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THE EFFECT OF ELEVATION AND FISH PREDATION ON THE DISTRIBUTION OF CHAOBORUS IN ROCKY MOUNTAIN LAKES: PALEOLIMNOLOGICAL APPLICATIONS.

by

Sébastien Lamontagne

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SPRING 1993

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UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled THE EFFECT OF ELEVATION AND FISH PREDATION ON THE DISTRIBUTION OF CHAOBORUS IN ROCKY MOUNTAIN LAKES: PALEOLIMNOLOGICAL APPLICATIONS submitted by Sébastien Lamontagne in partial fulfillment of the requirements for the degree of Master of Science.

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Date: 31 March 1993

Abstract

Cabin, Celestine and Caledonia lakes, Jasper National Park, contain naturally reproducing populations of rainbow trout (Oncorhynchus mykiss) and lake chub (Couesius plumbeus), but whether these populations are native was not known. I used subfossil Chaoborus mandibles retrieved from sediment cores to determine if planktivorous fish were present in these lakes prior to this century. To achieve this, I have first defined the extant distribution of Chaoborus species relative to elevation and the presence of fishes in Rocky Mountain lakes. I determined that C. (subgenus Chaoborus) americanus is the only species found in fishless lakes, while C. (C.) flavicans is only found in lakes containing fishes. The genus Chaoborus also had a restricted distribution along the elevation-temperature gradient of mountain lakes. C. americanus and C. flavicans only occurred in lakes with a mid-summer surface water temperature (MSSWT) $\geq$ 16°C, corresponding to lakes of elevations lower than 1 600 m. The subgenus Schadonophasma (C. trivittatus and C. cooki) was not as common, but seemed to be more tolerant of cold water temperatures. C. (Sayomia) punctipennis was found in lakes adjacent to the national parks and was restricted to relatively warm water temperatures (MSSWT $\geq$ 21°C).

Cabin and Celestine lakes were fishless prior to this century. In these lakes, C. americanus was present prior to this century but was eliminated when fish were first stocked. C. flavicans has replaced C. americanus in Celestine Lake but Chaoborus are presently rare in Cabin Lake. The occurrence of C. flavicans throughout the Caledonia Lake core suggests that this lake had native fish(es) prior to this century.

The fish species originally present cannot presently be determined. However, the paleolimnological analysis supports the hypothesis of the past occurrence of the Athabasca rainbow trout (O. mykiss athabascae) in Caledonia Lake. Paleolimnology appears to be a useful tool to determine the status of past fish populations in lakes with no early records.

Acknowledgements

I would like to thank R.S. Anderson, D.B. Donald, D.W. Mayhood, and E.E. Prepas for the use of their unpublished data. A. Paul and R. Vitic provided assistance during field collections. P. Leavitt, J. Curtis, B. Miskimmin and A. Paul provided challenging criticisms at various stages of my work. Special thanks to my supervisor, D.W. Schindler, for his support and editing of the thesis. This work was supported by a Boreal Alberta Grant from the Canadian Circumpolar Institute, a ’Fonds pour la Formation de Chercheur et d’Aide à la Recherche’ from the province of Quebec, and a Postgraduate Scholarship from the province of Alberta.

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Introduction

It is now recognized that many past fisheries management practices have been detrimental to native fish and invertebrate populations in lakes and rivers of the Rocky Mountain national parks (Plate 1, Harvey et al. 1989, Schindler et al. in prep.). Unfortunately, due to the lack of historical records, it is presently difficult to determine the extent of change that has occurred (Mayhood 1992). For example, in many lakes of the parks it is not known whether the present fish populations are native, stocked, or a combination of native and stocked fishes.

In the absence of historical records, paleolimnology can be a useful method of obtaining long-term information on the past environmental conditions and community composition of lakes (Schindler 1987, Magnuson 1990, Smol 1990). Paleolimnology uses the contemporary relationships between species and their environment to make inferences about past environmental conditions from plant and animal remains preserved in lake sediments.

I have used Chaoborus subfossil mandibles to determine if Cabin, Caledonia and Celestine lakes, Jasper National Park, had fish prior to this century. I have demonstrated that chaoborids are distributed as a function of lake temperature (Chapter 1) and the presence of predatory fishes (Chapter 2) in Rocky Mountain lakes. These relationships helped me in the interpretation of the sedimentary records of the three

Plate 1. Early fishing success in Banff, ca. 1900 (the fish are probably mostly lake trout, Salvelinus namaycush). In these early days, it was often a matter of pride to catch and kill as many trout as possible. Despite bag limits and season closures, even in the 1890's many native fish populations had been severely depleted (McIllree and White-Fraser 1983). Photo from Archives of Canadian Rockies, Peter Whyte Foundation.

lakes (Chapter 2). The relationship between Chaoborus and lake temperature deserves further study, and I have outlined this and other problems worth investigating in the General Discussion. I hope the result of this study will be helpful to those responsible for the management and the restoration of native lake communities in the mountain parks.

The thesis is written in paper format. Consequently, Chapters 1 and 2 have been written as two independent units. There is some overlap of material, but I tried to keep redundancy to a minimum.

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Chapter 1

The distribution of four Chaoborus species along an elevation gradient in Canadian Rocky Mountain lakes

Introduction

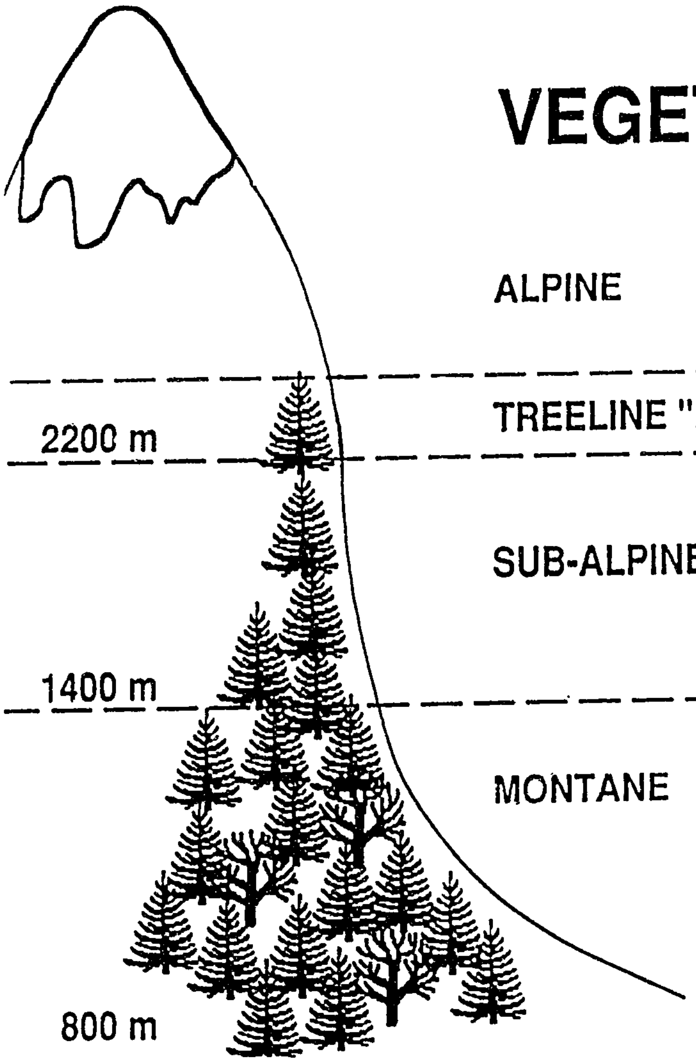
Chaoborus species, the phantom midges, have a limited northern distribution in North America, Europe and Asia (Borkent 1979, 1981, Walker 1991). The climatic factors responsible for this distribution are not known, however, they are probably related to the thermal cycles of the lakes and ponds that Chaoborus inhabit (Walker and Mathewes 1989a). The northern range of different species is variable (Borkent 1979, 1981) and it has not been precisely related to limnological variables. Studies on the distribution of plant and animals along latitudinal temperature gradients can be logistically complicated. However, similar temperature gradients can be found over shorter distances in mountainous regions (Thomasson 1956, Luckman 1990, Walker 1991). I have hypothesized that the distribution of chaoborids along an elevation gradient in Rocky Mountain lakes will be similar to that observed for latitude.

Like most midges, Chaoborus spend most of their lives in aquatic habitats. Adult midges are terrestrial and live for short period of times (hours to several days). Eggs are laid on top of the water and may float in rafts or sink depending of the species (Saether 1972). The larval stage consists of four instars of increasing duration (Fedorenko and Swift 1972, Saether 1972, Walker 1987). Chaoborus larvae have unique adaptations among aquatic insects that allow them to permanently occupy the open water regions of lakes and ponds. Most chaoborid larvae can tolerate long periods of anoxia, and they possess two sets of air sacs to facilitate hydrostatic compensation (Saether 1972). The third and fourth instars of some lake-dwelling species undergo strong diurnal vertical migrations to avoid the illuminated region of the water column during the day (Teraguchi and Northcote 1966, Roth 1968, Fedorenko and Swift 1972, Carter and Kwik 1977). The migrating behaviour, and nearly transparent bodies, limit predation by planktivorous fishes (Pope et al. 1973, Northcote et al. 1978, von Ende 1979). The pupal stage is also pelagic and is relatively active (Saether 1972). Depending on the species and latitude, generation time spans from 0.5 to 2 years (Fedorenko and Swift 1972, Carter and Kwik 1977, Luecke 1988). The rates of development and the metabolism of the aquatic life-stages of Chaoborus have been shown to be strongly influenced by water temperature (Parma 1969, Saether 1972, Swift 1976, Giguère 1980, 1981, Giguère and Dill 1980, Luecke 1988).

Walker and Mathewes (1989a) did not collect Chaoborus remains in surficial sediments of mountain lakes higher than 1 600 m in British Columbia and Alberta. In this study, I compared the distribution of four Chaoborus species along an elevation gradient extending from 600 to 2 400 m in the Canadian Rocky Mountain of Alberta (Fig. 1.1). I related the distribution of the chaoborids to the Mid-Summer Surface Water Temperature (MSSWT) of the lakes and, for a larger data set, the combination of lake elevation and lake maximum depth as an approximate measure of lake temperature. Because fishes strongly influence the distribution of Chaoborus species (Pope et al. 1973, von Ende 1979, Anderson 1980, Chapter 2), an effort was made to

Fig. 1.1. The 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, Jasper National Park (Gadd 1986). 'Krummholz' are the stunted trees found at treeline.

