992). Second, large antifreeze proteins inhibit freezing by preventing ice growth at the ice–water interface and by masking potential sites of nucleation (review by Duman 2001), and thus are most effective at temperatures relatively close to freezing. Their effectiveness is greatly enhanced by interactions with each other and with small molecules such as glycerol (Wang and Duman 2005). Although not yet reported from Diptera (the dominant northern group), antifreeze proteins are widely distributed in Alaskan insects, including the gerrid *Limnoporus dissortis* (Drake and Harris) (Duman *et al.* 2004), and are presumed to occur in eggs of a northern stonefly (Gehrken and Sømme 1987).

Other insect species can survive actual freezing within the body ("freezing tolerance"). The various cryoprotectants, including "antifreeze" proteins, serve to protect membranes and other structures while they are frozen (*e.g.*, Duman 2001). This freezing is extracellular, not intracellular (with limited exceptions), because water is drawn out of the cells to freeze on ice between them. If the freezing takes place too rapidly, water cannot leave the cells in this way, and the resulting intracellular freezing is normally fatal. Processes that draw water out of cells onto intercellular ice have parallels with dehydration, and indeed water and temperature relationships are closely linked (Ring and Danks 1994). Extensive supercooling in some Arctic terrestrial insects appears to depend on marked dehydration, which increases cryoprotectant concentrations (Bennett *et al.* 2005).

Some small soil organisms with permeable cuticles avoid freezing by extensive dehydration as water is lost to external ice, thereby progressively lowering the temperature at which the body contents would freeze (review by Holmstrup *et al.* 2002). Some frozen chironomid larvae show marked wrinkling and dehydration that presumably precedes freezing (Danks 1971*b* for an Arctic pond; Lencioni 2004 for an alpine stream), in addition to any physiological dehydration in preparation for winter.

Unfortunately, few detailed physiological or biochemical experiments have been done with aquatic species, so we do not know what combinations of cryoprotectants might be used. Presumably they would be similar to profiles in terrestrial species.

Many terrestrial insects also manufacture proteinaceous ice-nucleating agents for the winter (reviews by Duman 2001 and Lundheim 2002), which are supposed to limit supercooling in freezing-tolerant insects. The very rapid and damaging formation of ice that takes place once freezing is initiated in supercooled insects is thereby avoided, including the intracellular freezing that is more likely under such conditions. Some freezing-tolerant terrestrial species lack ice-nucleating agents, however, and in most of these species inoculative freezing from the environment at relatively high subfreezing temperatures is required to permit survival (review by Duman *et al.* 1991, pp. 397–398). Similar inoculation of freezing by ice could occur easily in species overwintering in aquatic habitats, and so ice-nucleating agents would not be expected.

How aquatic insects cope with ice in the immediate environment is of particular interest (Moore and Lee 1991; Oswood *et al.* 1991; Irons *et al.* 1993; Frisbie and Lee 1997) because, unlike most terrestrial insects, they live in water or wet substrates. When surrounding ice is only at about 0 °C, as in the case of frazil and anchor ice, its temperature is above the true freezing point (or melting point) of all organisms because ordinary cell constituents provide some freezing-point depression, and supercooling is not required. Some alpine chironomids, stoneflies, mayflies, caddisflies, and other species survive in anchor ice but not in more severe conditions (Brown *et al.* 1953; Benson 1955).

Many aquatic insects are known to survive winter in habitats in which all of the water is frozen. For example, aquatic insects from several different orders live in Arctic ponds that freeze completely (Danks 1981). However, when minimum habitat temperatures are relatively close to the freezing point, it may not be possible to distinguish species that survive by supercooling even when encased in ice from those that are freezing tolerant. Nevertheless, freezing tolerance has been demonstrated unequivocally in the larvae of many species of chironomids (Danks 1971*b* lists more than 25 species of many genera in different subfamilies that are certainly freezing tolerant, and many more that survive in freezing habitats and may be freezing tolerant) as well as in some empidids, mosquitoes, and other flies and caddisflies, and it may occur in some other taxa including dragonflies. For example, chironomids survive the winter frozen solid in Arctic sediments. Larvae of pond species studied by Scholander *et al.* (1953) and Danks (1971*b*) survive –20 °C in nature, and species collected frozen from high-Arctic ponds survived short experimental treatments of –32 °C (Scholander *et al.* 1953) and several weeks at –18 °C (Danks 1971*b*). In high-Arctic Char Lake, several species of chironomids showed substantial survival following overwintering at temperatures down to –18 °C (Andrews and Rigler 1985). Freezing tolerance of cold-temperate species is less extreme, but some species survived experimental freezing at –4 °C, with much better survival in winter cocoons (Danks 1971*b*). Some lotic species likewise are freezing tolerant. Oswood *et al.* (1991) and Olsson (1981, 1982) found diverse chironomid species alive after a winter frozen in the bed of northern streams. Larvae of *Diamesa mendotae* from northern streams are freezing tolerant (Bouchard *et al.* 2006*b*), and so are other *Diamesa* species from alpine habitats (*e.g.*, Lencioni 2004).

Several species of caddisflies appear to be freezing tolerant, notably species that overwinter as larvae in frozen tundra pools. The limnephilid caddisfly *Sphagnophylax meiops* Wiggins and Winchester, for example, spends more than 8 months as a larva frozen in the wet substrate, where the mean temperature in April (late winter) is –12.3 °C (Wiggins and Winchester 1984; Winchester *et al.* 1993). Lotic species are less cold hardy than lentic ones in the north (Wiggins and Parker 1997), although

Olsson (1981, 1982) reported survival of several species from frozen river sediments.

Another set of species that may be freezing tolerant comes from small container habitats that hold so little water that they are not buffered from winter temperatures. Larvae of mosquitoes survive in tree holes that may freeze to –15.5 °C (Copeland and Craig 1990). Larvae of *Orthopodomyia alba* Baker, for example, frozen experimentally, survived 24 h at –25 °C and 16 days at –15 °C, at least in some instars. Pitcher-plant inhabitants that overwinter as larvae include the mosquito *Wyeomia smithii* (Coquillett) and the chironomid midge *Metriocnemus knabi* (Coquillett) (Giberson and Hardwick 1999). Both species can overwinter encased in ice, and many larvae of *M. knabi* withstood exposure to –16.5 °C for 116 days (Paterson 1971). In contrast, larvae of *W. smithii* are not freezing tolerant and supercool only to about –5 °C (Evans and Brust 1972). They rely on insulation of the pitcher by overlying snow, so survival varies according to snowfall patterns as well as winter temperatures (Farkas and Brust 1986).

Other species survive temperatures below 0 °C as overwintering eggs, as in some *Aedes* mosquitoes (Copeland and Craig 1990), stream black flies (Kurtak 1974 for eggs laid in terrestrial habitats), and mayflies (Clifford 1969; Giberson and Galloway 1985), including the Arctic species *Baetis bundyae* Lehmkuhl (Giberson *et al*. 2007). Some aquatic insect eggs, such as those of *Lestes* dragonflies, survive temperatures below –20 °C, and as low as –28 °C in *L. congener* (Sawchyn and Gillott 1974*a*, 1974*b*), although snow cover too is necessary for winter survival. In some caddisflies from temporary pools, the gelatinous egg matrix resists freezing and drying and perhaps even gives freezing tolerance to the eggs (Wiggins 1973). However, in frozen streams eggs of the stonefly *Arcynopteryx compacta*, although encased in ice, overwinter down to –29 °C not by freezing but by supercooling through loss of up to two-thirds of the normal water content (Gehrken and Sømme 1987). There may be parallels here with the resistance against freezing of soil forms that depend on extensive dehydration by loss of water to external ice (see above). Resistance to inoculative freezing might also be possible because of antifreeze proteins, as shown experimentally for terrestrial species (Olsen *et al.* 1998; Zettel 2000). These proteins are most effective when the potential seed ice crystals are very small (Zachariassen and Husby 1982) and so might be able to prevent inoculation through cuticular pores that are very small (Duman 2001).

Aquatic species that survive in frozen habitats that do not get very cold probably supercool rather than freeze. For example, dragonfly larvae survive exposure to –1 °C (Duffy and Liston 1985). Species from prairie pond sediments have been reported to survive natural winter temperatures as low as –6 or –8 °C (Daborn 1971; Sawchyn and Gillott 1975), but survival is not very high as temperatures approach the supercooling point of about –4 to –8 °C (Moore and Lee 1991). Empidid larvae, which like chironomid larvae do not appear to move away before winter from sites likely to be frozen, also showed good survival after freezing in a sub-Arctic stream in Alaska (Irons *et al.* 1993). Nevertheless, experiments by Oswood *et al.* (1991) found that even wet empidid larvae have supercooling points between –5 and –10 °C.

In all of these species a period of preparation for overwintering in frozen habitats seems to be required. For example, dehydration of freezing-resistant stonefly eggs takes time: eggs cooled rapidly are killed (Gehrken and Sømme 1987).

In addition to cryoprotection, supercooling, and other physiological elements of cold hardiness, some aquatic insects withstand the mechanical effects of ice or move to avoid it. In some habitats, too, insects cope with high solute concentrations or anoxia beneath the ice.

The expansion of water as it freezes to form ice can damage aquatic insects. Unprotected individuals are usually injured by the mechanical forces resulting from this marked expansion (about 8%). As a result, most organisms that are simply frozen in containers in the laboratory do not survive (*e.g.*, Scholander *et al.* 1953; Danks 1971*b*; Olsson 1981). Freezing in sediments and plant material, which modify the mechanical forces, is likely to be less disruptive than freezing in water alone. In addition, many aquatic species overwinter in substrates within burrows or cocoons, which are presumed to provide protection against mechanical forces. For example, some species of chironomids build special winter cocoons that differ from the summer feeding cases. In temperate and Arctic shallow pond species these winter cocoons appear to be built in response to temperatures close to 0 °C (Danks 1971*b*). Moreover, the larvae may leave them again after the coldest period of winter (compare Danks and Jones

1978, Table 2). Such cocoons were also commonly encountered in a lake by Danell (1981) and in a river by Olsson (1981, 1982), although Andrews and Rigler (1985) found that only one of the chironomid species overwintering in a high-Arctic lake, *Chaetocladius* sp., made winter cocoons. Winter cocoons are tightly applied to the bodies of the larvae, which are folded up within the cocoons in ways characteristic of each species (review by Danks 1971*b*; Madder *et al.* 1977; Danks and Jones 1978). Such a posture would limit mechanical damage to the body and anal processes. Other insects, including some chironomids and caddisflies, simply seal their relatively robust summer cases for overwintering on or in the substrate (Olsson 1981).

As already noted, many aquatic species move in autumn to avoid areas where ice will form. Other species move in winter itself only as temperatures fall or in response to the ice front, as observed for the mayfly *Leptophlebia vespertina* (Linn.) by Olsson (1983) and experimentally for a range of groups by Oswood *et al.* (1991). Such "last-minute" responses are possible because temperature changes in most aquatic habitats are very slow.

