

The distribution of four *Chaoborus* species (Diptera: Chaoboridae) along an elevation gradient in Canadian Rocky Mountain lakes

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We tested the hypothesis that the distribution of four species of *Chaoborus* is limited by water temperature in Rocky Mountain lakes. Midsummer surface water temperature (MSSWT) of Rocky Mountain lakes varied between 25 and 5°C along an elevation gradient spanning 600–2400 m above sea level. *Chaoborus* (subgenus *Chaoborus*) *americanus* and *C. (C.) flavicans* were collected in lakes with MSSWT $\geq 16^\circ\text{C}$, generally corresponding to lakes at elevations lower than 1600 m above sea level. *Chaoborus (Sayomyia) punctipennis* was only collected in warm lakes (MSSWT $\geq 21^\circ\text{C}$). Species of the subgenus *Schadonophasma* (*C. trivittatus* and possibly *C. cooki*) were not commonly collected, but preliminary data suggest that they may be more tolerant of low water temperatures than the other species. On a qualitative basis, the distribution of these chaoborids in the Rockies is similar to their latitudinal distribution. However, MSSWT as a valid predictor of *Chaoborus* species distribution with latitude remains to be tested. The gradient in lake temperature found in mountainous environments appears to be a useful gauge for obtaining information about the distribution of invertebrates relative to temperature.

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Nous avons testé l'hypothèse que quatre espèces de chaoboridés ont une répartition limitée par la température dans les lacs des Rocheuses. La température estivale de l'eau à la surface (TEES) varie entre 25 et 5°C le long d'un gradient d'altitude de 600 à 2400 m dans les lacs des Rocheuses. *Chaoborus* (sous-genre *Chaoborus*) *americanus* et *C. (C.) flavicans* étaient retrouvés dans les lacs avec une TEES $\geq 16^\circ\text{C}$, correspondant généralement à une altitude de moins de 1600 m. *Chaoborus (Sayomyia) punctipennis* a seulement été retrouvé dans les lacs les plus chauds (TEES $\geq 21^\circ\text{C}$). Les espèces du sous-genre *Schadonophasma* (*C. trivittatus* et possiblement *C. cooki*) n'étaient pas communes, mais il est possible qu'elles soient plus tolérantes aux températures froides que les autres espèces. Qualitativement, la répartition des espèces par rapport à l'altitude est similaire à leur répartition en fonction de la latitude. Cependant, il reste à déterminer si TEES sera une mesure précise de la répartition de ces chaoboridés selon la latitude. Le gradient de température des lacs de montagne semble une avenue pratique pour obtenir de l'information sur la répartition des invertébrés relativement à la température.

Introduction

Most *Chaoborus* species have a limited northern distribution in North America, Europe, and Asia (Borkent 1979, 1981; Walker 1991). This pattern is identifiable at the subgeneric level; for example, most species of the subgenus *Schadonophasma* are arctic–subarctic, most species of *Chaoborus* s.str. are temperate, and most species of *Sayomyia* are tropical to subtropical (Borkent 1979, 1981). Although temperature-dependent processes appear to be important regulators of species distribution, there are presently few quantitative data available for predicting the northern limit for most species. Information on *Chaoborus* species distribution relative to temperature could be used to predict future distributions in the event of climatic change (Schindler et al. 1990), or to infer past climates through paleoecological studies (Frey 1976; Walker and Mathewes 1989; Walker 1991). We defined the distribution of four *Chaoborus* species relative to water tem-

perature using the gradient in lake temperature found in Rocky Mountain lakes and ponds.