ALPINE ZONATION



	VEGETATION	BREAK-UP/ FREEZE-OVER
ALPINE	-ALPINE MEADOWS -NO TREES	LATE-JUNE MID-JULY / EARLY-OCT
TREELINE "KRUMMHOLZ"		
SUB-ALPINE	- ENGELMANN SPRUCE - ALPINE FIR	MID-MAY MID-JUNE / MID-OCT
MONTANE	- MIXED FOREST	LATE-APRIL EARLY-MAY / EARLY-NOV

obtain data from lakes with and without fishes at all elevations. The information gathered in this study better defines the distribution of *Chaoborus* relative to lake temperature, and will provides background information for the use of subfossil *Chaoborus* as past climate indicators.

Methods

Data Collection

Data on the presence or absence of *Chaoborus* species was obtained from published and unpublished literature (Anderson 1974, 1980, Anderson and Raasvelt 1974, Mitchell and Prepas 1990, E.E. Prepas and D.B. Donald, unpubl. data; Appendix 1) and from recent sampling. In each lake, *Chaoborus* were collected with zooplankton nets hauled vertically from 1 m above the bottom to the lake surface (Anderson 1974, Anderson and Raasvelt 1974). In most lakes, chaoborids were also sampled with benthic grabs (Donald and Anderson 1982). I used the presence or absence of each species rather than quantitative data to avoid calibration problems between methods. Most of Anderson's (1974, 1980) zooplankton collection is archived in the Zoology Museum of the University of Alberta. Using Saether (1972), I confirmed species identification of archived samples.

The environmental variables used in the analysis (MSSWT, lake elevation and lake maximum depth) were mainly obtained from published (Anderson 1974, Anderson and Raasvelt 1974, Donald *et al.* 1980) and unpublished literature (Appendix

1). MSSWT was the average temperature between the surface and two meters 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. Both methods of measuring MSSWT gave similar results, except in colored lakes which can be 2 or 3 °C warmer at the surface than at two meters during sunny days (S. Lamontagne pers. obs.). MSSWT was usually taken in the last two weeks of July or first two weeks of August because previous studies have shown that seasonal temperature maxima in Rocky Mountain lakes occur in early August (Anderson 1970). In previous surveys by the Canadian Wildlife Service, an effort was made to sample the lakes at least once during that period (D.B. Donald, Environment Canada, 1901 Victoria Ave, Regina, Sask., S4P 3R4, pers. comm.)

Analysis

Logistic regressions were used to test the relationship between presence or absence of Chaoborus 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 1988).

Results

As expected, there is a strong relationship between lake elevation and MSSWT in lakes of the Rocky Mountains, with 73% of the variability in MSSWT explained by elevation (Fig. 1.2). In a multiple regression with lake elevation, lake maximum depth was negatively correlated to MSSWT, but only accounted for an additional 1% of the variance (Fig. 1.2). The effect of lake morphometry on the thermal regime of lakes 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 a MSSWT ≥ 16°C, and C. (Sayomia) punctipennis to lakes with a MSSWT ≥ 21°C (Table 1.1 and Fig. 1.3). Species were also clearly distributed along the lake elevation gradient. C. americanus and C. flavicans seldom occurred in lakes higher than 1600 m and C. punctipennis was only collected at elevations lower than 800 m (Table 1.1 and Fig. 1.4). Overall, the genus Chaoborus preferred warm, low-elevation lakes. At high elevations, Chaoborus tended to occupy only shallower bodies of water (Table 1.1 and Fig. 1.5).

Discussion

The distribution of chaoborids is strongly related to indices of the thermal regime of lakes in the Rocky Mountains of Alberta. Other invertebrate taxa have distributions restricted by temperature 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 1989a). 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).

Fig. 1.2. The relationship between-elevation and Mid-Summer Surface Water Temperature (MSSWT) in lakes of the Canadian Rocky Mountains. MSSWT (°C) = 29.3 - 0.00923 Elevation (m), $F = 299$, $P < 0.0001$, $R^2 = 0.73$, $s_{x \cdot y} = 2.62$, $n = 112$. Lake maximum depth further accounted for a further 1% of the variability in MSSWT: MSSWT = 31.0 - 0.00924 Elevation - 1.62 $\log_{10}$ Maximum Depth (m), $R^2 = 0.74$, $F = 162$, $P < 0.0001$, $s_{x \cdot y} = 2.55$. Other factors such as the relative importance of groundwater in the hydrological budget, the proximity of glaciers or glacier meltwater inflow are likely to influence MSSWT.

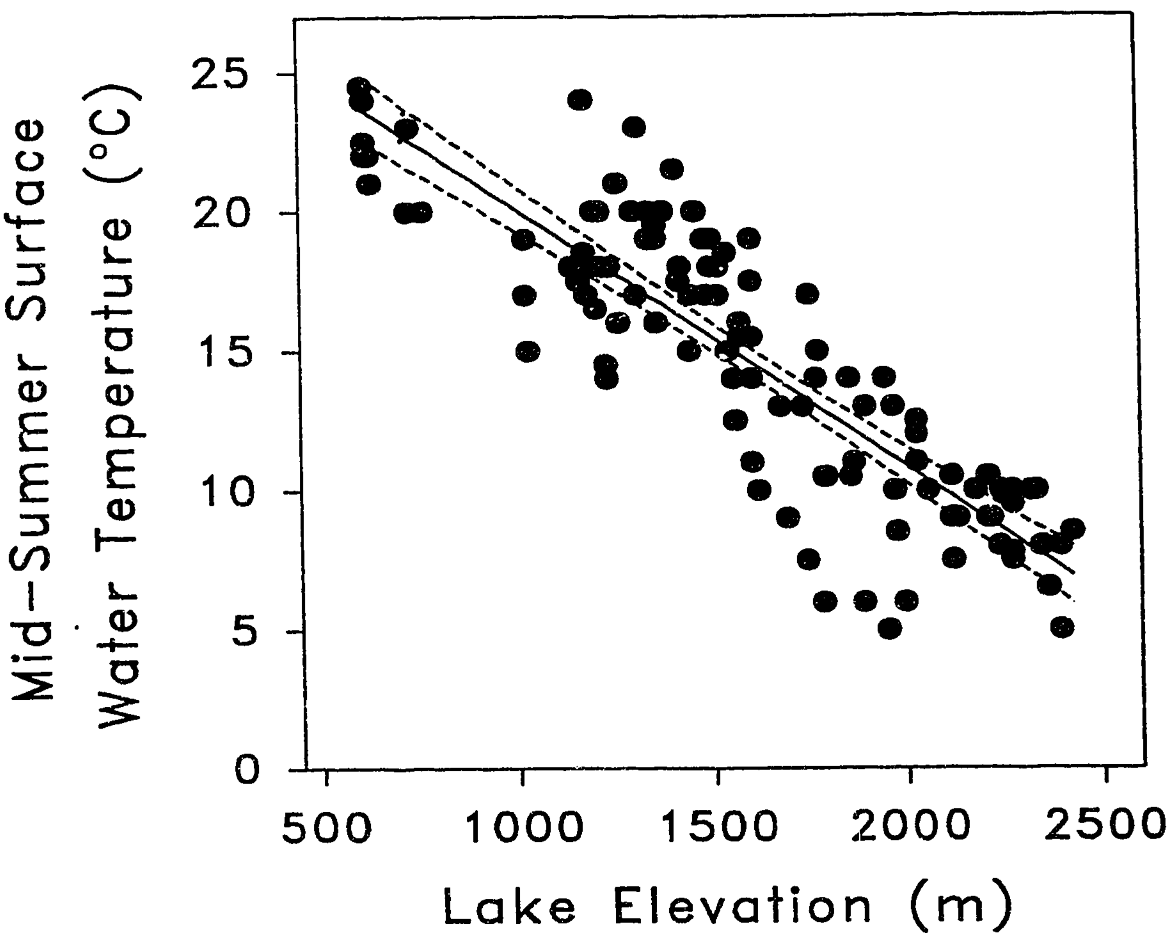

Mid-Summer Surface
Water Temperature (°C)
0
5
10
15
20
25
500
1000
1500
2000
2500
Lake Elevation (m)

Table 1.1. Logistic regressions describing the probability of occurrence of three Chaoborus species relative to Mid-Summer Surface Water Temperature (MSSWT; °C), Elevation (m) and maximum depth (Z_{max}; m) in lakes of the Canadian Rocky Mountains. The probability (Pr) of Chaoborus being present (1.0) or absent (0) can be estimated using the equation $Pr = 1 / (1 + e^{-(b + ax)})$, with x the environmental variable and b,a the fitted parameters of the logistic regression. *** = P<0.0001, ** = P<0.01, * = P<0.05. The Wald's statistic, which approximate a Chi-square distribution, was used to test the statistical significance of the parameter estimates (SAS 1988). Sample size (n) is given as the number of time the species occurred (y) and total number of lakes used in the analysis (z).

	Model	Chi-Square	n (y,z)
Pr (C. americanus)	$= -6.03 + 0.261$ MSSWT $(0.0759)^{***}$	11.8	17,112
	$= 1.28 - 0.00195$ Elevation $(0.000562)^{***}$	12.0	22,137
Pr (C. flavicans)	$= -6.85 + 0.360$ MSSWT $(0.0772)^{***}$	21.5	30,112
	$= 3.77 - 0.00390$ Elevation $(0.000694)^{***}$	23.9	30,137
Pr (C. punctipennis)	$= -25.1 + 1.09$ MSSWT $(0.400)^{**}$	7.44	5,112
	$= 9.95 - 0.0148$ Elevation $(0.00893)^{n.s.}$	2.86	5,137
Pr (Chaoborus)	$= 7.91 - 0.00454$ Elevation $(0.000821)^{***}$	30.5	53,137
	$- 1.71 \log_{10} Z_{max} (0.644)^{**}$	7.01	

Fig. 1.3. The distribution of three Chaoborus species relative to Mid-Summer Surface Water Temperature (MSSWT) of 112 lakes from Jasper and Banff National parks and neighbouring prairie regions. C. trivittatus (not shown) was also collected from three lakes (MSSWT = 11, 16.5, 18 °C). The two lakes in the 14-15.9 °C range where C. flavicans was found had MSSWTs = 15.5 °C.