Even in unfrozen areas, conditions beneath surface ice include concentration of solutes by freezing out. Concentrations can be high in small lentic habitats (Daborn and Clifford 1974). The distinct wrinkling and dehydration of chironomid larvae from frozen high-Arctic ponds and alpine streams may therefore result from the osmotic effects of solute concentration (Danks 1971*b*), but in any event would serve to enhance cold hardiness. Moreover, dehydration by passive processes, such as loss of water to external ice or to hyperosmotic solutions, is not energetically costly, as pointed out by Gehrken and Sømme (1987).

Resistance to anoxia varies widely among insect species (Hoback and Stanley 2001 and Hodkinson and Bird 2004 provide recent reviews emphasizing terrestrial species). In aquatic habitats, the amount of oxygen depletion beneath surface ice and thus its effect on insects varies from year to year, but some species survive many months in anoxia (*e.g.*, Nagell 1977, 1980; Nagell and Brittain 1977). Other species survive by moving to microhabitats such as pond edges which have more oxygen than elsewhere (Brittain and Nagell 1981). Some aquatic habitats experience anoxia in summer too, especially in the sediments. Some insects are well adapted to such conditions, including chironomid larvae that contain haemoglobin.

In less severe habitats, even in cold regions, some species are active rather than dormant during winter (review by Danks 1991*a*). The chief adaptations of the species that remain active in winter are low thresholds for development and activity (*e.g.*, Brittain 1980, 1983; Bengtsson 1981). In the same way, adults active in late winter show low activity thresholds and good supercooling abilities. For example, the supercooling point of adult *Diamesa mendotae* is –21.6 °C, similar to the lethal limit (Carillo *et al.* 2004; Bouchard *et al.* 2006*a*, 2006*b*).

Finally, it is worth noting that by no means all aquatic species in cold climates remain in water for the winter. Adults of the species that overwinter on land shelter chiefly in litter and similar habitats insulated by overlying snow, as in gerrids and some limnephilid caddisflies (see above). Sarcophagid larvae from pitcher plants leave the pitchers in autumn and pupate in the soil (Dahlem and Naczi 2006). These species survive by supercooling.

## Spring challenges

In spring, frozen habitats begin to thaw, challenging aquatic insects in different ways than they experienced during winter freezing. As frozen insects warm up prior to thawing, internal ice-crystal structure can change and potentially injurious recrystallizations and reorganizations can occur. One of the potential roles of cryoprotectants such as antifreeze proteins is to withstand or mitigate the effects of these rearrangements (Duman 2001). However, there is no information about this process in aquatic insects.

The manner in which ice melts in different aquatic habitats also influences the insects there. Melting of the snow accumulated during the long winter leads to very high flows in running water and to the temporary flooding of lower-lying land. Spring flows can be 100 times greater than the annual minimum in Lapland streams (Ulfstrand 1969). Increasing the impact in running waters is the breakup of ice, which accentuates disturbance during the thaw (Prowse 1994; Scrimgeour *et al.* 1994; Prowse and Culp 2003). Ice stores water but releases it rapidly on melting. Ice dams water behind it even when partially broken up, so that high-order streams back up during the thaw and flood larger areas than would otherwise be the case. Finally, all of the held-up water is released, increasing flows and the potential for floods downstream. For example, 27% of Mackenzie River flows have been attributed to ice-induced water storage (Prowse and Carter 2002). These spring events lead to very high currents, scouring of the bottom by rapidly moving water and current-borne ice, high suspended sediment loads and subsequent deposition, loss of fine particles, and flooding. Temperatures may stay low for some time but subsequently the water warms up relatively rapidly (Prowse and Culp 2003, p. 133). In lentic waters, on the other hand, ice melts gradually and although the melted ice and snow enlarge the area or depth and influence temperatures, and broken-up, wind-driven ice on large lakes can strike the shore, the dramatic disturbances typical of lotic systems are lacking.

Cold meltwater flowing into lakes under the ice is lighter than the 4 °C bottom water in cold stratified lakes and so influences insects in the littoral rather than the profundal zone. This water may contain pollutants such as acid rain, giving an "acid pulse" in regions that receive acid snow in winter. Acidified melting snow also influences insects in running waters (*e.g.*, Lepori *et al.* 2003).

In large river systems the direction of flow greatly influences the pattern of ice breakup because of climatic differences between lower and higher latitudes. Rivers flowing towards warmer regions (*i.e.*, south in the northern hemisphere) break up much more smoothly than those flowing in the other direction. In the latter, the water from melted tributaries adds to the build up behind accumulations of ice that have not yet melted (Prowse and Culp 2003). In smaller rivers and streams, however, much of the flow from snowmelt may be discharged before most of the channel ice or substrate melts. Meltwater then flows over ice or frozen ground, which protects the fauna from the worst effects (Miller and Stout 1989, p. 117).

Insect reponses to these spring challenges, including ways to compensate for the shortness of the subsequent summer, are summarized in Table 4. They vary according to habitat and latitude but are generally much less well known than are the physical challenges themselves (compare the reviews cited above).

A few species can exploit the very rapid currents and the food they carry during maximum discharge, as in the Swedish black fly *Metacnephia lyra* (Lundström), which consequently grows very fast at that time (Malmqvist 1999). Nevertheless, spring floods typically displace large numbers of some species (Brittain and Eikeland 1988). Other species avoid the breakup and peak flow, such as those that remain dormant in the hyporheos until after these major disturbances are over. Unlike most species (see Preparations for winter), a few species overwinter at the stream edge, not the centre, following autumn movements (Messner *et al.* 1983 for a hydrocorisid bug) or bankside oviposition (Kurtak 1974 for a black fly). Such placement may be related to avoidance of spring flushing rather than to winter conditions. Some species occupy other habitats during this spate. For example, larvae of the mayfly *Leptophlebia cupida* (Say) move from under river ice to safer tributaries as breakup starts (Clifford 1969; Clifford *et al.* 1979). Other species overwinter in lakes, colonizing the streams below them only by drifting down after the breakup ends and returning to the lakes in autumn by flight (Müller *et al.* 1976; Mendl and Müller 1978).

Timing of the life cycle allows these species to withstand or avoid the worst winter and spring conditions, but typically aquatic insects from cold climates nevertheless have to emerge in spring as early as possible to take advantage of the short summer season for adult reproductive activity. Two examples from high-Arctic ponds illustrate how this early emergence is achieved. Although these high-Arctic examples are especially striking, there is a marked general tendency for Arctic and boreal species to emerge in spring rather than later in the year (Downes 1962; Danks 1981, pp. 282–284).

Many investigated species of chironomids from Arctic ponds do not emerge unless they have completed growth the previous year (Danks and Oliver 1972*a* for the high Arctic; Butler 1982*b*). Any individuals that must feed in spring, even a little, defer emergence until the next spring, thereby entering the adult stage as early as possible in the short summer ("absolute spring species" of Danks and Oliver 1972*a*). However, preliminary information suggests that stream chironomids in the same high-Arctic locality do not have this type of life cycle (Hayes and Murray 1987), perhaps reflecting the wide differences among different aquatic habitats in cold climates already noted, and in particular the fact that lotic habitats are

**Table 4.** Sample responses of aquatic insects to spring challenges in cold climates (for examples and references see text).

| Constraint or threat | Sample response |
|---|---|
| Ice recrystallization in freezing-tolerant species | Presumed cryoprotectants |
| Scour of the stream or river bottom by ice or spring flows | Wintering in other habitats |
| | Choice of smaller habitats or tributaries, or those with lower flow |
| | Movement to edges before spring, or overwintering at edges |
| | Penetration into substrate |
| | Start of activity only after peak flow |
| Rapid currents | Adaptations to maintain position and feed in fast flows |
| Shortness of summer season | Emerge as early as possible in the spring through life-cycle controls |
| | Diapause to prevent emergence later than spring |
| | Overwinter in the warmest spring sites through oviposition-site selection the previous year |

greatly disturbed in the spring, whereas shallow ponds are not.

High-Arctic mosquitoes provide a second example of how early emergence is favoured. Like all northern species of *Aedes*, these mosquitoes must ensure that the egg stage, the only viable overwintering stage, is reached again in the same season. The high-Arctic species assist early egg development in the spring through specific oviposition behaviour, which has been characterized in particular detail for *Aedes nigripes* (Zetterstedt) (Corbet 1964; Corbet and Danks 1975). The females choose warm, moist sites near the temporary ponds that are the larval habitat, but with very exacting requirements. Areas with minor surface irregularities appear to be favoured. The sites must be protected from wind by bank contour and especially by stands of emergent sedges growing in shallow water near the pond edges, although these cannot be too dense or grow too close or the oviposition site might be shaded. Females of *A. nigripes* lay eggs only in direct sunshine and on banks that slope such that they are normal to the sun's rays and hence warmer than more gently sloping or steeper banks. Moreover, this choice of the warmest sites is enhanced because females oviposit only around the middle of the day and not at other times (Corbet 1965, 1966). Such very particular requirements of ovipositing females produce very high densities of eggs in a few favoured sites, whilst other places adjacent to the larval habitat, and even the whole shoreline of some ponds, carry no eggs at all. When the ponds fill in spring, the eggs hatch quickly because they are in the warmest possible places that thaw first.

## Summer activity

Although summers can be relatively hot in the interiors of continents that experience very cold winters, summers in regions with cool climates typically are short and heat-limited. Most aquatic insects must complete development, emerge, and reproduce under these conditions. Some of them compensate by extending the life cycle for more than one year (see Seasonality and insect life cycles). Depending on the habitat, insects may offset the low temperatures and short growing seasons by functioning even when heat is limited, notably through low thresholds or heat demands, or by gaining or seeking out heat through morphological, metabolic, and behavioural adaptations. Relevant challenges and responses are summarized in Table 5.

Some species select summer habitats or parts of the habitat that allow faster development. Movements may bring them to warmer and richer tributaries or flooded areas, although such movements have been interpreted as a response to spring disturbance (see Spring challenges) because growth there is no faster than in the main channel (Clifford *et al.* 1979). Even some chironomids from high-Arctic lakes show evidence of seasonal movements between lotic and lentic habitats (Oliver 1976). However, subsequent movements of *Parameletus* mayflies from the river edges colonized in spring to

**Table 5.** Sample responses of aquatic insects to summer constraints in cold climates (for examples and references see text).

| Constraint or threat | Sample response |
|---|---|
| Low habitat temperatures | Choice of habitats that are warm and have rich food supplies |
| | Choice of warm microhabitats within a given water body |
| Summers cool and short | Low temperature thresholds and heat requirements for development (including thermal compensation at higher latitudes) |
| | Small size |
| Cool air temperatures | Thermoregulation by adults, including dark colours, microhabitat choice, basking behaviour, and endothermy |
| | Low temperature thresholds for flight and other activities |
| | Activity on the ground or water surface with reduced wings and modified legs |
| | Mating behaviour curtailed with modification of genitalia, antennae, *etc.* |
| | Diel activity geared to temperature |

adjacent temporary ponds serve to reduce predation (Söderström and Nilsson 1987).