The thermal regime of lakes and ponds in mountainous environment varies significantly with elevation (Thomasson 1956; Fig. 1). We compared the distribution of the four species along an elevation gradient extending from 600 m in the boreal and aspen parkland ecoregions to 2400 m in the alpine ecoregion of Canadian Rocky Mountains of Alberta and British Columbia. We related the distribution of the chaoborids to the midsummer surface water temperature (MSSWT) of the lakes and, for a larger data set, the combination of lake elevation and maximum lake depth as an approximate measure of lake temperature. Because fishes strongly influence the distribution of some *Chaoborus* species (Pope et al. 1973; von Ende 1979; Anderson 1980; Lamontagne and Schindler 1994), data from lakes with and without fishes were obtained from all elevations. Although the specific mechanisms regulating distribution were not identified, this survey of Rocky Mountain lakes and ponds enable us to formulate testable predictions on the maximum northern distribution of these *Chaoborus* species.

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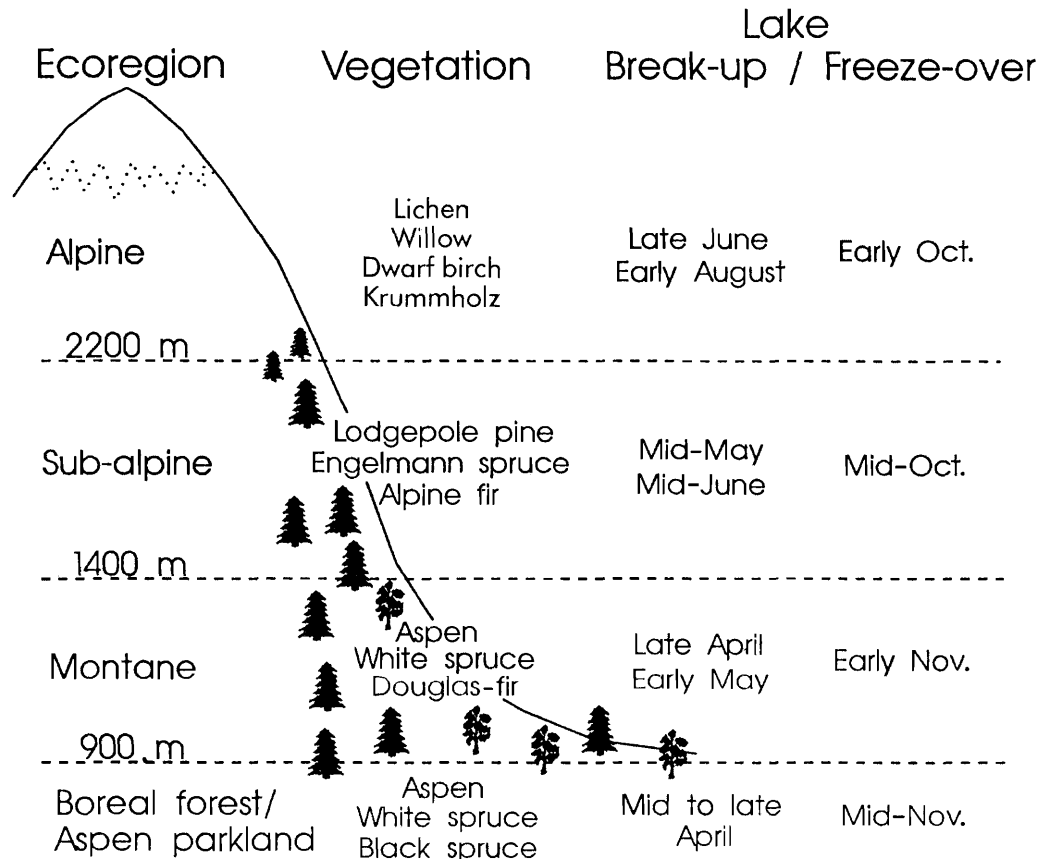


FIG. 1. Ecological classification of lakes relative to elevation in the Canadian Rocky Mountains. This zonation varies with latitude and topography but it is representative of the conditions in the vicinity of Jasper in Jasper National Park. "Krummholz" are the stunted trees found at treeline (adapted from Holland and Coen 1983).