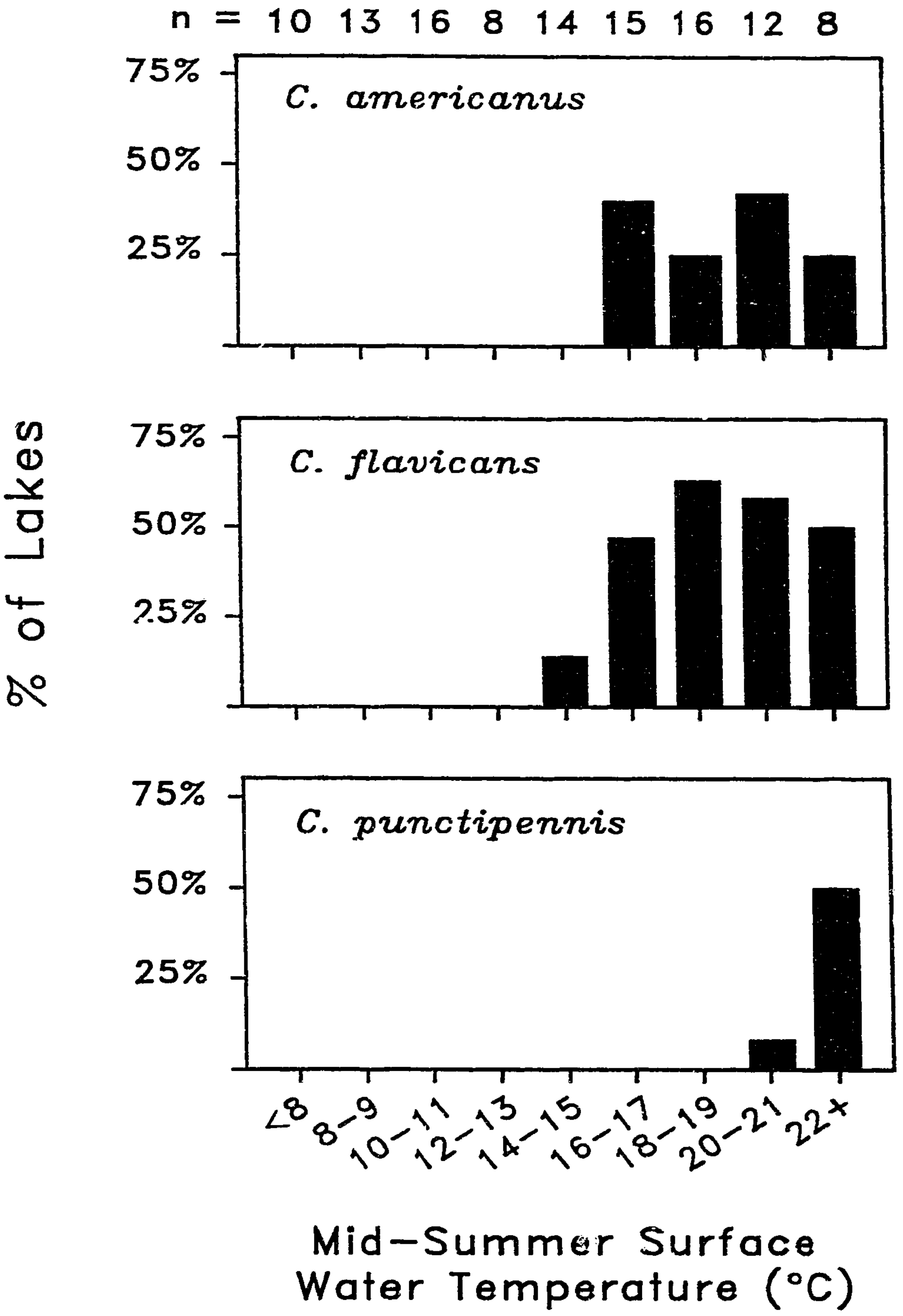

n = 10 13 16 8 14 15 16 12 8
% of Lakes
75%
50%
25%
C. americanus
C. flavicans
C. punctipennis
<8
8-9
10-11
12-13
14-15
16-17
18-19
20-21
22+
Mid-Summer Surface Water Temperature (°C)

Fig. 1.4. The distribution of four Chaoborus species in relation to lake elevation in 137 lakes from Banff, Jasper, Yoho and Kootenay National parks and neighbouring prairie regions.

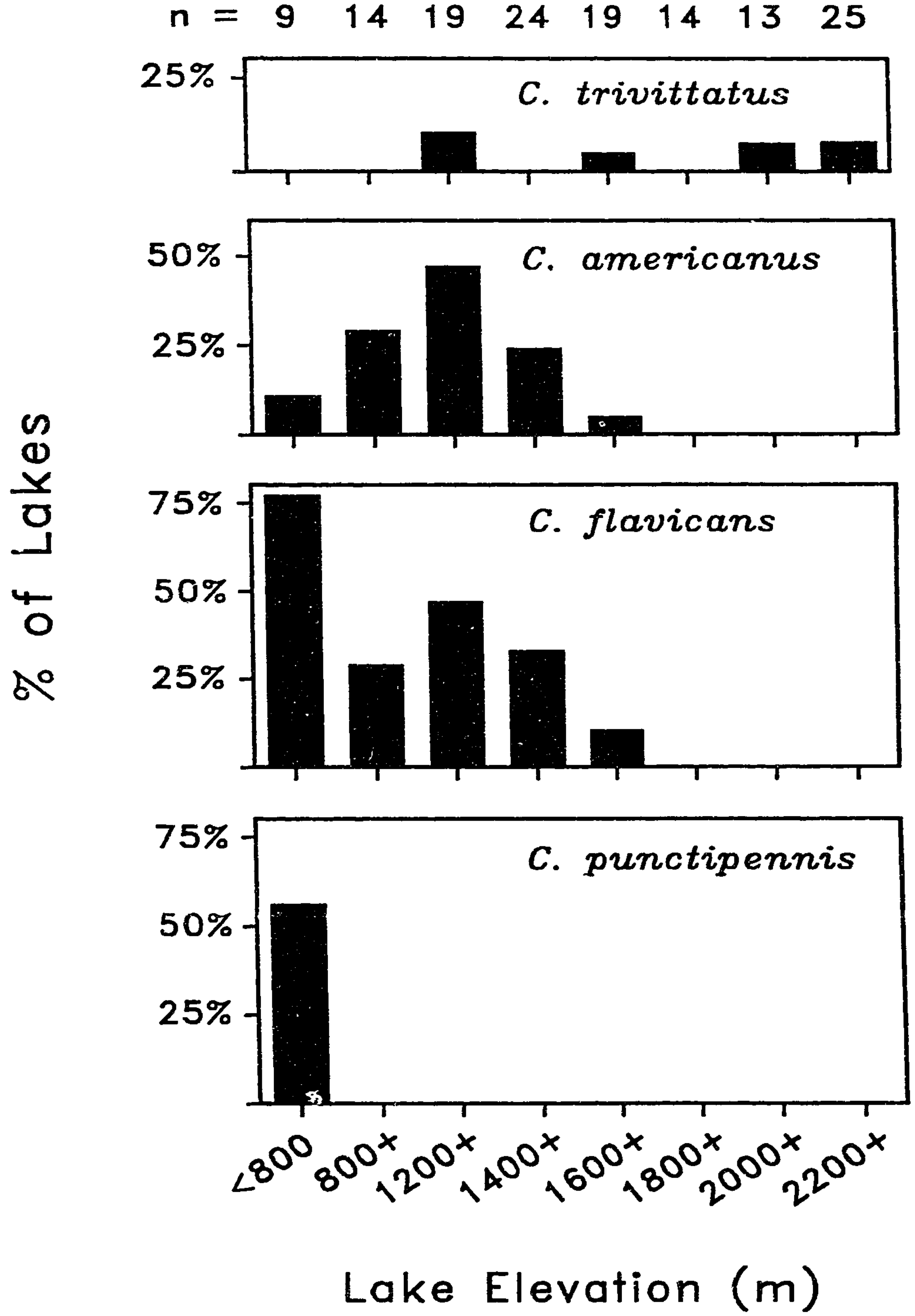
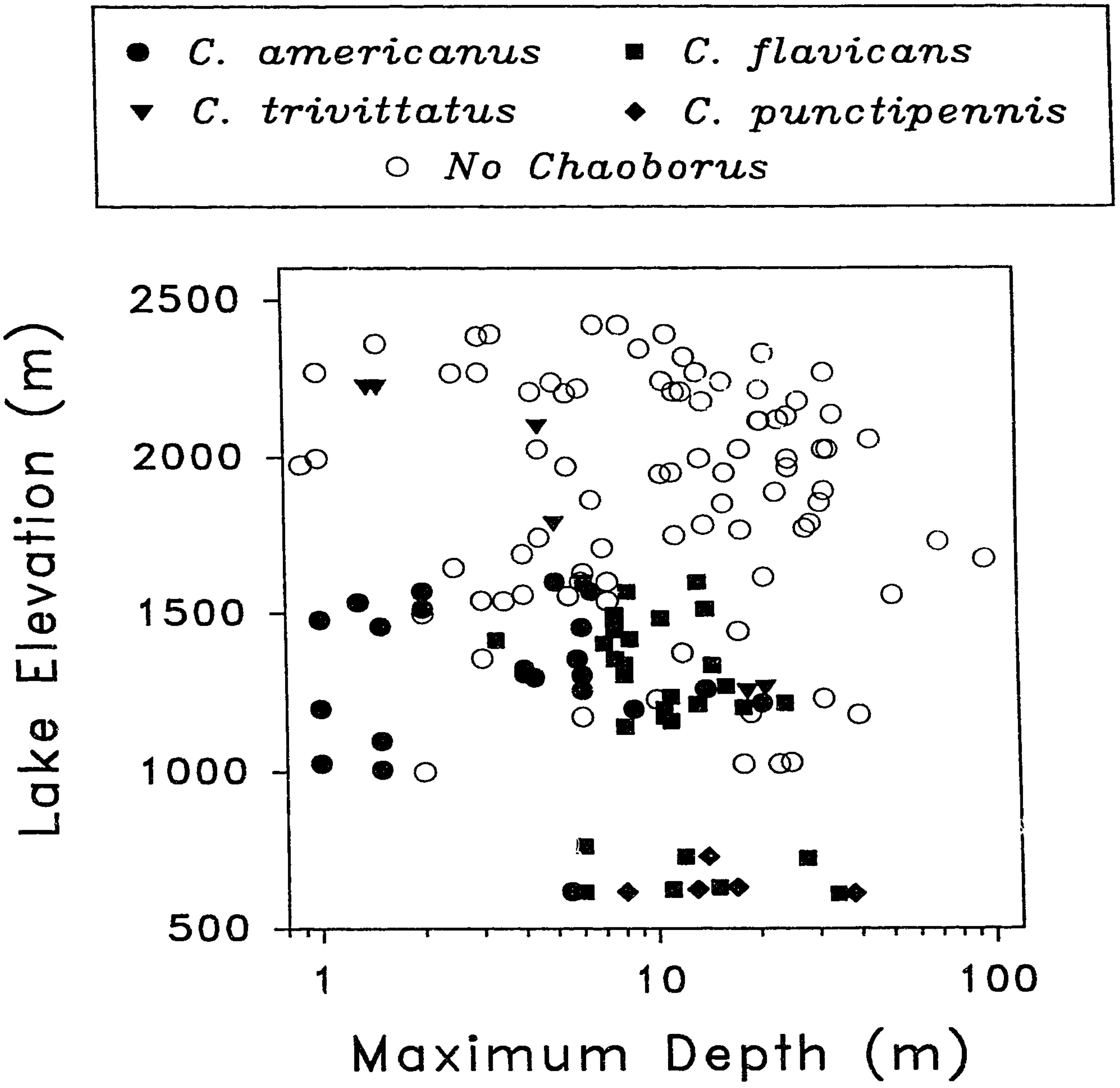