Although in most habitats options for heat gain by aquatic immature stages are limited, site selection plays a key role in ponds. The importance of oviposition-site selection has already been exemplified by high-Arctic mosquitoes, which lay eggs on the warmest and earliest-thawing sites. Furthermore, as demonstrated for some sub-Arctic species, mosquito larvae aggregate in the warmest places within the pools in which they develop, preferring sunny to shaded locations and even adjusting their depth to select places closer to the preferred temperature (Haufe 1957). Chosen sunny sites can be as much as 6 or 7 °C warmer at the same time of day than other parts of the same pond that are cooled by permafrost and lack insolation.

Many species from cool streams are cold stenotherms with low limits for activity and low temperature sums for development. Larvae of *Diamesa* chironomids from alpine glacial streams develop at temperatures below 2 °C (Milner and Petts 1994; Ward 1994). Eggs of stoneflies are cold adapted (Pritchard *et al.* 1996), and many larval stoneflies develop at very low temperatures (*e.g.*, Mutch and Pritchard 1986). Some larval mayflies and caddisflies are active at temperatures below 0.5 °C (Brittain and Nagell 1981; Solem 1983). Arctic mosquito larvae develop down to about 1 °C (Haufe and Burgess 1956). Similar adaptations occur in adults that remain active when it is very cold, as in high-alpine *Diamesa* chironomids that are active at temperatures as low as –16 °C (Kohshima 1984). Many rapidly developing species are small, a trait that reduces requirements of heat as well as food (*cf.* Danks 2006*c*).

Some cold-climate species have evolved metabolism that is relatively rapid at a given temperature, and such temperature compensation or thermal adaptation occurs most commonly in northern compared with southern species in a group (*e.g.*, Van Doorslaer and Stoks 2005 for *Coenagrion* dragonflies). However, such adaptation is by no means common even in Arctic insects (Danks 1981). Also reported in Arctic chironomids is shorter-term acclimation, whereby individuals compensate after transfer to a lower temperature by increasing respiratory metabolism (Bierle 1971; Butler *et al.* 1981). In *Hexagenia* mayflies, lower day-degree requirements for development have been reported for northern populations, even though temperature thresholds apparently are the same as those in more southern populations (Giberson and Rosenberg 1994).

Adaptations to cold summers are common in adult aquatic insects. Arctic dragonflies illustrate the ways in which species include or combine different strategies. (In dragonflies, too, post-emergence maturation would be slower in colder places.) Adaptations for dragonfly activity are closely tied not only with size, because insects can thermoregulate more easily when body size is larger, but also with behaviour (Sformo and Doak 2006). Small dragonflies keep flying by means of low minimum flight temperatures, whereas large ones fly at elevated temperatures by using wing muscles to produce heat; but dragonflies that spend much time perching generate less metabolic heat than those species that remain in flight for long periods.

One way of reducing heat requirements is to telescope or eliminate behaviours that are difficult when summers are cold, such as those requiring aerial activity. Indeed, many Arctic and alpine species of chironomids and other flies with southern relatives that normally mate in aerial swarms mate instead on the ground or water surface. Associated with this habit, to varying degrees depending on species, are modifications to some or all of the wings, thorax, antennae, palps, eyes, legs, and genitalia (*e.g.*, Downes 1962; Oliver 1983; Sæther and Willassen 1987; Oliver and Dillon 1997; Butler 2000). Several species of Arctic chironomids have male antennae modified to a greater or lesser extent towards the female form by loss of the long setae that are part of the system used by normal flying males to amplify and detect female wing-beat frequencies. One but not the other male morph of the Arctic chironomid *Oliveridia tricornis* (Oliver) has this adaptation (Oliver 1976, as *Trissocladius*). Wings are relatively reduced in the flightless tundra caddisfly *Sphagnophylax meiops* (Winchester *et al.* 1993). Northern *Gymnopais* black flies mate on the ground and have reduced eyes and other unusual characteristics (Currie 1997). Parthenogenesis, which is prevalent in Arctic insects (see Variability), also eliminates the need for mating.

Heat is acquired in the aerial adults of many aquatic insects, as in terrestrial species, by various forms of thermoregulation. For example, relatively large, melanic, and hairy adults bask in sunshine to raise body temperature (Danks 1981). In the high Arctic, even mosquitoes bask in the parabolic corollas of certain flowers, such as Arctic poppies, that track the sun during the day (Kevan 1989 and references cited there), thereby allowing enhanced activity and egg development.

Finally, diel patterns of adult emergence and activity accord with habitat temperatures. Whereas these temporal patterns in warmer climates are programmed by endogenous circadian rhythms geared to photoperiod, in cold and unpredictable habitats direct responses to temperature seem to be prevalent (*cf.* Danks and Oliver 1972*b* for high-Arctic chironomids).

## Aquatic communities in cold climates

Aquatic habitats in cold regions are comparatively poor in species compared with warmer regions, as might be expected, but diversity varies widely with latitude and depends on the habitat features already noted, especially productivity, habitat complexity, hydrological disturbance, channel stability, and freezing (*e.g.*, Lee and Hershey 2000; Voelz and McArthur 2000; Vinson and Hawkins 2003; Huryn *et al.* 2005; Füreder *et al.* 2006). The composition of aquatic faunas in boreal and alpine regions, and especially in Arctic regions, suggests that they have been selected by the constraints that result from cold climates. For example, Diptera, especially aquatic species, dominate the Arctic fauna as a whole and Chironomidae dominate the high Arctic (Danks 1990). This pattern is repeated in Arctic Alaska (Miller and Stout 1989; Oswood 1989, 1997; Hershey *et al.* 1995) and in alpine streams (Füreder *et al.* 2005). Such phylogenetic patterns, confirmed on a wider scale for Arctic insects as a whole (*e.g.*, Danks 1981, 1993*b*), suggest that certain groups are at an advantage in cold areas, owing to traits of physiology, habitats, and habits. Thus, changes in composition would reflect pre-existing advantages of particular taxa. For example, Chironomidae are even supposed to have evolved in cold mountain streams, and freezing tolerance is very widely distributed in the family (Danks 1971*b*). Stoneflies with winter adults (Nemouridae) are well represented in Alaskan streams (Oswood 1989). Stoneflies that survive in the Yukon Territory belong to groups that develop in hyporheic and other unfrozen habitats or have a long life cycle with winter diapause, live in permanent ponds well supplied with detritus or feed when litter is in peak supply, and lack the less favourable habitats and large vulnerable gills of the taxa that are absent (Stewart and Ricker 1997). Among northern caddisflies, species from cold lotic habitats that have unstable substrates, highly variable flows, and limited food are reduced (Wiggins and Parker 1997), although, as in dytiscid beetles (Larson 1997), many species from generally warmer, more stable, and richer lentic habitats persist.

The abundance of species in these attenuated faunas appears to vary more from one year to the next than in warmer regions because of abiotic disturbances (Miller and Stout 1989; Hershey *et al.* 1997). Year-to-year variation in discharge greatly influences black fly populations in an Alaskan river (Hershey *et al.* 1997). Indeed, the emergence and abundance of insect species in Alaskan streams varies so much from year to year that a simple index based on proportions of taxa is useless for indicating stream condition (Milner *et al.* 2006). Communities might therefore be expected to result to a greater degree from abiotic factors than from competition, predation, or anthropogenic influences. Nevertheless, interactions with other organisms are complex. Temporal and spatial separation of related species is known even in cold-climate habitats (*e.g.*, Butler 1982*a*, 2000 for Arctic chironomids; Solem 1983 for alpine caddisflies; Irons 1988 for Alaskan caddisflies). Litter processing in cold streams may depend to a greater degree on shredder insects than on microbes (Irons *et al.* 1994). Predation by fish is important (Hershey 1985*b*; O'Brien *et al.* 1997): in sub-Arctic lakes it can change the composition of chironomids (Mousavi *et al.* 2002) or eliminate larger predatory invertebrates such as dytiscids and modify the macrobenthos (Tate and Hershey 2003). However, predation by fish may vary because fish are more susceptible to winter anoxia beneath ice than are invertebrates; anoxia may thus enhance insect populations in some habitats by removing these predators (*e.g.*, Tonn *et al.* 2004).

Despite relatively low diversity in northern aquatic habitats, food webs can be complex, even in high-Arctic locations (*e.g.*, Danks 1990, Fig. 1). Terrestrial and aquatic habitats are linked extensively. Energy is transferred from aquatic to terrestrial habitats through emergence of aquatic insects as terrestrial adults and because birds and other terrestrial predators such as spiders eat aquatic insect larvae or adults. Energy and nutrients are transferred in the other direction by terrestrial detritus that washes into ponds and rivers during snowmelt, providing food for aquatic insects, and by vertebrates that defecate in or near aquatic habitats, for example.

Again, despite the many abiotic constraints on abundance and development, aquatic species from cold climates appear to disperse readily and recolonize habitats after populations have been eliminated (Miller and Stout 1989), which would lead to interactions among the colonists. Indeed, most Arctic species appear to be distributed widely in all of the regions and habitats one might expect (Danks 1981, 1990). Except when separated by marked relief, and at least within individual catchments, populations of many alpine taxa too do not appear to be especially isolated (*e.g.*, Hughes *et al.* 1999; Monaghan *et al.* 2002), suggesting dispersal and mixing of local populations. Therefore, the adaptations of aquatic insects to cold climates are by no means exclusively ruled by the need to meet abiotic challenges related to cold temperatures.

## Conclusions

Aquatic habitats in cold climates are influenced by cold winters with ice and snow and by disturbed springs with high flows, ice scour, and flooding. Most areas also have short, cool summers that are unpredictable.

Many adaptations to such conditions are shown by individual species of insects (see above) but, even in the same habitat, different species use different means to overcome these challenges, such as synchrony or asynchrony, winter growth or winter dormancy, diapause or quiescence, supercooling or freezing tolerance, and greater or lesser heat requirements for egg hatch or emergence. Even in individual species, the adaptations are best considered not alone but in sets, because typically they work together either for a given purpose (*e.g.*, behaviour and dark colour for heat gain by basking adults; reduced wings and antennae and modified genitalia and behaviour for ground mating; change of location, penetration into the substrate, and cocoon building for larval overwintering) or to allow the life cycle as a whole to be completed. For example, individual species combine such traits as food and microhabitat selection by larvae, pre-winter dispersal and habitat choice, cold hardiness and dormancy, optimum timing of spring emergence, curtailed mating to offset low air temperatures, and selection of warm oviposition sites. Most of these traits derive from more general ones used for various purposes elsewhere, such as penetration into the substrate for protection against various factors; others result from previous relevant evolution, as for the phylogenetically based cold hardiness of chironomid midges or the use of widely distributed detrital food particles by many pond species. These traits combine to form more specialized sets that allow species to exploit particular cold-climate habitats such as tundra ponds.