Methods

Study site

The survey included 128 lakes located in Jasper (84), Banff (41), Yoho (2), and Kootenay (1) national parks, Canada, and 9 lakes from the adjacent boreal and aspen parkland regions near Edmonton, Canada. Detailed limnological information on Rocky Mountain lakes can be found in Rawson (1942, 1953) and Anderson (1968, 1970, 1974). In general, Canadian Rocky Mountain lakes are oligotrophic to ultra-oligotrophic, circumneutral to alkaline (pH 7.0–8.5), and transparent (Secchi >5 m), except for lakes receiving glacial meltwater, which can be very turbid during summer (Smith 1978).

Data collection

Data on the presence or absence of *Chaoborus* species were obtained from published and unpublished literature (Anderson 1974, 1980; Anderson and Raasvelt 1974; Mitchell and Prepas 1990) and from recent sampling (Lamontagne 1993). In each lake, *Chaoborus* sp. were collected by means of replicated (2–5) zooplankton net hauls from 1 m over the bottom to the lake surface at maximum lake depth (Anderson 1974; Anderson and Raasvelt 1974). In most lakes, chaoborids were also sampled with replicated (9–15) benthic grabs along depth transects (Donald and Anderson 1982). On average, each lake was sampled twice for zooplankton and once for benthos because of large year-to-year variability and the use of different types of sampling gear, we used the presence or absence of each species in the analysis. Most of Anderson's (1974, 1980) zooplankton collection is archived in the Zoology Museum of the University of Alberta. Using Sæther (1972) and Borkent (1979), we confirmed species identification of archived samples.

The environmental variables used in the analysis (MSSWT, lake elevation, and maximum lake depth) were mainly obtained from

Anderson (1974), Anderson and Raasvelt (1974), Mitchell and Prepas (1990), Donald et al. (1980), Lamontagne (1993); and our unpublished data. MSSWT was the average temperature between the surface and 2 m depth, measured with a thermistor. When temperature profiles were not available, MSSWT was the temperature obtained with a hand thermometer held ≈ 25 cm below the surface. The two methods of measuring MSSWT gave similar results, except for lakes coloured by glacial meltwater, which can be 2 or 3°C warmer at the surface than at 2 m depth during warm, calm days. MSSWT was usually taken in the last 2 weeks of July or first 2 weeks of August because previous studies have shown that maximum seasonal temperatures in Rocky Mountain lakes occur in early August (Anderson 1970; Fabris and Hammer 1975). An effort was made to sample the lakes at least once during that period. The complete data set can be found in Lamontagne (1993) or obtained upon request to the authors.

Analysis

Logistic regressions were used to test the relationship between the presence or absence of *Chaoborus* spp. and the environmental variables. Logistic regression is the equivalent of linear regression for categorical response variables, such as presence/absence (Reckow et al. 1987; SAS Institute Inc. 1988; Trexler and Travis 1993).

Results

As expected, there is a strong relationship between lake elevation and MSSWT in lakes in the Rocky Mountains, with 73% of the variability in MSSWT explained by elevation (Fig. 2). In a multiple regression with lake elevation, maximum lake depth was negatively correlated with MSSWT, but only accounted for an additional 1% of the variance (Fig. 2). The effect of lake morphometry on the thermal regime of lakes