n = 9 14 19 24 19 14 13 25
C. trivittatus
25%
C. americanus
50%
25%
C. flavicans
75%
50%
25%
C. punctipennis
75%
50%
25%
% of Lakes
<800
800+
1200+
1400+
1600+
1800+
2000+
2200+
Lake Elevation (m)

Fig. 1.5. The distribution of four Chaoborus species relative to lake elevation and lake maximum depth in 137 lakes from the Canadian Rockies. Overall, the genus is restricted to low elevations and is most common in shallower lakes and ponds (Table 1). Chaoborids may be absent from some lakes due to fish predation (Chapter 2).


● C. americanus
■ C. flavicans
▼ C. trivittatus
◆ C. punctipennis
○ No Chaoborus
Lake Elevation (m)
2500
2000
1500
1000
500
Maximum Depth (m)
1
10
100

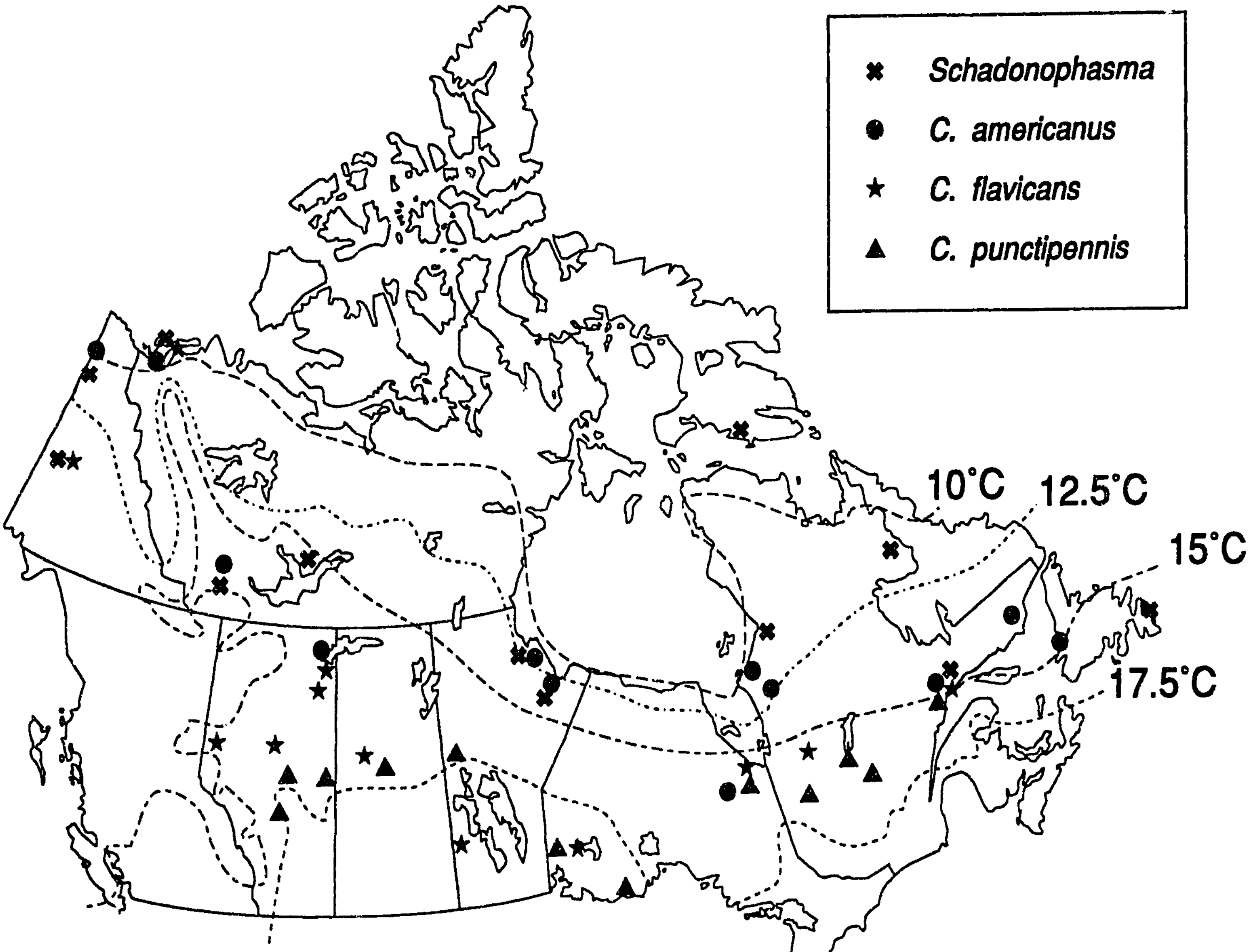
C. (*Schadonophasma*) *trivittatus* is a common lake-dwelling species but was seldom collected in our study area. However, based on the few records obtained from shallow high-elevation ponds, *C*. *trivittatus* may be more tolerant to cold climatic conditions than the other three species (Fig. 1.5). It is possible that some of the larvae identified as *C*. *trivittatus* were *C*. *cooki*, another species of the sub-genus *Schadonophasma*. *C*. *cooki* typically occurs in temporary bodies of water but is occasionally found in permanent habitats (Borkent 1979). Because of the difficulty of separating the larvae of the two species (Borkent 1979), it is possible that *C*. *cooki* was present in some of the small lakes.

Chaoborus may be absent from cold lakes because they do not 'accumulate' enough degree-days above a certain temperature threshold, even under their physiological maximal life-span (Danks 1971, Danks and Oliver 1972, Begon *et al*. 1986 pp. 44-46, Büns and Ratte 1991). The sensitivity of different stages of the *Chaoborus* life-cycle to temperature is not known. It is possible that cold temperature completely inhibits one particular life-stage of *Chaoborus*, for example egg hatching, or that cumulative effects over the entire life-cycle prevent successful maturation or reproduction. Of all life-stages, it is possible that pupae require the highest temperature threshold for emergence (Danks 1971, Danks and Oliver 1972, Walker 1991), but this needs to be confirmed. As for arctic chironomids, it is probable that chaoborids cope with marginal temperature regimes by lengthening their life-cycle (Downes 1964). This and other aspects of chaoborid life-history relative to the thermal regime of their habitat require further investigation.

I presently do not have enough limnological data from arctic and sub-arctic lakes to test whether the thresholds in MSSWT defined in the Rockies also apply to chaoborids in northern lakes. However, the relative distribution of *Chaoborus* species along the elevation-temperature gradient of Rocky Mountain lakes is similar to their latitudinal distribution. In Canada, *C. americanus* and *C. flavicans*, range as far north as the James Bay region and the MacKenzie delta (Fig. 1.6). In contrast, *C. punctipennis* is limited to the southernmost regions of Canada. In the Matamek River system, at the northern limit of its distribution, *C. punctipennis* was collected in the low-elevation lakes of the Saint-Lawrence Valley but was absent from nearby shield lakes at higher elevations (Pope *et al* 1973). There are records of *C. trivittatus* being found as far north as the MacKenzie Delta, Baffin Island and Labrador (Borkent 1979, Walker *et al*. 1991). The known range of *C. cooki* extends well into northern Quebec and Labrador (Borkent 1979).

There are also differences between latitudinal and elevation distributions. For example, the northern limit in the distribution of *C. americanus* and *C. trivittatus* has been associated with treeline (Borkent 1979, 1981). Treeline, however, was not a good marker of *Chaoborus* distribution in the Rockies. *C. americanus* was not found in lakes above 1 600 m while treeline is at approximately 2 200 m. Some of the factors influencing treeline may be different between the alpine and arctic

Fig. 1.6. The latitudinal distribution of four Chaoborus species in Canada relative to mean July air temperature (Fisheries and Environment Canada 1978). The twelve northernmost records of each species from Borkent (1979, 1981) are plotted. Schadonophasma species (C. trivittatus and C. cooki) were pooled together because of the difficulty in separating the two species. Treeline is approximately located between the 10 and 12.5°C isotherms.