Moreover, some adaptations play multiple roles. Cocoons are made by many different taxa and, like the cocoons of temperate species, protect them and modify their habitats (Danks 2002, 2004). In cold aquatic habitats cocoons may not only provide protection from predation and a way to control oxygen supply, but also permit anchorage to the substrate (which avoids displacement and abrasion), protect against mechanical damage from water-borne substrate or ice particles as well as from surrounding ice, and act as a barrier against inoculative freezing by ice in some circumstances.

Given this diversity of simultaneous and alternative adaptations there are few absolute declarations to be made about how aquatic insects live in cold climates. Nevertheless, several general trends can be identified. The first such generalization recognizes the great diversity of available habitats with different conditions, from large lakes and rivers to temporary pools and streams. Alpine and lowland habitats are different; conditions for insects in water bodies of different sizes and hydrological signatures vary widely even in one location. Therefore, faunal composition varies widely from place to place.

A second generalization is that aquatic and terrestrial habitats are closely linked, not only because the temperature and moisture profiles of the smallest water bodies grade into those of adjacent terrestrial habitats, but also because aquatic larvae emerge as terrestrial adults, terrestrially produced organic matter falls or is washed into water bodies, terrestrial animals prey on aquatic biota, and so on. Components of the aquatic fauna that fare best in these circumstances belong to taxa that are generally cold hardy and have other adaptations to cold habitats (*e.g.*, Chironomidae), occupy the most favourable habitats among those available (those that are more stable, warmer, and more productive), and eat foods that are widely available (*e.g.*, FPOM rather than CPOM where autumn leaf fall is reduced).

Low productivity characterizes most of these systems and reduces diversity, and seasonality and disturbance diminish it further. Even so, the systems have surprising ecological complexity (*e.g.*, Oswood 1997, Fig. 1). As this review makes clear, enough fascinating adaptations, temporal patterns, and interrelationships have already been identified in aquatic insects from cold climates to suggest that their further study will continue to be rewarding from physiological, ecological, and other points of view. However, our knowledge lags far behind that for terrestrial species. Among many particular needs is the study of the physiological and biochemical basis of cold hardiness in selected aquatic insects, alongside measurements of the actual winter conditions in the different habitats and substrates they occupy.

Required physiological and biochemical studies include even the most basic elements, such as whether insects supercool or freeze in frozen substrates, how acclimatization is achieved, how well insects tolerate low temperatures, the occurrence and roles of various cryoprotectants, and the potential involvement of dehydration. Required ecological components of these studies include examination of exactly where different species spend the winter, how winter shelters contribute to survival, and the detailed patterns of temperature change, snow cover, and other habitat characteristics from fall to spring of known overwintering sites.

## Acknowledgements

I thank Donna Giberson, University of Prince Edward Island, for a variety of helpful comments on the manuscript.

## References

Aagaard, K., Solem, J.O., Nøst, T., and Hanssen, O. 1997. The macrobenthos of the pristine stream, Skiftesåa, Høylandet, Norway. Hydrobiologia, **348**: 81–94.

Andrews, D., and Rigler, F.H. 1985. The effects of an Arctic winter on benthic invertebrates in the littoral zone of Char Lake, Northwest Territories. Canadian Journal of Zoology, **63**: 2825–2834.

Arnekleiv, J.V. 1996. Life cycle strategies and seasonal distribution of mayflies (Ephemeroptera) in a small stream in central Norway. Fauna Norvegica Series B, **43**: 19–30.

Bale, J.S. 2002. Insects and low temperatures: from molecular biology to distributions and abundance. Philosophical Transactions of the Royal Society of London B Biological Sciences, **357**: 849–862.

Barton, D.R. 1980. Obserservations [sic] on the life histories and biology of Ephemeroptera and Plecoptera in northeastern Alberta, Canada. Aquatic Insects, **2**: 97–111.

Barton, D.R., Pugsley, C.W., and Hynes, H.B.N. 1987. The life history and occurrence of *Parachaetocladius abnobaeus* (Diptera: Chironomidae). Aquatic Insects, **9**: 189–194.

Beltaos, S., Calkins, D.J., Gatto, L.W., Prowse, T.D., Reedyk, S., Scrimgeour, G.J., and Wilkins, S.P. 1993. Physical effects of river ice. Chapter 2. *In* Environmental aspects of river ice. *Edited by* T.D. Prowse and N.C. Gridley. National Hydrology Research Institute, Saskatoon, Saskatchewan. pp. 3–74.

Bengtsson, B.E. 1981. The growth of some ephemeropteran nymphs during winter in a north Swedish river. Aquatic Insects, **3**: 199–208.

Bennett, V.A., Sformo, T., Walters, K., Toien, O., Jeannet, K., Hochstrasser, R., Pan, Q., Serianni, A.S., Barnes, B.M., and Duman, J.G. 2005. Comparative overwintering physiology of Alaska and Indiana populations of the beetle *Cucujus clavipes* (Fabricius): roles of antifreeze proteins, polyols, dehydration and diapause. Journal of Experimental Biology, **208**: 4467–4477.

Benson, N.G. 1955. Observations on anchor ice in a Michigan trout stream. Ecology, **36**: 529–530.

Benstead, J.P., Deegan, L.A., Peterson, B.J., Huryn, A.D., Bowden, W.B., Suberkropp, K., Buzby, K.M., Green, A.C., and Vacca, J.A. 2005. Responses of a beaded Arctic stream to short-term N and P fertilisation. Freshwater Biology, **50**: 277–290.

Berté, S.B., and Pritchard, G. 1983. The life history of *Glyphopsyche irrorata* (Trichoptera, Limnephilidae): a caddisfly that overwinters as an adult. Holarctic Ecology, **6**: 69–73.

Bierle, D.A. 1971. Dynamics of freshwater macrobenthic communities in arctic Alaska ponds and lakes. *In* The structure and function of the tundra ecosystem, Vol. 1. *Edited by* J. Brown and S. Bowen. U.S. Tundra Biome Program, U.S. International Biological Program. pp. 228–233.

Blenckner, T. 2005. A conceptual model of climate-related effects on lake ecosystems. Hydrobiologia, **533**: 1–14.

Bouchard, R.W., Jr., Carrillo, M.A., and Ferrington, L.C., Jr. 2006*a*. Lower lethal temperature for adult male *Diamesa mendotae* Muttkowski (Diptera: Chironomidae), a winter-emerging aquatic insect. Aquatic Insects, **28**: 57–66.

Bouchard, R.W., Jr., Carillo, M.A., Kells, S.A., and Ferrington, L.C., Jr. 2006*b*. Freeze tolerance in larvae of the winter-active *Diamesa mendotae* Muttkowski (Diptera: Chironomidae): a contrast to adult strategy for survival at low temperatures. Hydrobiologia, **568**: 403–416.

Brittain, J.E. 1980. Mayfly strategies in a Norwegian subalpine lake. *In* Advances in Ephemeroptera biology. *Edited by* J.F. Flannagan and K.E. Marshall. Plenum Press, New York. pp. 179–186.

Brittain, J.E. 1983. The influence of temperature on nymphal growth rates in mountain stoneflies (Plecoptera). Ecology, **64**: 440–446.

Brittain, J.E., and Eikeland, T.J. 1988. Invertebrate drift — a review. Hydrobiologia, **166**: 77–93.

Brittain, J.E., and Milner, A.M. 2001. Ecology of glacier-fed rivers: current status and concepts. Freshwater Biology, **46**: 1571–1578.

Brittain, J.E., and Nagell, B. 1981. Overwintering at low oxygen concentrations in the mayfly *Leptophlebia vespertina*. Oikos, **36**: 45–50.

Brown, C.J.D., Clothier, W.D., and Alvord, W. 1953. Observations on ice conditions and bottom organisms in the West Gallatin River, Montana. Proceedings of the Montana Academy of Sciences, **13**: 21–27.

Brown, L.E., Hannah, D.M., and Milner, A.M. 2003. Alpine stream habitat classification: an alternative approach incorporating the role of dynamic water source contributions. Arctic, Antarctic and Alpine Research, **35**: 313–322.

Brown, L.E., Milner, A.M., and Hannah, D.M. 2006. Stability and persistence of alpine stream macroinvertebrate communities and the role of physicochemical habitat variables. Hydrobiologia, **560**: 159–173.

Butler, M.G. 1982*a*. A 7-year life cycle for two *Chironomus* species in arctic Alaskan tundra ponds (Diptera: Chironomidae). Canadian Journal of Zoology, **60**: 58–70.

Butler, M.G. 1982*b*. Morphological and phenological delimitation of *Chironomus prior* sp.n., and *C. tardus* sp.n. (Diptera: Chironomidae), sibling species from arctic Alaska. Aquatic Insects, **4**: 219–235.

Butler, M.G. 2000. *Tanytarsus aquavolans*, spec. nov., and *Tanytarsus nearcticus*, spec. nov., two surface-swarming midges from arctic tundra ponds (Insecta, Diptera, Chironomidae). Spixiana, **23**: 211–218.

Butler, M., Miller, M.C., and Mozley, S. 1981. Macrobenthos. *In* Limnology of tundra ponds, Barrow, Alaska. US/IBP Synthesis Series 13. *Edited by* J.E. Hobbie. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania. pp. 297–339.

Cannings, S.G., and Cannings, R.A. 1997. Dragonflies (Odonata) of the Yukon. *In* Insects of the Yukon. *Edited by* H.V. Danks and J.A. Downes. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, Ontario. pp. 169–200.

Carrillo, M.A., Cannon, C.A., and Ferrington, L.C., Jr. 2004. Effect of sex and age on the supercooling point of the winter-active *Diamesa mendotae* Muttkowski (Diptera: Chironomidae). Aquatic Insects, **26**: 243–251.

Chernov, Yu.I. 1978. Adaptive features of the life cycles of tundra zone insects. Zhurnal Obshchei Biologii, **39**: 394–402. [In Russian.]

Clifford, H.F. 1969. Limnological features of a northern brown-water stream, with special reference to the life-histories of the aquatic insects. American Midland Naturalist, **82**: 578–597.

Clifford, H.F., Hamilton, H., and Killins, B.A. 1979. Biology of the mayfly *Leptophlebia cupida* (Say) (Ephemeroptera: Leptophlebiidae). Canadian Journal of Zoology, **57**: 1026–1045.

Convey, P., and Block, W. 1996. Antarctic Diptera: ecology, physiology and distribution. European Journal of Entomology, **93**: 1–13.