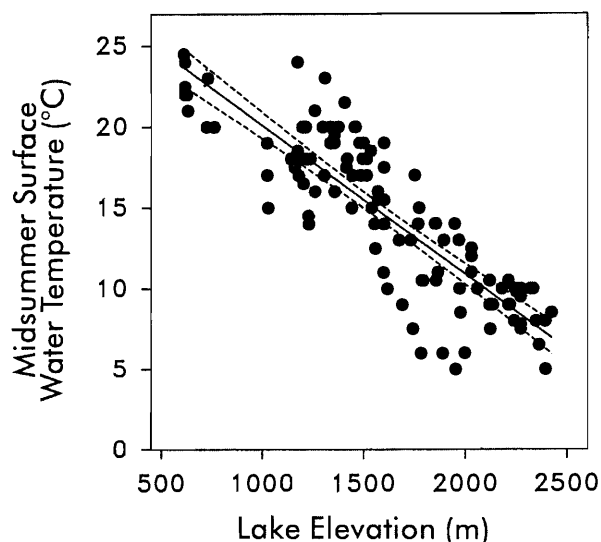


FIG. 2. Relationship between elevation and midsummer surface water temperature (MSSWT) in lakes in the Canadian Rocky Mountains. $MSSWT (^{\circ}C) = 29.3 - 0.00923 \times \text{elevation (m)}$; $F = 299$, $P < 0.0001$, $R^2 = 0.73$, $S_{x,y} = 2.62$; $n = 112$. Maximum lake depth further accounted for 1% of the variability in MSSWT: $MSSWT = 31.0 - 0.00924 \times \text{elevation} - 1.62 \log_{10} \text{maximum depth (m)}$; $R^2 = 0.74$, $F = 162$, $P < 0.0001$, $S_{x,y} = 2.55$.

may be underestimated by MSSWT because the whole water column is not considered.

Chaoborus (subgenus *Chaoborus*) *flavicans* and *C. (C.) americanus* were restricted to lakes with $MSSWT \geq 16^{\circ}C$ and *Chaoborus (Sayomyia) punctipennis* to lakes with $MSSWT \geq 21^{\circ}C$ (Table 1 and Fig. 3). For *C. americanus* and *C. flavicans*, this corresponded to lakes at elevations lower than 1600 m. More data are needed to define the elevation threshold for *C. punctipennis* (Table 1), but it is approximately 800 m (Fig. 4). *Chaoborus (Schadonophasma) trivittatus* was not commonly collected but was the only species found at elevations higher than 1600 m (Fig. 4). Overall, the four species of *Chaoborus* preferred warm, low-elevation lakes and tended to occupy shallower bodies of water at high elevations (Table 1 and Fig. 5).

Discussion

The distribution of the four chaoborids studied is strongly related to indices of lake thermal regime in the Rocky Mountains of Alberta. Other invertebrate taxa have been shown to have restricted distributions in lakes of the Canadian Rockies, including zooplankton (Anderson 1974), and benthic insects such as stoneflies (Donald and Anderson 1977, 1980) and chironomids (Walker and Mathewes 1989). Similar patterns have been observed for a variety of invertebrate taxa in other mountainous regions (Patalas 1964; Hynes 1970; Kawecka and Szczesny 1984; Ward 1986).

Chaoborus trivittatus was not very common in lakes in this survey, but it was common in ponds in the Jasper area sampled by Borkent (1979). *Chaoborus trivittatus* may be more tolerant of cold climatic conditions than the other three species (Fig. 4), notably, it was collected in some high-elevation ponds (Fig. 5). Some of the larvae identified as *C. trivittatus* may have been *C. cooki*, another species of the subgenus *Schadonophasma*. *Chaoborus cooki* typically occurs in temporary bodies of water but is occasionally found in permanent