✖ Schadonophasma
● C. americanus
★ C. flavicans
▲ C. punctipennis
10°C
12.5°C
15°C
17.5°C

environments (Walker and Mathewes 1989a). For example, the Canadian northern limit of trees is related to the mean summer position of the arctic front (Bryson 1966). In contrast, in the Rockies the position of treeline is related to the July 10°C isotherm (Wardel 1974, Tranquillini 1979), and is also influenced by winter conditions such as snowpack depth and wind exposure (Gadd 1986). Solar insolation is also higher in the arctic during summer, and this could be a significant factor in small bodies of water (see below). On the other hand, high UV light levels may limit the distribution of organisms at high elevations (Thomasson 1956). Despite these differences, elevation gradients appear to be a useful mean of obtaining information about the distribution of organisms relative to temperature.

Under marginal climates, chaoborids may survive in small water bodies because these are warmer during summer than deeper lakes of similar surface area. In general, the temperature of water bodies is dependent on average air temperature and solar insolation (Thomasson 1956). Because solar insolation is a more important part of the heat budget of small lakes in summer, these will tend to be warmer than nearby larger ones (Thomasson 1956, Danks 1971, Rigler 1978). The difference in temperature is significant enough that many species of chironomids are restricted to ponds in the arctic (Danks 1971, Danks and Oliver 1972).

Other factors

Fish predation affects the structure of Chaoborus communities greatly in temperate lakes (Pope et al. 1973, Northcote et al. 1978, von Ende 1979, Chapter 2). Chaoborus populations may be less able to sustain predation under cold thermal regimes due to slower developmental rates (Luecke 1988) and lower food availability. Chaoborus were less likely to be found in lakes with high densities of planktivorous fish in our study area (Chapter 2). However, because approximately one half of the lakes above 1 600 m were fishless in this study, increased susceptibility to fish predation alone cannot account for the absence of Chaoborus in cold lakes.

Anderson and Raasvelt (1974) proposed that predation by Gammarus lacustris may limit Chaoborus distribution in alpine lakes. Gammarus are occasionally pelagic in fishless lakes and may compete with Chaoborus for food or even prey on them. Under laboratory conditions, G. lacustris preyed on Chaoborus americanus larvae (Anderson and Raasvelt 1974). The abundance of Gammarus and Chaoborus was also negatively correlated in 50 lakes in Alberta and British Columbia (Anderson and Raasvelt 1974). However, Gammarus and Chaoborus coexist in many montane and sub-alpine lakes (Anderson and Raasvelt 1974) and Gammarus is not present in all alpine lakes of the Rockies (Anderson 1974, Anderson and Raasvelt 1974). Determining the importance of Gammarus competition or predation on Chaoborus in the absence of predatory fishes requires field experiments.

Implications for Paleoecology

Chaoborids have been used as markers of past climatic conditions in Quaternary paleoecology (Kerfoot 1981, Frey 1988, Walker and Mathewes 1989b). Their presence is usually interpreted as an evidence of relatively warm climatic conditions and higher lake productivity (Frey 1986, Walker 1987, Walker and Mathewes 1989a). Based on the results of this study and other biogeographical information (Borkent 1979, 1981), identification to species would increase the precision of deducing past lake temperatures. The most common Chaoborus subfossils are their mandibles; these can be identified to species or to pairs of taxonomically related species (Uutala 1990). Further resolution could probably be gained by relating the presence or absence of Chaoborus to degree-day models.

Chaoborus subfossils are also used as indicators of the presence or absence of planktivorous fishes in lakes through time (Uutala 1990, Chapter 2). This technique will need to be restricted to lakes with MSSWT's of at least 16°C in the Canadian Rockies to avoid confounding temperature and predation effects. Fortunately, the two key species for this type of study in the Rockies (the fish-sensitive C. americanus and the fish-tolerant C. flavicans) have similar distributions relative to temperature. Therefore, changes from one species to the other observed in the sedimentary record will be due to changes in fish predation rather than lake temperature. It is possible, however, that even fish-tolerant species will be eliminated by fish predation in cold lakes, due to low productivity of the populations and longer larval and pupal developmental rates (Luecke 1988, Chapter 2). In this case, Chaoborus americanus (and possibly C. trivittatus) will be found during periods when the lake was fishless, but no Chaoborus may be found when fishes were present.

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Chapter 2

Historical status of fish populations in Canadian Rocky Mountain lakes inferred from subfossil Chaoborus mandibles.

Introduction

The native fish and invertebrate communities of the lakes and rivers of the Rocky Mountain national parks have been modified substantially by past fisheries management practices (Donald 1987, Harvey et al. 1989, Mayhood 1992a, Schindler et al. in prep.). When the mountain parks were created at the beginning of the century, their role was primarily for recreation, tourism and the exploitation of natural resources (Rawson 1940, Scace 1968). Because angling attracted numbers of tourist and generated large revenues, considerable effort was spent to supplement declining native fisheries with hatchery stocks (Rawson 1940, McIllree and White-Fraser 1983, Donald 1987). When exotic fishes were believed to provide better sport, they were often introduced into park waters over native species (Rawson 1941). In addition, 'undesirable' fish populations were frequently eliminated using fish toxicants or other methods (Anderson 1970, Rawson and Elsey 1948, Mayhood 1992a). Many lakes that were originally fishless were stocked with a variety of salmonids (Rawson 1940, 1941, Donald 1987) without regard for invertebrate populations sensitive to fish predation (Anderson 1972, 1980). Some of the parks' native fishes are currently threatened outside of park boundaries (Roberts 1982, 1991) and the current status of many fishes in the parks is uncertain (Mayhood 1992a). In addition, due to the proximity of a possible ice-free refugium (Crossman and McAllister 1986, Mayhood 1992a), Jasper and Banff national parks may have had several unusual fish populations that are currently either extinct or severely threatened (Bajkov 1927, Mayhood 1992a).

The mandate of National Parks has changed in recent years. Although providing recreational opportunities is still viewed as important, the main goal of national parks is to protect representative ecosystems in a state as pristine as possible (Canadian Parks Service 1991, Mayhood 1992b). Exotic species cannot be introduced anymore and measures must be taken to protect and restore native fish and invertebrate populations (Parks Canada 1983). Unfortunately, due to the lack of historical records, the original community composition of park's water is not known. For example, it is not known whether many fish populations in the parks are native, introduced, or a mixture of both native and stocked fishes (Mayhood 1992a). Baseline information on the original distribution of fishes in the parks is needed to implement measures to protect or restore native populations.

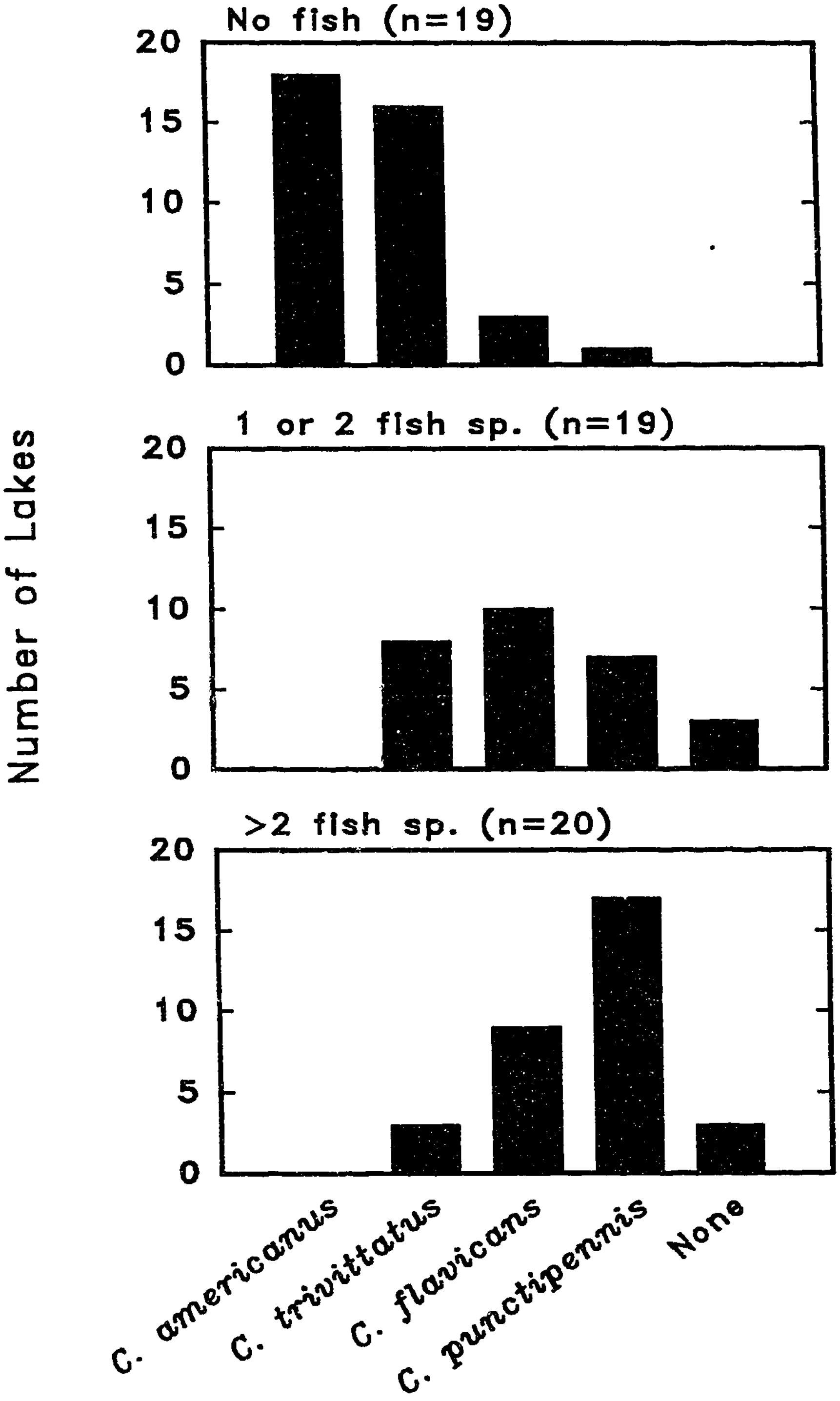
Cabin, Caledonia and Celestine lakes, Jasper National Park, were stocked with salmonids in the 1920's and 30's. There is some evidence that these lakes may have had native fish populations prior to stocking (Mayhood 1992a). Caledonia and Celestine lakes may have contained Athabasca rainbow trout (Oncorhynchus mykiss v. athabascae), a proposed subspecies endemic to the headwaters of the Athabasca River (Bajkov 1927, Mayhood 1992a, Nelson and Paetz 1992) and lake chub (Couesius plumbeus), while Cabin Lake may have contained lake chub (Ward 1974, Mayhood 1992a). Because some of the fish species that were stocked or introduced are native to the drainage, whether fish were originally present is unclear. We used subfossil Chaoborus mandibles preserved in lake sediments to determine whether Cabin, Caledonia and Celestine lakes had fish prior to 1900.