Copeland, R.S., and Craig, G.B., Jr. 1990. Cold hardiness of tree-hole mosquitoes in the Great Lakes region of the United States. Canadian Journal of Zoology, **68**: 1307–1314.

Corbet, P.S. 1964. Autogeny and oviposition in arctic mosquitoes. Nature (London), **203**: 668.

Corbet, P.S. 1965. Reproduction in mosquitoes of the high arctic. Proceedings of the International Congress of Entomology (London 1964): 817–818.

Corbet, P.S. 1966. Diel patterns of mosquito activity in a high arctic locality: Hazen Camp, Ellesmere Island, N.W.T. The Canadian Entomologist, **98**: 1238–1252.

Corbet, P.S. 1967. Facultative autogeny in arctic mosquitoes. Nature (London), **215**: 662–663.

Corbet, P.S., and Danks, H.V. 1973. Seasonal emergence and activity of mosquitoes (Diptera: Culicidae) in a high arctic locality. The Canadian Entomologist, **105**: 837–872.

Corbet, P.S., and Danks, H.V. 1975. Egg-laying habits of mosquitoes in the high arctic. Mosquito News, **35**: 8–14.

Corbet, P.S., and Downe, A.E.R. 1966. Natural hosts of mosquitoes in Northern Ellesmere Island. Arctic, **19**: 153–161.

Cowan, C.A., and Oswood, M.W. 1984. Spatial and seasonal associations of benthic macroinvertebrates and detritus in an Alaskan subarctic stream. Polar Biology, **3**: 211–215.

Currie, D.C. 1997. Black flies (Diptera: Simuliide) of the Yukon, with reference to the black-fly fauna of northwestern North America. *In* Insects of the Yukon. *Edited by* H.V. Danks and J.A. Downes. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, Ontario. pp. 563–614.

Currie, D.C., and Craig, D.A. 1988. Feeding strategies of larval black flies. *In* Black flies: ecology, population management, and annotated world list. *Edited by* K.C. Kim and R.W. Merritt. Pennsylvania State University Press, University Park. pp. 155–170.

Daborn, G.R. 1971. Survival and mortality of coenagrionid nymphs (Odonata: Zygoptera) from the ice of an aestival pond. Canadian Journal of Zoology, **49**: 569–571.

Daborn, G.R., and Clifford, H.F. 1974. Physical and chemical features of an aestival pond in western Canada. Hydrobiologia, **44**: 43–59.

Dahlem, G.A., and Naczi, R.F.C. 2006. Flesh flies (Diptera: Sarcophagidae) associated with North American pitcher plants (Sarraceniaceae), with descriptions of three new species. Annals of the Entomological Society of America, **99**: 218–240.

Danell, K. 1981. Overwintering of invertebrates in a shallow northern Swedish lake. Internationale Revue der Gesamten Hydrobiologie, **66**: 837–845.

Danks, H.V. 1971*a*. Overwintering of some north temperate and arctic Chironomidae. I. The winter environment. The Canadian Entomologist, **103**: 589–604.

Danks, H.V. 1971*b*. Overwintering of some north temperate and arctic Chironomidae. II. Chironomid biology. The Canadian Entomologist, **103**: 1875–1910.

Danks, H.V 1981. Arctic arthropods: a review of systematics and ecology with particular reference to North American fauna. Entomological Society of Canada, Ottawa, Ontario.

Danks, H.V. 1983. Extreme individuals in natural populations. Bulletin of the Entomological Society of America, **29**: 41–46.

Danks, H.V. 1987. Insect dormancy: an ecological perspective. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, Ontario.

Danks, H.V. 1990. Arctic insects: instructive diversity. *In* Canada's missing dimension: science and history in the Canadian arctic islands, Vol. II. *Edited by* C.R. Harington. Canadian Museum of Nature, Ottawa, Ontario. pp. 444–470.

Danks, H.V. 1991*a*. Winter habitats and ecological adaptations for winter survival. *In* Insects at low temperature. *Edited by* R.E. Lee and D.L. Denlinger. Chapman and Hall, New York and London. pp. 231–259.

Danks, H.V. 1991*b*. Life-cycle pathways and the analysis of complex life cycles in insects. The Canadian Entomologist, **123**: 23–40.

Danks, H.V. 1992. Long life cycles in insects. The Canadian Entomologist, **124**: 167–187.

Danks, H.V. 1993*a*. Seasonal adaptations in insects from the high arctic. *In* Seasonal adaptation and diapause in insects. *Edited by* M. Takeda and S. Tanaka. Bun-ichi-Sogo Publishers, Ltd., Tokyo. pp. 54–66. [In Japanese.]

Danks, H.V. 1993*b*. Patterns of diversity in the Canadian insect fauna. *In* Systematics and entomology: diversity, distribution, adaptation and application. *Edited by* G.E. Ball and H.V. Danks. Memoirs of the Entomological Society of Canada, **165**: 51–74.

Danks, H.V. 1996. The wider integration of studies on insect cold-hardiness. European Journal of Entomology, **93**: 383–403.

Danks, H.V. 1999. Life cycles in polar arthropods — flexible or programmed? European Journal of Entomology, **96**: 83–102.

Danks, H.V. 2002. Modification of adverse conditions by insects. Oikos, **99**: 10–24.

Danks, H.V. 2004. The roles of insect cocoons in cold conditions. European Journal of Entomology, **101**: 433–437.

Danks, H.V. 2005. Key themes in the study of seasonal adaptations in insects I. Patterns of cold hardiness. Applied Entomology and Zoology, **40**: 199–211.

Danks, H.V. 2006*a*. Insect adaptations to cold and changing environments. The Canadian Entomologist, **138**: 1–23.

Danks, H.V. 2006*b*. Key themes in the study of seasonal adaptations in insects II. Life cycle patterns. Applied Entomology and Zoology, **41**: 1–13.

Danks, H.V. 2006*c*. Short life cycles in insects and mites. The Canadian Entomologist, **138**: 407–463.

Danks, H.V. 2007. The elements of seasonal adaptations in insects. The Canadian Entomologist, **139**: 1–44.

Danks, H.V., and Jones, J.W. 1978. Further observations on winter cocoons in Chironomidae (Diptera). The Canadian Entomologist, **110**: 667–669.

Danks, H.V., and Oliver, D.R. 1972*a*. Seasonal emergence of some high arctic Chironomidae (Diptera). The Canadian Entomologist, **104**: 661–686.

Danks, H.V., and Oliver, D.R. 1972*b*. Diel periodicities of emergence of some high arctic Chironomidae (Diptera). The Canadian Entomologist, **104**: 903–916.

DeBruyn, A.M.H., and Ring, R.A. 1999. Comparative ecology of two species of *Hydroporus* (Coleoptera: Dytiscidae) in a high arctic oasis. The Canadian Entomologist, **131**: 405–420.

Dolmen, D., and Solem, J.O. 2002. Life history of *Ilybius fenestratus* (Fabricius) (Coleoptera, Dytiscidae) in a central Norwegian lake. Aquatic Insects, **24**: 199–205.

Downes, J.A. 1962. What is an arctic insect? The Canadian Entomologist, **94**: 143–162.

Downes, J.A. 1965. Adaptations of insects in the arctic. Annual Review of Entomology, **10**: 257–274.

Duffy, W.G., and Liston, C.R. 1985. Survival following exposure to subzero temperatures and respiration in cold acclimatized larvae of *Enallagma boreale* (Odonata: Zygoptera). Freshwater Invertebrate Biology, **4**: 1–7.

Duman, J.G. 2001. Antifreeze and ice nucleator proteins in terrestrial arthropods. Annual Review of Physiology, **63**: 327–357.

Duman, J.G., Wu, D.W., Xu, L., Tursman, D., and Olsen, T.M. 1991. Adaptations of insects to subzero temperatures. Quarterly Review of Biology, **66**: 387–410.

Duman, J.G., Bennett, V., Sformo, T., Hochstrasser, R., and Barnes, B.M. 2004. Antifreeze proteins in Alaskan insects and spiders. Journal of Insect Physiology, **50**: 259–266.

Ellis, R.J. 1978. Over-winter occurrence and maturation of gonads in adult *Psychoglypha subborealis* (Banks) and *Glyphopsyche irrorata* (Fabricius). Pan-Pacific Entomologist, **54**: 178–180.

Evans, K.W., and Brust, R.A. 1972. Induction and termination of diapause in *Wyeomyia smithii* (Diptera: Culicidae), and larval survival studies at low and subzero temperatures. The Canadian Entomologist, **104**: 1937–1950.

Farkas, M.J., and Brust, R.A. 1986. Phenology of the mosquito *Wyeomyia smithii* in Manitoba and Ontario. Canadian Journal of Zoology, **64**: 285–290.

Friberg, N., Milner, A.M., Svendsen, L.M., Lindegaard, C., and Larsen, S.E. 2001. Macroinvertebrate stream communities along regional and physico-chemical gradients in western Greenland. Freshwater Biology, **46**: 1753–1764.

Frisbie, M.P., and Lee, R.E., Jr. 1997. Inoculative freezing and the problem of winter survival for freshwater macroinvertebrates. Journal of the North American Benthological Society, **16**: 635–650.

Frutiger, A., and Buergisser, G.M. 2002. Life history variability of a grazing stream insect (*Liponeura cinerascens minor*; Diptera: Blephariceridae). Freshwater Biology, **47**: 1618–1632.

Füreder, L. 1999. High alpine streams: cold habitats for insect larvae. *In* Cold-adapted organisms. Ecology, physiology, enzymology, and molecular biology. *Edited by* R. Margesin and F. Schinner. Springer-Verlag, Berlin. pp. 181–196.

Füreder, L., Schütz, C., Wallinger, M., and Burger, R. 2001. Physico-chemistry and aquatic insects of a glacier-fed and a spring-fed alpine stream. Freshwater Biology, **46**: 1673–1690.

Füreder, L., Wallinger, M., and Burger, R. 2005. Longitudinal and seasonal pattern of insect emergence in alpine streams. Aquatic Ecology, **39**: 67–78.

Füreder, L., Ettinger, R., Boggero, A., Thaler, B., and Thies, H. 2006. Macroinvertebrate diversity in alpine lakes: effects of altitude and catchment properties. Hydrobiologia, **562**: 123–144.

Gehrken, U. 1989. Diapause termination in eggs of the stonefly *Arcynopteryx compacta* (McLachland) in relation to dehydration and cold hardiness. Journal of Insect Physiology, **35**: 377–385.

Gehrken, U., and Sømme, L. 1987. Increased cold hardiness in eggs of *Arcynopteryx compacta* (Plecoptera) by dehydration. Journal of Insect Physiology, **33**: 987–991.