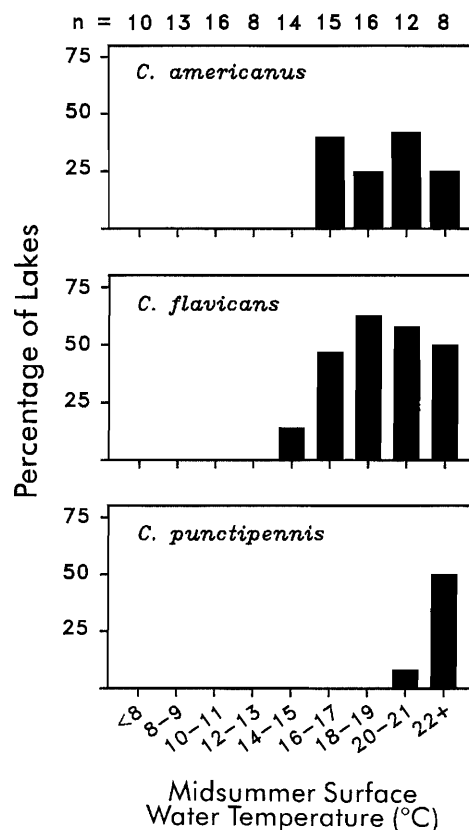


FIG. 3. Distribution of three *Chaoborus* species relative to midsummer surface water temperature (MSSWT) of 112 lakes in Jasper and Banff national parks and neighbouring aspen parkland region. *Chaoborus trivittatus* (not shown) was also collected from three lakes ($MSSWT = 11, 16.5, 18^{\circ}C$). The number of lakes sampled per category of lake temperature regime (n) is indicated at the top.

habitats (Borkent 1979). It was difficult to separate the larvae of the two species (Borkent 1979), so *C. cooki* may have been present in some of the small lakes and ponds.

Chaoborus may be absent from cold lakes because they do not "accumulate" enough degree-days above a certain temperature threshold, even at their maximum physiological life-span (Danks 1971; Danks and Oliver 1972; Begon et al. 1986, pp. 44–46; Büns and Ratte 1991). Water temperature can have a strong influence on metabolism of *Chaoborus* species; for example, *C. trivittatus* has a lower food-assimilation efficiency and feeding rate at low temperatures (Fedorenko 1975; Swift 1976; Giguère 1981). Like arctic chironomids (also dipterans) perhaps, chaoborids may cope with marginal temperature regimes by lengthening their life cycle (Downes 1964). *Chaoborus trivittatus* and *C. americanus* have a 2-year instead of a 1-year life cycle in some lakes (Fedorenko and Swift 1972; Carter and Kwik 1977). Alternatively, the life cycle of *Chaoborus* spp. may also be lengthened by the short supply of food in oligotrophic lakes (Neill 1988).

Presently, we do not have enough limnological data from arctic and subarctic lakes to test whether the MSSWT thresholds defined in the Rockies also apply to these *Chaoborus* species in northern lakes. On a relative basis, however, the distribution of the *Chaoborus* species along the elevation–temperature gradient of Rocky Mountain lakes is similar to their latitudinal distribution (Fig. 6). Species of the subgenus

TABLE 1. Logistic regressions describing the probability of occurrence of three *Chaoborus* species relative to midsummer surface water temperature (MSSWT; °C), Elevation (m) and maximum depth (Z_{max} ; m) in lakes of the Canadian Rocky Mountains

	Model	χ^2	$n(y, z)^a$
<i>Chaoborus americanus</i>	$P = -6.03 + 0.261 \times \text{MSSWT} (0.0759)^{***}$ $= 1.28 - 0.00195 \text{ elevation} (0.000562)^{***}$	11.8 12.0	17, 112 22, 137
<i>Chaoborus flavicans</i>	$P = -6.85 + 0.360 \times \text{MSSWT} (0.0772)^{***}$ $P = 3.77 - 0.00390 \times \text{elevation} (0.000694)^{***}$	21.7 23.9	30, 112 30, 137
<i>Chaoborus punctipennis</i>	$P = -25.1 + 1.09 \times \text{MSSWT} (0.400)^{**}$ $P = 9.95 - 0.0148 \times \text{elevation} (0.00893)^{(P=0.06)}$	7.44 2.86	5, 112 5, 137
<i>Chaoborus</i> spp.	$P = 7.91 - 0.00454 \times \text{elevation} (0.000821)^{***}$ $- 1.71 \log_{10} Z_{max} (0.644)^{**}$	30.5 7.01	53, 137

NOTE: The probability (P) of *Chaoborus* being present (1.0) or absent (0) can be estimated using the equation P (species present) = $1/(1 + e^{-(b+ax)})$, where x is the environmental variable and b and a are the fitted parameters of the logistic regression (standard error of a is given in parentheses).