Chaoborus as Indicators of Fish Presence or Absence

Chaoborus species are sensitive to the presence of insectivorous fishes (Pope *et al*. 1973, von Ende 1979). The larvae of *Chaoborus*, the phantom midge, are widespread inhabitants of the pelagic and profundal zones of temperate lakes (Borkent 1981). In lakes without planktivorous fishes, large species such as *C. americanus* and *C. trivittatus* dominate (Fig. 2.1; Pope *et al*. 1973, Northcote *et al*. 1978, Borkent 1981, Bendell and McNicol 1987). *C. americanus* and *C. trivittatus* exclude smaller *Chaoborus* species by preying on their early instars (von Ende 1979). *C. americanus*, however, is vulnerable to predation by fish and can be rapidly extirpated when fish are present because the older instars are planktonic throughout the day (Fedorenko and Swift 1972, Northcote *et al*. 1978, von Ende 1979, Evans 1989). Similarly, *C. trivittatus* larvae undergo weak vertical migrations and only withstand slight planktivory (Pope *et al*. 1973, Uutala 1990). These two species are referred to as "fish-sensitive" in the following analysis.

Other *Chaoborus* spp. can coexist with vertebrate planktivores, relying on their small size, high transparency and on vertical migration to limit predation. The most common species associated with fishes are *C. flavicans* and *C. punctipennis* (Fig. 2.1; Pope *et al*. 1973, von Ende 1979). These species undergo strong diurnal vertical migrations, spending daylight hours in deep water or in lake sediments, where

Fig. 2.1. The distribution of Chaoborus spp. in 58 North American lakes relative to the presence or absence of fish. Lakes with fish were separated into low (one or two fish species) and high (more than two species) fish diversity groups, assuming that higher fish diversity resulted in higher planktivory. In most lakes more than one Chaoborus species was found. Data are gathered from Hamilton (1971), Pope et al. (1973), Northcote and Clarotto (1975), Beamish et al. (1976), Northcote et al. (1978), von Ende (1979), Elser et al. (1987) and Johnson and McNeil (1988).


No fish (n=19)
1 or 2 fish sp. (n=19)
>2 fish sp. (n=20)
Number of Lakes
20
15
10
5
0
C. americanus
C. trivittatus
C. flavicans
C. punctipennis
None

visibility is poor (Teraguchi and Northcote 1966, LaRow 1968, Carter and Kwik 1977). Where they coexist with fish, *Chaoborus* population density is dependent on the intensity of fish predation (Kitchell and Carpenter 1988) and on the density of prey, normally small rotifers and crustaceans (Neill 1988). The range of *C. punctipennis* does not include the mountain parks (Chapter 1, Borkent 1981). Therefore, *C. flavicans* will be the species referred to as 'fish-tolerant' in the following analysis.

Subfossil *Chaoborus* mandibles are preserved in lake sediments and are diagnostic of species or pairs of taxonomically related species (Uutala 1990). *Chaoborus* mandibles have been used to infer the loss of fish populations in recently acidified lakes in eastern North America (Johnson and McNeil 1988, Johnson *et al.* 1990, Uutala 1990, Kingston *et al.* 1992).

In this study, I first reviewed the contemporary distribution of *Chaoborus* species relative to fish density in lakes of the Canadian Rocky Mountains. I then used the relationship between *Chaoborus* and fish density to interpret changes observed in paleolimnological records obtained by enumerating and identifying *Chaoborus* mandibles retrieved from sediment cores from Cabin, Caledonia and Celestine lakes.

Methods

Study sites

Cabin, Caledonia and Celestine lakes are located in the vicinity of the town of Jasper, Jasper National Park, Canada (Fig. 2.2). Limnological and fisheries information for the lakes is available from Anderson (1970, 1974), Donald et al. (1980), Donald and Anderson (1982), Donald and Alger (1987) and unpublished reports. The lakes are at montane elevations (1161 - 1260 m above sea level), are small, relatively deep and sheltered by surrounding forests and topography (Table 2.1). The drainage basins are fully forested with lodgepole pine (Pinus contorta), white spruce (Picea glauca), and trembling aspen (Populus tremuloides). Hiking trails and wilderness camping sites are the only signs of activity in the catchment, except that the water level of Cabin Lake was raised by several feet in the 1940's by the building of a dike and weir at the lake outlet to provide water for the town of Jasper (Clarkson 1990).

A total of four fish species presently occupy the lakes. Rainbow trout were stocked in all three lakes by 1933 and brook trout (Salvelinus fontinalis) in Caledonia Lake in 1964 (Fig. 2.3). Lake chub occurs in the three lakes and burbot (Lota lota) is present in Celestine Lake. It is most likely that lake chub were introduced by anglers using them as bait (Donald 1987, Mayhood 1992a), but based on the available information it cannot be ruled out that they were native. Burbot appeared in gill net catches for the first time in 1980 (D.B. Donald, Environment Canada, Inland Waters Directorate, 1901 Victoria Avenue, Regina, Saskatchewan, S4P 3R4, pers. comm.) and

Fig. 2.2. Location of Jasper National Park, Canada, and the three study lakes.

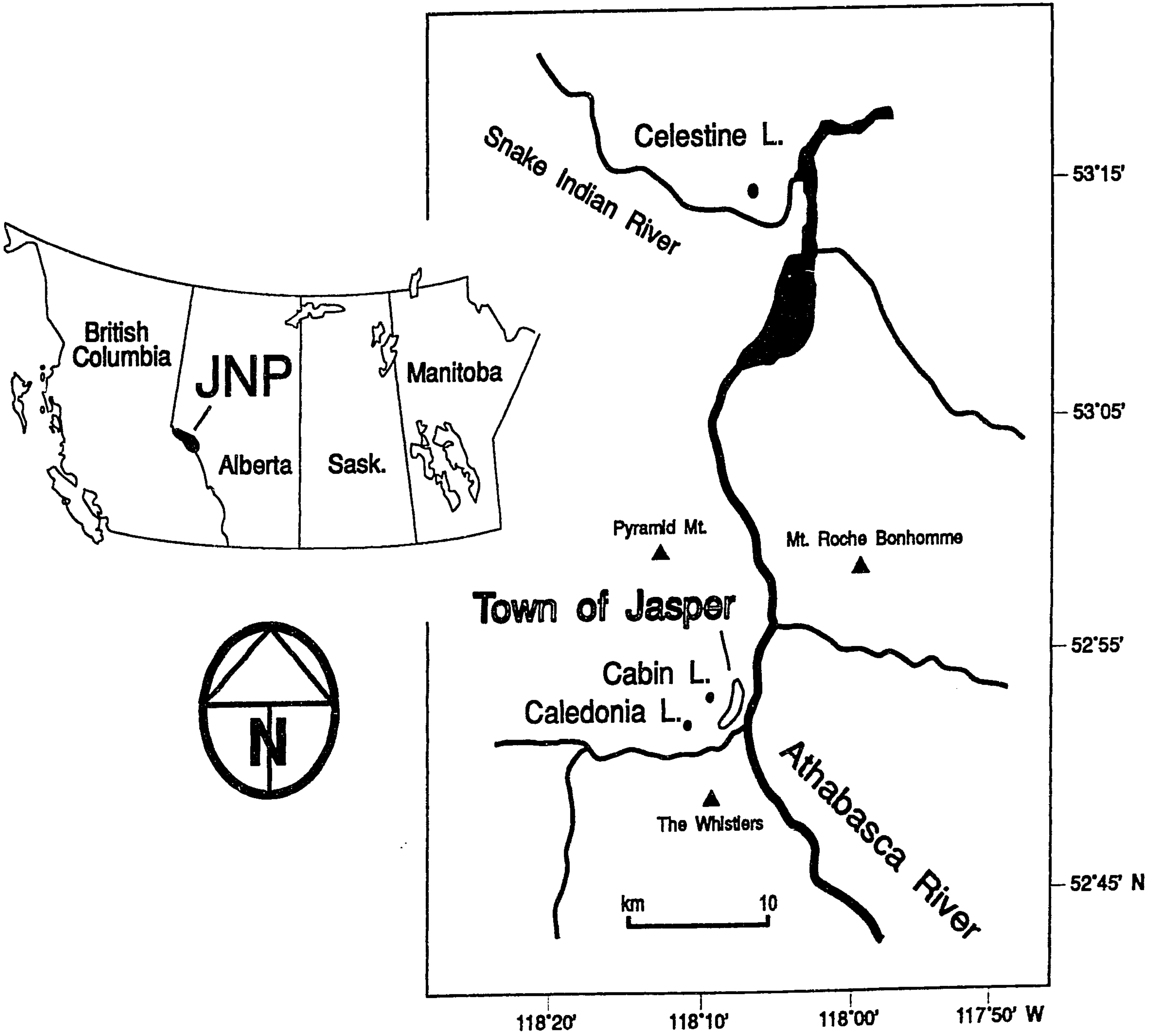
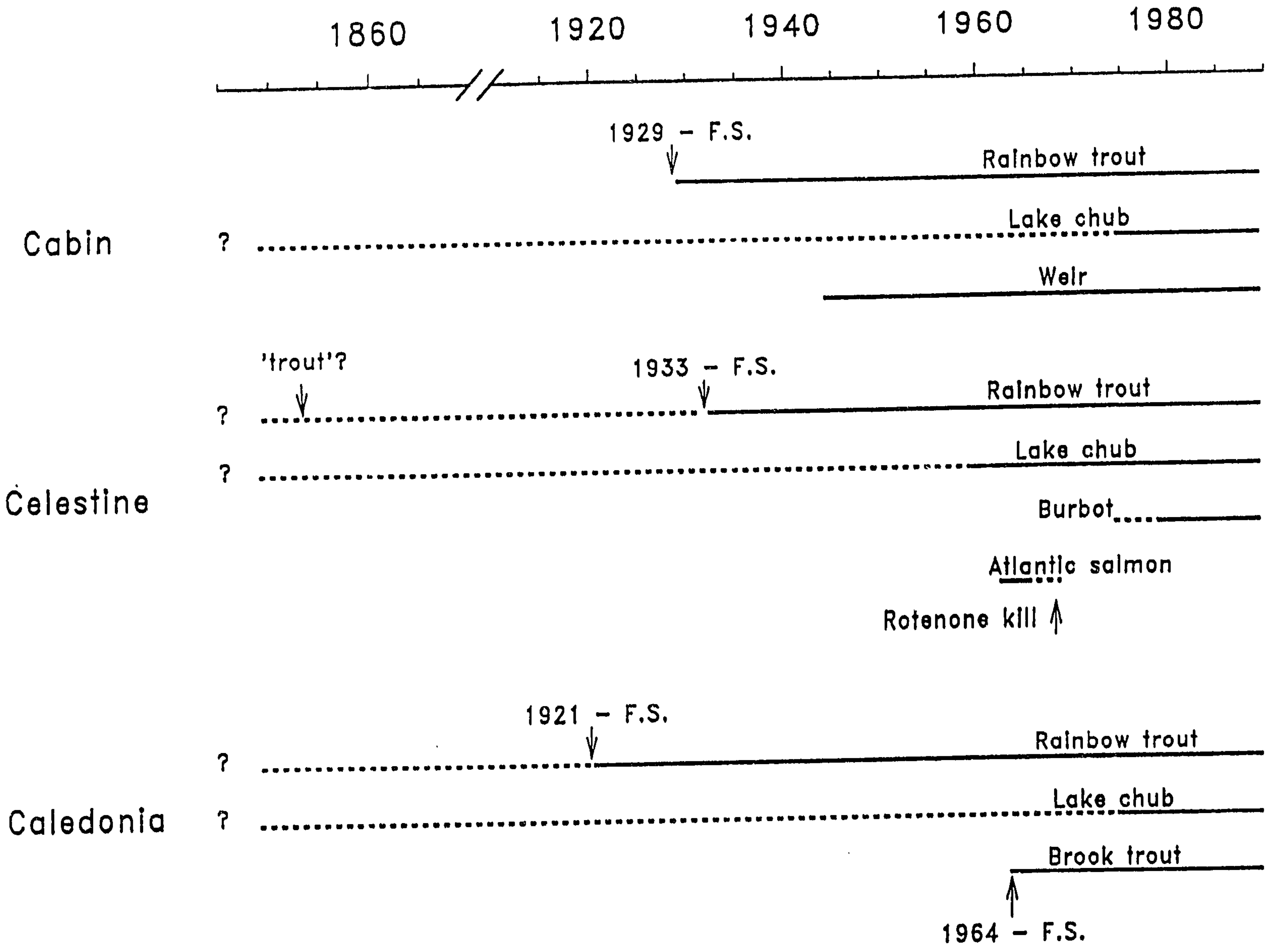