Gibbs, K.E. 1979. Ovoviviparity and nymphal seasonal movements of *Callibaetis* spp. (Ephemeroptera: Baetidae) in a pond in southwestern Quebec. The Canadian Entomologist, **111**: 927–931.

Giberson, D.J., and Galloway, T.D. 1985. Life history and production of *Ephoron album* (Say) (Ephemeroptera: Polymitarcidae) in the Valley River, Manitoba. Canadian Journal of Zoology, **63**: 1668–1674.

Giberson, D., and Hardwick, M.L. 1999. Pitcher plants (*Sarracenia purpurea*) in eastern Canadian peatlands: ecology and conservation of the invertebrate inquilines. *In* Invertebrates in freshwater wetlands of North America: ecology and management. *Edited by* D.P. Batzer, R.B. Rader, and S.A. Wissinger. John Wiley and Sons, Inc., New York. pp. 401–422.

Giberson, D.J., and Rosenberg, D.M. 1992*a*. Effects of temperature, food quantity, and nymphal rearing density on life-history traits of a northern population of *Hexagenia* (Ephemeroptera:Ephemeridae). Journal of the North American Benthological Society, **11**: 181–193.

Giberson, D.J., and Rosenberg, D.M. 1992*b*. Egg development in *Hexagenia limbata* (Ephemeroptera:Ephemeridae) from Southern Indian Lake, Manitoba: temperature effects and diapause. Journal of the North American Benthological Society, **11**: 194–203.

Giberson, D.J., and Rosenberg, D.M. 1994. Life histories of burrowing mayflies (*Hexagenia limbata* and *H. rigida*, Ephemeroptera: Ephemeridae) in a northern Canadian reservoir. Freshwater Biology, **32**: 501–518.

Giberson, D.J., Burian, S.K., and Shouldice, M. 2007. Life history of the northern mayfly, *Baetis bundyae* (Ephemeroptera) in Rankin Inlet, Nunavut Territory, Canada, with updates to the mayflies of Canada list. The Canadian Entomologist. In press.

Gíslason, G.M., Ólafsson, J.S., and Adalsteinsson, H. 2000. Life in glacial and alpine rivers in central Iceland in relation to physical and chemical parameters. Nordic Hydrology, **31**: 411–422.

Gíslason, G.M., Ađalsteinsson, H., Hansen, I., Ólafsson, J.S., and Svavarsdóttir, K. 2001. Longitudinal changes in macroinvertebrate assemblages along a glacial river system in central Iceland. Freshwater Biology, **46**: 1737–1751.

Goddeeris, B. 2004. Diapause and ecological strategies in Chironomidae (Diptera). Journal of Limnology, **63**(Suppl. 1): 92.

Harper, P.P. 1981. Ecology of streams at high latitudes. *In* Perspectives in running water ecology. *Edited by* M.A. Lock and D.D. Williams. Plenum Press, New York. pp. 313–337.

Harvey, C.J., Peterson, B.J., Deegan, L.A., Bowden, W.B., Hershey, A.E., Miller, M.C., and Finlay, J.C. 1998. Biological responses to fertilization of Oksrukuyik Creek, a tundra stream. Journal of the North American Benthological Society, **17**: 190–209.

Haufe, W.O. 1957. Physical environment and behaviour of immature stages of *Aedes communis* (Deg.) (Diptera: Culicidae) in subarctic Canada. The Canadian Entomologist, **89**: 120–139.

Haufe, W.O., and Burgess, L. 1956. Development of *Aedes* (Diptera: Culicidae) at Fort Churchill, Manitoba, and prediction of dates of emergence. Ecology, **37**: 500–519.

Hayes, B.P., and Murray, D.A. 1987. Species composition and emergence of Chironomidae (Diptera) from three high arctic streams on Bathurst Island, Northwest Territories, Canada. Entomologica Scandinavica Supplementum, **29**: 355–360.

Heino, J. 2005. Functional biodiversity of macroinvertebrate assemblages along major ecological gradients of boreal headwater streams. Freshwater Biology, **50**: 1578–1587.

Hershey, A.E. 1985*a*. Littoral chironomid communities in an arctic Alaskan lake. Holarctic Ecology, **8**: 39–48.

Hershey, A.E. 1985*b*. Effects of predatory sculpin on the chironomid communities in an arctic lake. Ecology, **66**: 1131–1138.

Hershey, A.E., Hiltner, A.L., Hullar, M.A.J., Miller, M.C., Vestal, J.R., Lock, M.A., Rundle, S., and Peterson, B.J. 1988. Nutrient influence on a stream grazer: *Orthocladius* microcommunities respond to nutrient input. Ecology, **69**: 1383–1392.

Hershey, A.E., Merritt, R.W., and Miller, M.C. 1995. Insect diversity, life history, and trophic dynamics in arctic streams, with particular emphasis on black flies (Diptera: Simuliidae). *In* Arctic and alpine biodiversity: patterns, causes and ecosystem consequences. *Edited by* F.S. Chapin, III and C. Körner. Ecological Studies Vol. 113. Springer-Verlag, Berlin, Heidelberg. pp. 283–295.

Hershey, A.E., Bowden, W.B., Deegan, L.A., Hobbie, J.E., Peterson, B.J., Kipphut, G.W., Kling, G.W., Lock, M.A., Merritt, R.W., Miller, M.C., Vestal, J.R., and Schuldt, J.A. 1997. The Kuparuk River: a long-term study of biological and chemical processes in an arctic river. *In* Freshwaters of Alaska: ecological syntheses. *Edited by* A.M. Milner and M.W. Oswood. Springer-Verlag, New York. pp. 107–130.

Hershey, A.E., Beaty, S., Fortino, K., Kelly, S., Keyse, M., Luecke, C., O'Brien, W.J., and Whalen, S.C. 2006. Stable isotope signatures of benthic invertebrates in arctic lakes indicate limited coupling to pelagic production. Limnology and Oceanography, **51**: 177–188.

Hieber, M., Robinson, C.T., Uehlinger, U., and Ward, J.V. 2002. Are alpine lake outlets less harsh than other alpine streams? Archiv für Hydrobiologie, **154**: 199–223.

Hieber, M., Robinson, C.T., and Uehlinger, U. 2003. Seasonal and diel patterns of invertebrate drift in different alpine stream types. Freshwater Biology, **48**: 1078–1092.

Hieber, M., Robinson, C.T., Uehlinger, U., and Ward, J.V. 2005. A comparison of benthic macroinvertebrate assemblages among different types of alpine streams. Freshwater Biology, **50**: 2087–2100.

Hoback, W.W., and Stanley, D.W. 2001. Insects in hypoxia. Journal of Insect Physiology, **47**: 533–542.

Hodkinson, I.D., and Bird, J.M. 2004. Anoxia tolerance in high Arctic terrestrial microarthropods. Ecological Entomology, **29**: 506–509.

Holmstrup, M., Bayley, M., and Ramløv, H. 2002. Supercool or dehydrate? An experimental analysis of overwintering strategies in small permeable arctic invertebrates. Proceedings of the National Academy of Sciences of the United States of America, **99**: 5716–5720.

Hughes, J.M., Mather, P.B., Sheldon, A.L., and Allendorf, F.W. 1999. Genetic structure of the stonefly, *Yoraperla brevis*, populations: the extent of gene flow among adjacent montane streams. Freshwater Biology, **41**: 63–72.

Huryn, A.D., Slavik, K.A., Lowe, R.L., Parker, S.M., Anderson, D.S., and Peterson, B.J. 2005. Landscape heterogeneity and the biodiversity of Arctic stream communities: a habitat template analysis. Canadian Journal of Fisheries and Aquatic Sciences, **62**: 1905–1919.

Irons, J.G., III. 1988. Life history patterns and trophic ecology of Trichoptera in two Alaska (U.S.A.) subarctic streams. Canadian Journal of Zoology, **66**: 1258–1265.

Irons, J.G., III, and Oswood, M.W. 1992. Seasonal temperature patterns in an arctic and two subarctic Alaskan (USA) headwater streams. Hydrobiologia, **237**: 147–157.

Irons, J.G., III, Ray, S.R., Miller, L.K., and Oswood, M.W. 1989. Spatial and seasonal patterns of streambed water temperatures in an Alaskan subarctic stream. *In* Proceedings of the symposium on headwaters hydrology, June 1989, Missoula, Montana. *Edited by* W.W. Woessner and D.F. Potts. American Water Resources Association, Bethesda, Maryland. pp. 381–390.

Irons, J.G., III, Miller, L.K., and Oswood, M.W. 1993. Ecological adaptations of aquatic macroinvertebrates to overwintering in interior Alaska (U.S.A.) subarctic streams. Canadian Journal of Zoology, **71**: 98–108.

Irons, J.G., III, Oswood, M.W., Stout, R.J., and Pringle, C.M. 1994. Latitudinal patterns in leaf litter breakdown: is temperature really important? Freshwater Biology, **32**: 401–411.

Johansson, F., and Rowe, L. 1999. Life history and behavioral responses to time constraints in a damselfly. Ecology, **80**: 1242–1252.

Johansson, F., Stoks, R., Rowe, L., and De Block, M. 2001. Life history plasticity in a damselfly: effects of combined time and biotic constraints. Ecology, **82**: 1857–1869.

Kevan, P.G. 1989. Thermoregulation in arctic insects and flowers: adaptation and co-adaptation in behaviour, anatomy, and physiology. *In* Thermal physiology. *Edited by* J.B. Mercer. Elsevier Science Publishers B.V. (Biomedical Division), Amsterdam. pp. 747–753.

Knispel, S., Sartori, M., and Brittain, J.E. 2006. Egg development in the mayflies of a Swiss glacial floodplain. Journal of the North American Benthological Society, **25**: 430–443.

Kohshima, S. 1984. A novel cold-tolerant insect found in a Himalayan glacier. Nature (London), **310**: 225–227.

Kurtak, D. 1974. Overwintering of *Simulium pictipes* Hagen (Diptera: Simuliidae) as eggs. Journal of Medical Entomology, **11**: 383–384.

Langton, P.H. 1998. *Micropsectra silvesterae* n. sp., and *Tanytarsus heliomesonyctios* n. sp., (Diptera: Chironomidae), two parthenogenetic species from Ellesmere Island, Arctic Canada. Journal of the Kansas Entomological Society, **71**: 208–215.

Larson, D.J. 1997. Dytiscid water beetles (Coleoptera: Dytiscidae) of the Yukon. *In* Insects of the Yukon. *Edited by* H.V. Danks and J.A. Downes. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, Ontario. pp. 491–522.

Lee, J.O., and Hershey, A.E. 2000. Effects of aquatic bryophytes and long-term fertilization on arctic stream insects. Journal of the North American Benthological Society, **19**: 697–708.

Lee, R.E., Jr. 1991. Principles of insect low temperature tolerance. *In* Insects at low temperature. *Edited by* R.E. Lee, Jr., and D.L. Denlinger. Chapman and Hall, New York. pp. 17–46.