Wald's statistic, which approximates a χ^2 distribution, was used to test the statistical significance of the parameter estimates (SAS Institute Inc. 1988).

^aSample size (n) is given as the number of times the species occurred (y) and total number of lakes used in the analysis (z).

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.0001$.

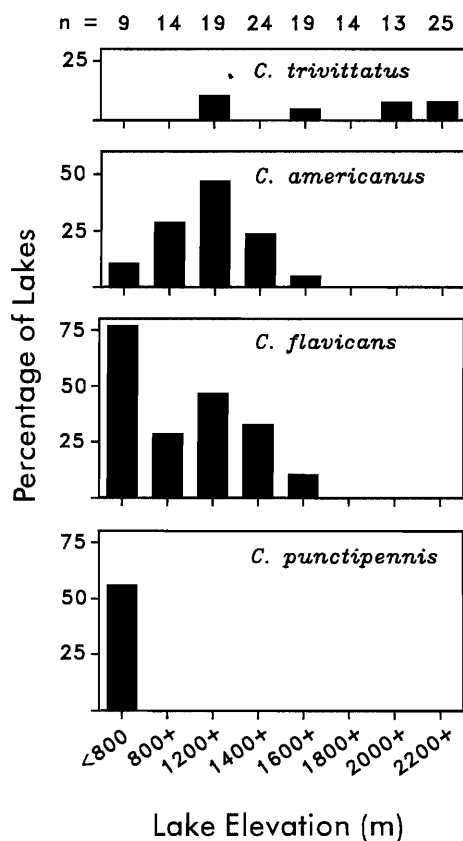


FIG. 4. Distribution of four *Chaoborus* species in relation to lake elevation in 137 lakes from Banff, Jasper, Yoho, and Kootenay national parks and neighbouring aspen parkland region.

Schadonophasma have the northernmost distribution (Fig. 6). Notably, *C. trivittatus* has been collected as far north as the MacKenzie River delta, Labrador, and Baffin Island (Borkent 1979, 1981). *Chaoborus* (*C.*) *americanus* and *C.* (*C.*) *flavicans* have an intermediate northern distribution, while the northern

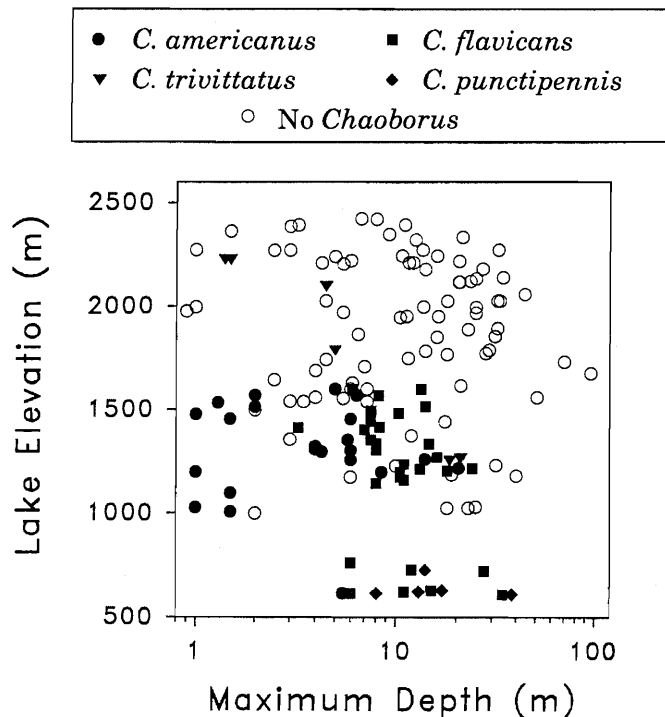


FIG. 5. Distribution of four *Chaoborus* species relative to lake elevation and lake maximum depth in 137 lakes from the Canadian Rockies.

limit of *C. (Say.) punctipennis* is restricted to the southern part of Canada (Fig. 6).