British Columbia
JNP
Alberta
Sask.
Manitoba
N
Snake Indian River
Celestine L.
Pyramid Mt.
Mt. Roche Bonhomme
Town of Jasper
Cabin L.
Caledonia L.
The Whistlers
Athabasca River
km
10
53°15'
53°05'
52°55'
52°45' N
118°20'
118°10'
118°00'
117°50' W

Table 2.1. Some limnological characteristics of Cabin, Caledonia and Celestine lakes, Jasper National Park.

	Cabin	Caledonia	Celestine
Surface area (ha)	32.2	13.0	39.0
Z_m (m)	20.5	11	14
Mid-Summer Surface Water Temperature (°C)	18	17.5	16
Present *Chaoborus* sp.	Rare or absent	*C. flavicans*	*C. flavicans*
Coring Date	16 April 1991	16 April 1991	8 August 1991

Fig. 2.3. Summary of the history of the fish populations in Cabin, Celestine and Caledonia lakes, Jasper National Park. Dashed lines indicate presence uncertain. Dates followed by F.S. indicate the first recorded stocking of species. A dike and a weir were built at the outflow of Cabin Lake in the 1940's and raised the water level by approximately 1 m. Celestine Lake was poisoned with rotenone in 1967 to eliminate a large population of lake chub, but pre-rotenone invertebrate and fish communities recovered within a few years (Anderson 1970). In Caledonia Lake, rainbow trout were stocked three times at an average of 1330 fry$\cdot$ha^{-1} and brook trout 4 times (480 fry$\cdot$ha^{-1}). One stocking of 45 387 rainbow trout fry (possibly a rainbow X cutthroat hybrid) is recorded for Cabin Lake, although unrecorded stockings might have occurred earlier (Mayhood 1992a). Celestine Lake was stocked with rainbow trout regularly from 1940 to 1980. Atlantic salmon (Salmo salar) were also stocked in Celestine Lake in 1962 and 1963.


1860
1920
1940
1960
1980
Cabin
?
1929 - F.S.
Rainbow trout
Lake chub
Weir
Celestine
?
'trout'?
1933 - F.S.
Rainbow trout
Lake chub
Burbot
Atlantic salmon
Rotenone kill
Caledonia
?
1921 - F.S.
Rainbow trout
Lake chub
Brook trout
1964 - F.S.

have also probably been introduced by anglers. There is at least some natural recruitment in the three lakes, but the exact amount is not known.

Historical Evidences for the Presence of Fishes

There is a record of 'trout' being present in 1854-55 for a lake in the vicinity and of the size of Celestine Lake (Mayhood 1992a from Moberly and Cameron 1929). However, whether the lake was Celestine is uncertain. The fishes of Caledonia Lake were sampled in 1925-26, five years after the initial stocking of rainbow trout (Bajkov 1927, Neave and Bajkov 1929). Bajkov (1927) described two "morphs" of rainbow trout from the lake based on morphometric and meristic characteristics. One of the morphs may have been native to the lake (Mayhood 1992a). There are accounts by early Jasper residents that trout were present in Caledonia Lake early this century (Ward 1974).

Chaoborus distribution

To assess the relationship between Chaoborus and fish distribution in montane lakes, we reviewed the distribution of Chaoborus spp. in 43 lakes of Jasper and Banff national parks, representing a gradient in salmonid density (mainly rainbow and brook trout). Data on Chaoborus distribution and limnological variables were obtained from Anderson (1970, 1974, 1980) and Anderson and Raasvelt (1974). In each lake, Chaoborus were sampled with zooplankton nets hauled from 1 m above the bottom to the surface (Anderson 1974, Anderson and Raasvelt 1974), and with benthic grabs

(Donald and Anderson 1982). We only used the presence or absence of Chaoborus spp. to avoid calibration problems between methods. Most zooplankton collections from Anderson (1974, 1980) are archived in the Zoology Museum of the University of Alberta. Chaoborus species identifications were confirmed from examination of archived material and from direct enumeration of recent zooplankton samples (Lamontagne unpubl. data). Catch-Per-Unit-Effort (CPUE) from mixed mesh size gill nets was measured to estimate salmonid density (Donald et al. 1980, Donald and Anderson 1982, Donald and Alger 1986, Donald 1987).

Chaoborus have a restricted distribution along the elevation gradient of mountain lakes (Chapter 1). C. americanus and C. flavicans do not occur in lakes with a mid-summer surface water temperature (MSSWT) colder than 16°C, generally corresponding to elevations higher than 1 600 m. We restricted the survey between fish and Chaoborus to lakes with a MSSWT of at least 16°C, hereafter referred to as montane lakes.

Coring Procedures

We collected sediment cores from the deepest part of each lake using a self-closing gravity corer fitted with 5 cm diameter core tubes. The cores were extruded on site in 1 cm intervals between 0 and 14 cm, and in 2 cm intervals below 14 cm. The outer 0.5 cm of each slice was discarded to reduce contamination from sediment smearing along the inner side of the core tube (Johnson et al. 1990, Chant and Cornett

1991). We collected 4 to 6 mL subsamples for ^{210}Pb analysis from the Cabin and Celestine cores (analysis by Flett Research Ltd, 440 DeSalaberry Ave, Winnipeg, Manitoba, Canada R2L OY7). Lead-210 derived sediment accumulation rates were determined using the constant rate of supply model (Oldfield and Appleby 1984, Binford 1990). In the lab, 4-5 mL subsamples were collected from each interval for analysis of subfossil *Chaoborus* mandibles. For each lake, we analyzed all intervals from one core and bulk samples from the lower portion of a duplicate. The subsamples were dispersed overnight in 10% KOH and filtered onto a 80 µm mesh. The material left on the screen was washed with 80% ethanol and the mandibles removed under a dissecting microscope. The mandibles were mounted on microscope slides with Euparal. *Chaoborus* mandibles were identified to species using Uutala (1990) and Saether (1972).

Results

Species Distribution

Chaoborus species were closely related to fish density in the montane lakes of Jasper and Banff National parks (Fig. 2.4). *C. americanus* was the only species collected in fishless lakes while *C. flavicans* was the most common species in lakes with intermediate CPUE. *C. americanus* was found in three lakes with fish, twice co-occurring with *C. flavicans* (Fig. 2.4). These lakes had stocked populations of rainbow or brook trout and fish density was low at the time of sampling, possibly because fish have not reproduced successfully. *Chaoborus* were rare in lakes with high CPUE (Fig. 2.4). C. trivittatus have been found within the mountain parks (Borkent 1979, Chapter 1) but were not present in the lakes studied.

There was a tendency for fishless lakes to be smaller and shallower than lakes with fish (Table 2.2). There are unfortunately few relatively large lakes that have been left fishless in Banff and Jasper national parks. This bias should not have affected the distribution of Chaoborus species. Elsewhere in North America, C. americanus occurs in large fishless lakes (Table 2.2; Pope et al. 1973, Northcote et al. 1978). In large lakes, C. americanus frequently co-occurs with C. trivittatus (Pope et al. 1973, Northcote et. al. 1978).