Lencioni, V. 2004. Survival strategies of freshwater insects in cold environments. Journal of Limnology, **63**(Suppl. 1): 45–55.

Lepori, F., Barbieri, A., and Ormerod, S.J. 2003. Effects of episodic acidification on macroinvertebrate assemblages in Swiss alpine streams. Freshwater Biology, **48**: 1873–1885.

Lillehammer, A. 1987. Diapause and quiescence in eggs of *Systellognatha* stonefly species (Plecoptera) occuring [sic] in alpine areas of Norway. Annales de Limnologie, **23**: 179–184.

Lods-Crozet, B., Lencioni, V., Ólafsson, J.S., Snook, D.L., Velle, G., Brittain, J.E., Castella, E., and Rossaro, B. 2001. Chironomid (Diptera: Chironomidae) communities in six European glacier-fed streams. Freshwater Biology, **46**: 1791–1809.

Lundheim, R. 2002. Physiological and ecological significance of biological ice nucleators. Philosophical Transactions of the Royal Society of London B Biological Sciences, **357**: 937–943.

Madder, D.J., Surgeoner, G.A., and Helson, B.V. 1983. Induction of diapause in *Culex pipiens* and *Culex restuans* (Diptera: Culicidae) in southern Ontario. The Canadian Entomologist, **115**: 877–883.

Madder, M.C.A., Rosenberg, D.M., and Wiens, A.P. 1977. Larval cocoons in *Eukiefferiella claripennis* (Diptera: Chironomidae). The Canadian Entomologist, **109**: 891–892.

Malmqvist, B. 1999. Life history of *Metacnephia lyra*, a blackfly highly characteristic of large Swedish river rapids at the time of maximum discharge (Diptera: Simuliidae). Aquatic Insects, **21**: 89–98.

Meier, G.M., Meyer, E.I., and Meyns, S. 2000. Lipid content of stream macroinvertebrates. Archiv für Hydrobiologie, **147**: 447–463.

Mendl, H., and Müller, K. 1978. The colonization cycle of *Amphinemura standfussi* Ris (Ins.: Plecoptera) in the Abisko area. Hydrobiologia, **60**: 109–111.

Messner, B., Groth, I., and Taschenberger, D. 1983. Zum jahreszeitlichen Wanderverhalten der Grundwanze *Aphelocheirus aestivalis*. Zoologische Jahrbücher, Abteilung für Systematik

Oekologie und Geographie der Tiere, **110**: 323–331.

Miller, M.C., and Stout, J.R. 1989. Variability of macroinvertebrate community composition in an arctic and subarctic stream. Hydrobiologia, **172**: 111–127.

Milner, A.M., and Petts, G.E. 1994. Glacial rivers: physical habitat and ecology. Freshwater Biology, **32**: 295–307.

Milner, A.M., Irons, J.G., III, and Oswood, M.W. 1997. The Alaskan landscape: an introduction for limnologists. *In* Freshwaters of Alaska: ecological syntheses. *Edited by* A.M. Milner and M.W. Oswood. Springer-Verlag, New York. pp. 1–44.

Milner, A.M., Conn, S.C., and Brown, L.E. 2006. Persistence and stability of macroinvertebrate communities in streams of Denali National Park, Alaska: implications for biological monitoring. Freshwater Biology, **51**: 373–387.

Monaghan, M.T., Spaak, P., Robinson, C.T., and Ward, J.V. 2002. Population genetic structure of 3 alpine stream insects: influences of gene flow, demographics, and habitat fragmentation. Journal of the North American Benthological Society, **21**: 114–131.

Moore, M.V., and Lee, R.E., Jr. 1991. Surviving the big chill: overwintering strategies of aquatic and terrestrial insects. American Entomologist, **37**: 111–118.

Mousavi, S.K., Sandring, S., and Amundsen, P.-A. 2002. Diversity of chironomid assemblages in contrasting subarctic lakes: impact of fish predation and lake size. Archiv für Hydrobiologie, **154**: 461–484.

Müller, K., Mendl, H., Dahl, M., and Müller-Haeckel, A. 1976. Biotopwahl und Colonization Cycle von Plecopteren in einem subarktischen Gewässersystem. Entomologisk Tidskrift, **97**: 1–6.

Mutch, R.A., and Pritchard, G. 1986. Development rates of eggs of some Canadian stoneflies (Plecoptera) in relation to temperature. Journal of the North American Benthological Society, **5**: 272–277.

Nagell, B. 1977. Survival of *Cloeon dipterum* (Ephemeroptera) larvae under anoxic conditions in winter. Oikos, **29**: 161–165.

Nagell, B. 1980. Overwintering strategy of *Cloeon dipterum* (L.) larvae. *In* Advances in Ephemeroptera biology. *Edited by* J.F. Flannagan and K.E. Marshall. Plenum Press, New York. pp. 259–264.

Nagell, B., and Brittain, J.E. 1977. Winter anoxia — a general feature of ponds in cold temperate regions. Internationale Revue der Gesamten Hydrobiologie, **62**: 821–824.

Nolte, U., and Hoffmann, T. 1992. Fast life in cold water: *Diamesa incallida* (Chironomidae). Ecography, **15**: 25–30.

Norling, U. 1976. Seasonal regulation in *Leucorrhinia dubia* (Vander Linden) (Anisoptera: Libellulidae). Odonatologica, **5**: 245–263.

Norling, U. 1984*a*. The life cycle and larval photoperiodic responses of *Coenagrion hastulatum* (Charpentier) in two climatically different areas (Zygoptera: Coenagrionidae). Odonatologica, **13**: 429–449.

Norling, U. 1984*b*. Photoperiodic control of larval development in *Leucorrhinia dubia* (Vander Linden): a comparison between populations from northern and southern Sweden (Anisoptera: Libellulidae). Odonatologica, **13**: 529–550.

Norling, U. 1984*c*. Life history patterns in the northern expansion of dragonflies. Advances in Odonatology, **2**: 127–156.

O'Brien, W.J., Bahr, M., Hershey, A.E., Hobbie, J.E., Kipphut, G.W., Kling, G.W., Kling, H., McDonald, M., Miller, M.C., Rublee, P., and Vestal, J.R. 1997. The limnology of Toolik Lake. *In* Freshwaters of Alaska: ecological syntheses. *Edited by* A.M. Milner and M.W. Oswood. Springer-Verlag, New York. pp. 61–106.

Økland, B. 1991. Laboratory studies of egg development and diapause in *Isoperla obscura* (Plecoptera) from a mountain stream in Norway. Freshwater Biology, **25**: 485–495.

Oliver, D.R. 1964. A limnological investigation of a large arctic lake, Nettilling Lake, Baffin Island. Arctic, **17**: 69–83.

Oliver, D.R. 1968. Adaptations of arctic Chironomidae. Annales Zoologici Fennici, **5**: 111–118.

Oliver, D.R. 1976. Chironomidae (Diptera) of Char Lake, Cornwallis Island, N.W.T., with descriptions of two new species. The Canadian Entomologist, **108**: 1053–1064.

Oliver, D.R. 1983. Male dimorphism in an arctic chironomid. Memoirs of the American Entomological Society, **34**: 235–240.

Oliver, D.R., and Corbet, P.S. 1966. Aquatic habitats in a high arctic locality: the Hazen Camp study area, Ellesmere Island, N.W.T. Defence Research Board of Canada, Directorate of Physical Research (G), Hazen 26, Ottawa, Ontario.

Oliver, D.R., and Dillon, M.E. 1997. Chironomids (Diptera: Chironomidae) of the Yukon Arctic North Slope and Herschel Island. *In* Insects of the Yukon. *Edited by* H.V. Danks and J.A. Downes. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, Ontario. pp. 615–636.

Olsen, T.M., Sass, S.J., Li, N., and Duman, J.G. 1998. Factors contributing to seasonal increases in inoculative freezing resistance in overwintering fire-colored beetle larvae *Dendroides canadensis* (Pyrochroidae). Journal of Experimental Biology, **201**: 1585–1594.

Olsson, T.I. 1981. Overwintering of benthic macroinvertebrates in ice and frozen sediment in a north Swedish river. Holarctic Ecology, **4**: 161–166.

Olsson, T.I. 1982. Overwintering sites and freezing tolerance of benthic invertebrates in a north Swedish river. Cryo-Letters, **3**: 297–298.

Olsson, T.I. 1983. Seasonal variation in the lateral distribution of mayfly nymphs in a boreal river. Holarctic Ecology, **6**: 333–339.

Oswood, M.W. 1989. Community structure of benthic invertebrates in interior Alaskan (USA) streams and rivers. Hydrobiologia, **172**: 97–110.

Oswood, M.W. 1997. Streams and rivers of Alaska: a high latitude perspective on running waters. *In* Freshwaters of Alaska: ecological syntheses. *Edited by* A.M. Milner and M.W. Oswood. Springer-Verlag, New York. pp. 331–356.

Oswood, M.W., Miller, L.K., and Irons, J.G., III. 1991. Overwintering of freshwater benthic macroinvertebrates. *In* Insects at low temperature. *Edited by* R.E. Lee, Jr. and D.L. Denlinger. Chapman and Hall, New York. pp. 360–375.

Paterson, C.G. 1971. Overwintering ecology of the aquatic fauna associated with the pitcher plant *Sarracenia purpurea* L. Canadian Journal of Zoology, **49**: 1455–1459.

Peterson, B., Fry, B., Deegan, L., and Hershey, A. 1993. The trophic significance of epilithic algal production in a fertilized tundra river ecosystem. Limnology and Oceanography, **38**: 872–878.

Power, G., Cunjak, R., Flanagan, J., and Katopodis, C. 1993. Biological effects of river ice. *In* Environmental aspects of river ice. Chapter 4. *Edited by* T.D. Prowse and N.C. Gridley. National Hydrology Research Institute, Saskatoon, Saskatchewan. pp. 97–119.

Pritchard, G., Harder, L.D., and Mutch, R.A. 1996. Development of aquatic insect eggs in relation to temperature and strategies for dealing with different thermal environments. Biological Journal of the Linnean Society, **58**: 221–244.

Prowse, T.D. 1994. Environmental significance of ice to streamflow in cold regions. Freshwater Biology, **32**: 241–259.

Prowse, T.D., and Carter, T. 2002. Significance of ice-induced storage to spring runoff: a case study of the Mackenzie River. Hydrological Processes, **16**: 779–788.

Prowse, T.D., and Culp, J.M. 2003. Ice breakup: a neglected factor in river ecology. Canadian Journal of Civil Engineering, **30**: 128–144.

Ramløv, H. 2000. Aspects of natural cold tolerance in ectothermic animals. Human Reproduction, **15**: 26–46.