Effect of predation and lake size

Fish predation greatly affects the structure of *Chaoborus* communities in temperate lakes (Pope et al. 1973; Northcote et al. 1978; von Ende 1979). *Chaoborus* populations may be less able to sustain predation in cold, oligotrophic lakes because of slower development rates (Luecke 1988) and low food availability (Neill 1988; Yan et al. 1982). *Chaoborus* spp.

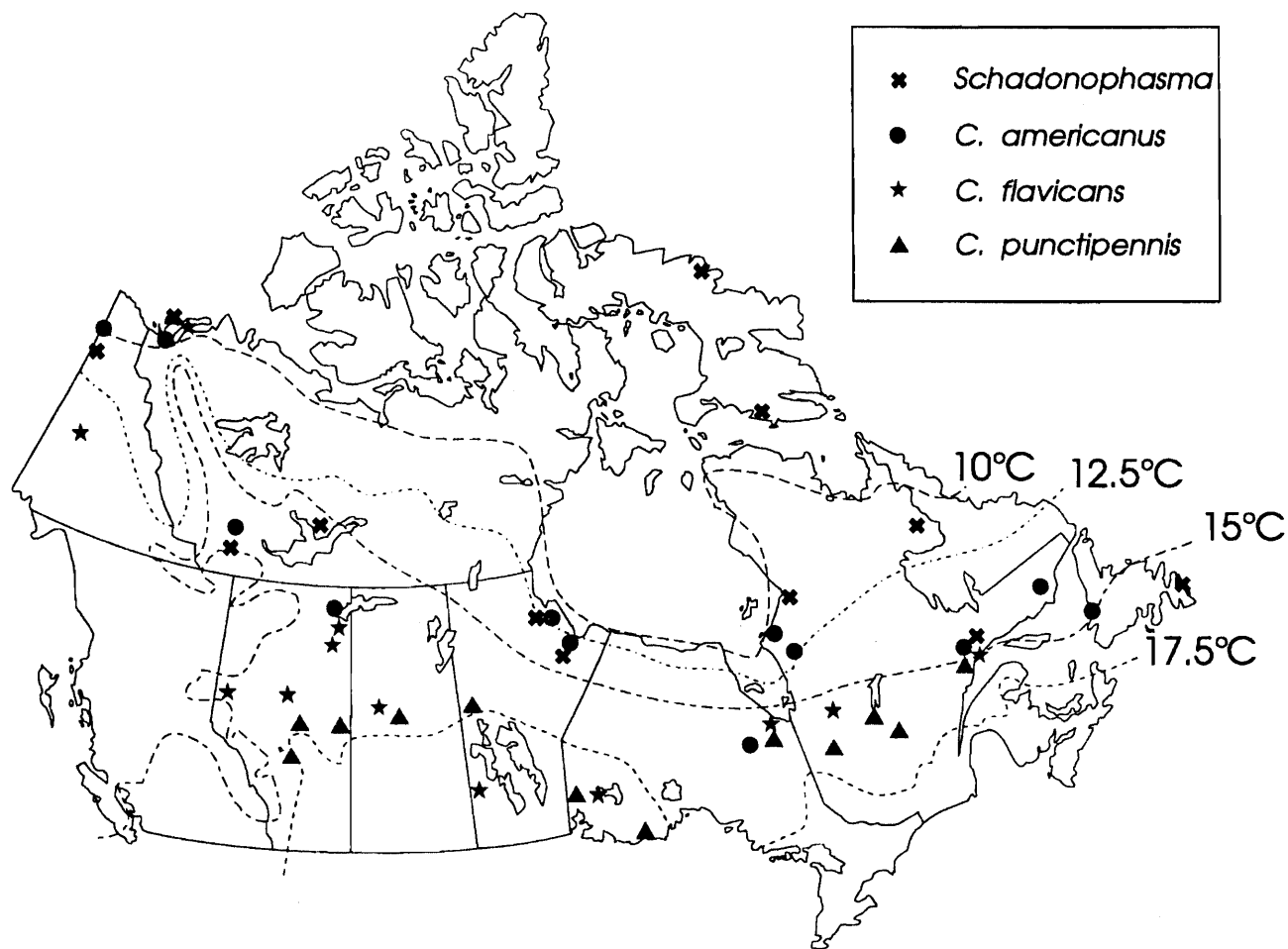


FIG. 6. Latitudinal distribution of four *Chaoborus* species in Canada relative to mean July air temperature (Fisheries and Environment Canada 1978). The 12 northernmost records of each species from Borkent (1979, 1981) are plotted. Subgenus *Schodonophasma* species (*C. trivittatus* and *C. cooki*) were pooled because of the difficulty of separating the two species.

were less likely to be found in lakes with a high density of fish in our study area (Lamontagne and Schindler 1994). However, because 42% of the lakes above 1600 m in this survey were fishless, increased susceptibility to fish predation alone cannot account for the absence of *Chaoborus* spp. in cold lakes.

Anderson and Raasvelt (1974) proposed that predation by *Gammarus lacustris* may limit *Chaoborus* spp. distribution in high-elevation lakes. *Gammarus* spp. are occasionally pelagic in fishless lakes and may compete with *Chaoborus* spp. for food, or even prey on them (Anderson and Raasvelt 1974). The importance of competition with or predation on *Chaoborus* spp. by *Gammarus* spp. in the absence of predatory fishes requires verification in the field.

Lake size is indirectly correlated with the distribution of the four *Chaoborus* species because of its influence on fish distribution (Lamontagne and Schindler 1994). *Chaoborus americanus* and *C. trivittatus* are sensitive to predation by fishes (Northcote et al. 1978; von Ende 1979) and occur more commonly in small water bodies because these more frequently have few or no fish species (Matuszek and Beggs 1988). However, in large fishless lakes (i.e., >25 ha in area) *C. americanus* and *C. trivittatus* are still the dominant species (Lamontagne and Schindler 1994). *Chaoborus flavicans*