Reid, R.A., Schindler, D.W., and Schmidt, R.V. 1975. Light measurements in the Experimental Lakes Area, 1969–1973. Technical Report 559, Canadian Fisheries and Marine Service. 167 pp.

Ring, R.A., and Danks, H.V. 1994. Desiccation and cryoprotection: overlapping adaptations. Cryo-Letters, **15**: 181–190.

Robinson, C.T., Gessner, M.O., and Ward, J.V. 1998. Leaf breakdown and associated macroinvertebrates in alpine glacial streams. Freshwater Biology, **40**: 215–228.

Robinson, C.T., Uehlinger, U., and Hieber, M. 2001. Spatio-temporal variation in macroinvertebrate assemblages of glacial streams in the Swiss Alps. Freshwater Biology, **46**: 1663–1672.

Sæther, O.A., and Willassen, E. 1987. Four new species of *Diamesa* Meigen, 1835 (Diptera: Chironomidae) from the glaciers of Nepal. Entomologica Scandinavica Supplementum, **29**: 189–203.

Sahlberg, J. 1988. Modelling the thermal regime of a lake during the winter season. Cold Regions Science and Technology, **15**: 151–159.

Sandberg, J.B., and Stewart, K.W. 2004. Capacity for extended egg diapause in six *Isogenoides* Klapalek species (Plecoptera: Perlodidae). Transactions of the American Entomological Society, **130**: 411–423.

Sawchyn, W.W., and Gillott, C. 1974*a*. The life history of *Lestes congener* (Odonata: Zygoptera) on the Canadian prairies. The Canadian Entomologist, **106**: 367–376.

Sawchyn, W.W., and Gillott, C. 1974*b*. The life histories of three species of *Lestes* (Odonata: Zygoptera) in Saskatchewan. The Canadian Entomologist, **106**: 1283–1293.

Sawchyn, W.W., and Gillott, C. 1975. The biology of two related species of coenagrionid dragonflies (Odonata: Zygoptera) in western Canada. The Canadian Entomologist, **107**: 119–128.

Schindler, D.W. 1972. Production of phytoplankton and zooplankton in Canadian Shield lakes. *In* Productivity problems of freshwaters. *Edited by* Z. Kajak and A. Hillbrich-Ilikowska. PWN [Polish Scientific Publishers], Krakow. pp. 311–331.

Scholander, P.F., Flagg, W., Hock, R.J., and Irving, L. 1953. Studies on the physiology of frozen plants and animals in the arctic. Journal of Cellular and Comparative Physiology, **42**(Suppl. 1): 1–56.

Schütz, C., Wallinger, M., Burger, R., and Füreder, L. 2001. Effects of snow cover on the benthic fauna in a glacier-fed stream. Freshwater Biology, **46**: 1691–1704.

Scrimgeour, G.J., Prowse, T.D., Culp, J.M., and Chambers, P.A. 1994. Ecological effects of river ice break-up: a review and perspective. Freshwater Biology, **32**: 261–275.

Sformo, T., and Doak, P. 2006. Thermal ecology of interior Alaska dragonflies (Odonata: Anisoptera). Functional Ecology, **20**: 114–123.

Shama, L.N.S., and Robinson, C.T. 2006. Sex-specific life-history responses to seasonal time constraints in an alpine caddisfly. Evolutionary Ecology Research, **8**: 169–180.

Shen, H.T. 2003. Research on river ice processes: progress and missing links. Journal of Cold Regions Engineering, **17**: 135–142.

Smidt, S., and Oswood, M.W. 2002. Landscape patterns and stream reaches in the Alaskan taiga forest: potential roles of permafrost in differentiating macroinvertebrate communities. Hydrobiologia, **468**: 95–105.

Snyder, C.D., Young, J.A., Lemarie, D.P., and Smith, D.R. 2002. Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. Canadian Journal of Fisheries and Aquatic Sciences, **59**: 262–275.

Söderström, O., and Nilsson, A.N. 1987. Do nymphs of *Parameletus chelifer* and *P. minor* (Ephemeroptera) reduce mortality from predation by occupying temporary habitats? Oecologia, **74**: 39–46.

Solem, J.O. 1983. Identification of the Norwegian larvae of the genus *Potomophylax* Wallengren, 1891 (Trichoptera, Limnephilidae), with data on life histories, habitats and food in the Kongsvoll area, Dovrefjell mountains, central Norway. Fauna Norvegica Series B, **30**: 69–76.

Solem, J.O. 1985. Norwegian *Apatania* Kolenati (Trichoptera: Limnephilidae): identification of larvae and aspects of their biology in a high-altitude zone. Entomologica Scandinavica, **16**: 161–174.

Spence, J.R., and Andersen, N.M. 1994. Biology of water striders: interactions between systematics and ecology. Annual Review of Entomology, **39**: 101–128.

Stewart, K.W., and Ricker, W.E. 1997. Stoneflies (Plecoptera) of the Yukon. *In* Insects of the Yukon. *Edited by* H.V. Danks and J.A. Downes. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, Ontario. pp. 201–222.

Storey, K.B., and Storey, J.M. 1992. Biochemical adaptations for winter survival in insects. Advances in Low-temperature Biology, **1**: 101–140.

Svensson, B.W. 2005. Seasonal fat content fluctuations in a gyrinid beetle: comparison between an arctic and a temperate zone population (Coleoptera: Gyrinidae). Aquatic Insects, **27**: 11–19.

Tate, A.W., and Hershey, A.E. 2003. Selective feeding by larval dytiscids (Coleoptera: Dytiscidae) and effects of fish predation on upper littoral zone macroinvertebrate communities of arctic lakes. Hydrobiologia, **497**: 13–23.

Taylor, B.W., Anderson, C.R., and Peckarsky, B.L. 1999. Delayed egg hatching and semivoltinism in the nearctic stonefly *Megarcys signata* (Plecoptera: Perlodidae). Aquatic Insects, **21**: 179–185.

Tonn, W.M., Langlois, P.W., Prepas, E.E., Danylchuk, A.J., and Boss, S.M. 2004. Winterkill cascade: indirect effects of a natural disturbance on littoral macroinvertebrates in boreal lakes. Journal of the North American Benthological Society, **23**: 237–250.

Townsend, G.D., and Pritchard, G. 1998. Larval growth and development of the stonefly *Pteronarcys californica* (Insecta: Plecoptera) in the Crowsnest River, Alberta. Canadian Journal of Zoology, **76**: 2274–2280.

Townsend, G.D., and Pritchard, G. 2000. Egg development in the stonefly *Pteronarcys californica* Newport (Plecoptera: Pteronarcyidae). Aquatic Insects, **22**: 19–26.

Tozer, W.E., Resh, V.H., and Solem, J.O. 1981. Bionomics and adult behavior of a lentic caddisfly, *Nectopsyche albida* (Walker). American Midland Naturalist, **106**: 133–144.

Ulfstrand, S. 1967. Microdistribution of benthic species (Ephemeroptera, Plecoptera, Trichoptera, Diptera: Simuliidae) in Lapland streams. Oikos, **18**: 293–310.

Ulfstrand, S. 1968. Life cycles of benthic insects in Lapland streams (Ephemeroptera, Plecoptera, Trichoptera, Diptera Simuliidae). Oikos, **19**: 167–190.

Ulfstrand, S. 1969. Ephemeroptera and Plecoptera from River Vindel ven in Swedish Lapland. Entomologisk Tidskrift, **90**: 145–165.

Vali, G. 1995. Principles of ice nucleation. *In* Biological ice nucleation and its applications. *Edited by* R.E. Lee, Jr., G.J. Warren, and L.V. Gusta. American Phytopathological Society, St. Paul, Minnesota. pp. 1–28.

Van Doorslaer, W., and Stoks, R. 2005. Thermal reaction norms in two *Coenagrion* damselfly species: contrasting embryonic and larval life-history traits. Freshwater Biology, **50**: 1982–1990.

Vinson, M.R., and Hawkins, C.P. 2003. Broad-scale geographical patterns in local stream insect genera richness. Ecography, **26**: 751–767.

Voelz, N.J., and McArthur, J.V. 2000. An exploration of factors influencing lotic insect species richness. Biodiversity and Conservation, **9**: 1543–1570.

Wang, L., and Duman, J.G. 2005. Antifreeze proteins of the beetle *Dendroides canadensis* enhance one another's activities. Biochemistry, **44**: 10305–10312.

Ward, J.V. 1994. Ecology of alpine streams. Freshwater Biology, **32**: 277–294.

Wiggins, G.B. 1973. A contribution to the biology of caddisflies (Trichoptera) in temporary pools. Life Sciences Contributions, Royal Ontario Museum, **88**: 1–28.

Wiggins, G.B., and Parker, C.R. 1997. Caddisflies (Trichoptera) of the Yukon, with analysis of the Beringian and Holarctic species of North America. *In* Insects of the Yukon. *Edited by* H.V. Danks and J.A. Downes. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, Ontario. pp. 787–866.

Wiggins, G.B., and Winchester, N.N. 1984. A remarkable new caddisfly genus from northwestern North America (Trichoptera, Limnephilidae, Limnephilinae). Canadian Journal of Zoology, **62**: 1853–1858.

Wiggins, G.B., Mackay, R.J., and Smith, I.M. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. Archiv für Hydrobiologie Supplementum, **58**: 97–206.

Winchester, N.N., Wiggins, G.B., and Ring, R.A. 1993. The immature stages and biology of the unusual North American arctic caddisfly *Sphagnophylax meiops*, with consideration of the phyletic relationships of the genus (Trichoptera: Limnephilidae). Canadian Journal of Zoology, **71**: 1212–1220.

Wise, E.J. 1980. Seasonal distribution and life histories of Ephemeroptera in a Northumbrian River. Freshwater Biology, **10**: 101–111.

Wodsedalek, J.E. 1912. Natural history and general behavior of the Ephemeridae nymphs, *Heptagenia interpunctata* (Say). Annals of the Entomological Society of America, **5**: 31–40.

Zachariassen, K.E., and Husby, J.A. 1982. Antifreeze effect of thermal hysteresis agents protects highly supercooled insects. Nature (London), **298**: 865–867.

Zachariassen, K.E., Kristiansen, E., Pedersen, S.A., and Hammel, H.T. 2004. Ice nucleation in solutions and freeze-avoiding insects — homogeneous or heterogeneous? Cryobiology, **48**: 309–321.

Zettel, J. 2000. Alpine Collembola: adaptations and strategies for survival in harsh environments. Zoology, **102**: 73–89.

Zwick, P. 1996. Variable egg development of *Dinocras* spp. (Plecoptera, Perlidae) and the stonefly seed bank theory. Freshwater Biology, **35**: 81–100.

Zwick, P., and Teslenko, V.A. 2002. Development and life history of Far Eastern Russian *Pteronarcys* spp. (Plecoptera, Pteronarcyidae). Archiv für Hydrobiologie, **153**: 503–528.