and *C. punctipennis* rarely co-occur with *C. americanus* (Lamontagne and Schindler 1994). Von Ende (1979) demonstrated that larger size and earlier emergence enabled *C. americanus* larvae to prey on *C. punctipennis* larvae. On the other hand, *C. flavicans* and *C. punctipennis* have several adaptations allowing them to coexist with predatory fishes (Uutala 1990), and therefore occur more frequently in larger lakes.

The tendency for *Chaoborus* spp. to occur in small water bodies at higher elevations suggests that small lake size influences their distribution directly through a more favourable temperature regime in the thermally limiting environments. In general, the temperature of water bodies is dependent on average air temperature and insolation (Thomasson 1956). Because insolation is a more important part of the heat budget of small lakes in summer, these will tend to be warmer than larger ones nearby (Thomasson 1956; Danks 1971; Rigler 1978). The difference in temperature is significant enough that many species of chironomids in the arctic are restricted to ponds (Danks 1971; Danks and Oliver 1972).

Variation in the timing and composition of irradiation may cause discrepancies in species distributions between elevation and latitudinal gradients. Insolation is higher in the arctic during summer, and this could be a significant factor for small

water bodies. In other words, some organisms may be found farther north than predicted from their elevational distribution. In addition, high ultraviolet light levels may limit the distribution of organisms at high elevations (Thomasson 1956). Despite these potential differences, elevation gradients appear to be a useful way of obtaining information about the distribution of organisms.

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