Core Profiles

Cabin and Celestine lakes originally had fish-sensitive chaoborids but there was a switch to fish-tolerant chaoborids in recent sediments (Fig. 2.5). In Cabin Lake, C. americanus and C. trivittatus mandibles were only present in samples below 4 cm depth. C. flavicans mandibles were also found at the 4 cm interval, but not at other levels. No mandibles were retrieved from the upper 3 cm of the core. This was not unexpected because Chaoborus are presently rare or absent in Cabin Lake (Lamontagne unpubl. data). In Celestine Lake, C. americanus in older sediments were progressively replaced by C. flavicans above 10 cm depth. In contrast, fish-tolerant C. flavicans were present in Caledonia Lake throughout recent history (Fig. 2.5). The

Fig. 2.4. The distribution of Chaoborus species in 43 lakes in Jasper and Banff National Parks, Canada, relative to fish density assessed by Catch Per Unit Effort (CPUE). Numbers in parentheses represent the number of lakes included in each CPUE class. Only lakes with a mid-summer surface water temperature 16°C or higher were included in this analysis.

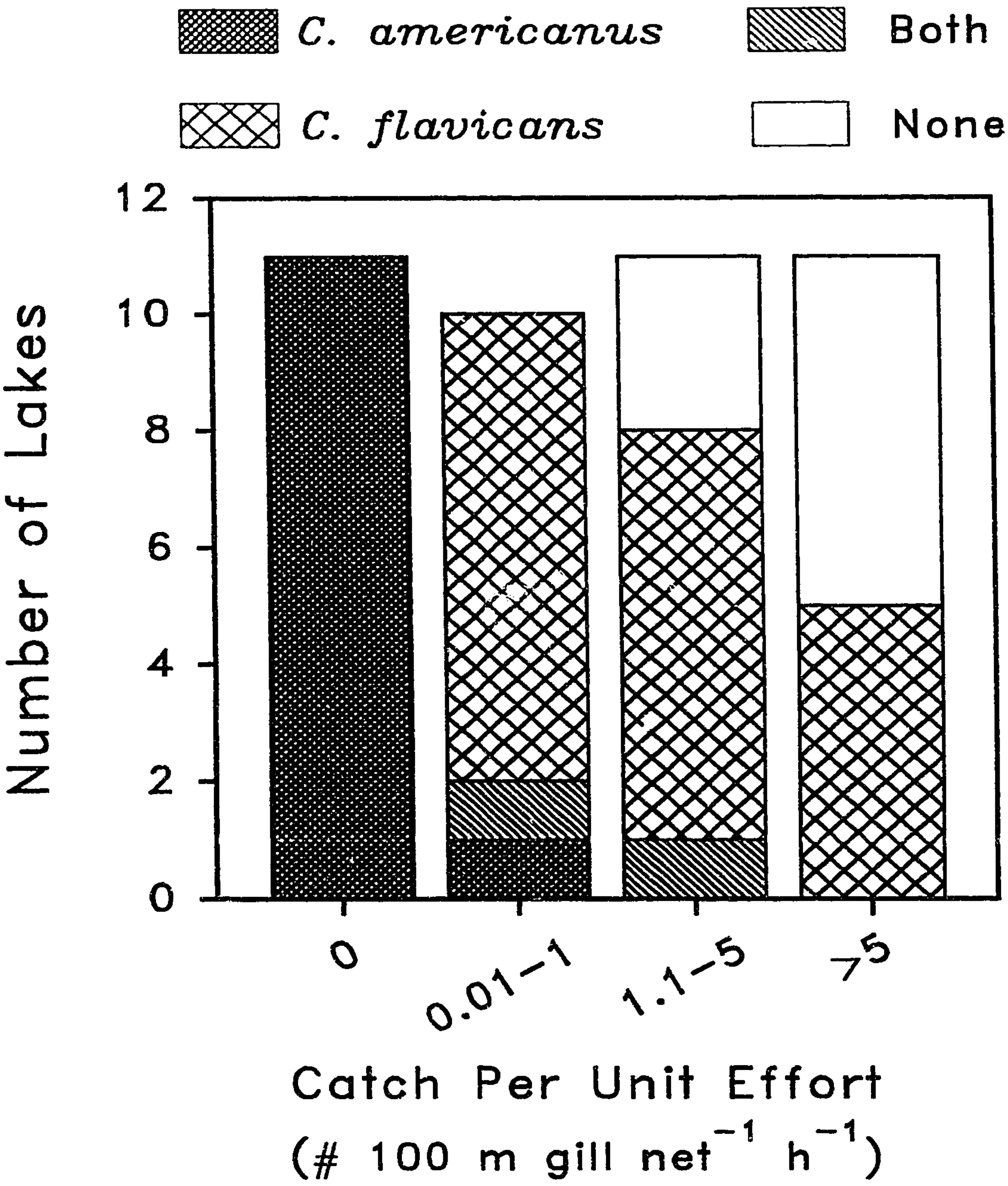
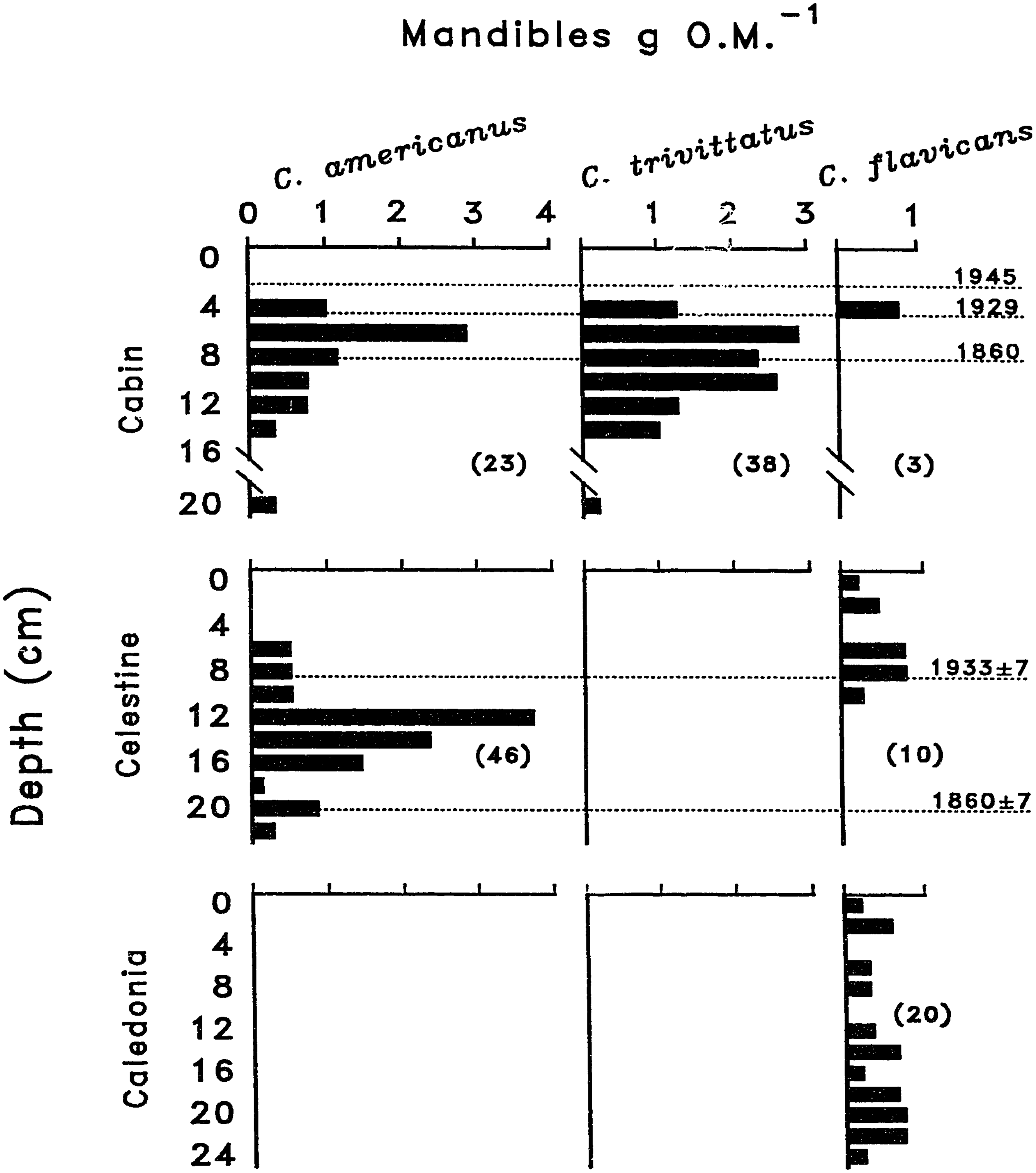

C. americanus
Both
C. flavicans
None
Number of Lakes
0
2
4
6
8
10
12
0
0.01–1
1.1–5
>5
Catch Per Unit Effort
(# 100 m gill net^{-1} h^{-1})

Table 2.2. Comparison of the mean and range in lake area and maximum depth of lakes with and without *Chaoborus americanus* in Jasper and Banff national parks and elsewhere in North America (reference in Fig. 2.1).

	Montane Lakes		North American Lakes	
	with *C. americanus*	without *C. americanus*	with *C. americanus*	without *C. americanus*
Area (ha)	2.7 (0.4 - 15)	34 (0.5 - 516)	28 (4.5 - 67)	48 (1.7 - 429)
Max. Depth (m)	3.6 (1.0 - 6.4)	11 (2 - 40)	51 (1.7 - 429)	27 (4.5 - 67)
n	11	33	39	18

Fig. 2.5. Chaoborus subfossil density per gram organic matter from the Cabin, Celestine and Caledonia cores. Numbers in parentheses represent the total number of mandibles retrieved per species. In Cabin Lake, 1945 represents the location of the debris band presumably left by the building of the weir and dike and 1929 the date of first recorded stocking. Dates in Cabin Lake are approximate. In Celestine Lake, 1933 is the date of first recorded stocking (± two standard deviation).


Mandibles g O.M.$^{-1}$
C. americanus
C. trivittatus
C. flavicans
0
1
2
3
4
1
2
3
1
Depth (cm)
Cabin
0
4
8
12
16
20
(23)
(38)
(3)
1945
1929
1860
Celestine
0
4
8
12
16
20
(46)
(10)
1933±7
1860±7
Caledonia
0
4
8
12
16
20
24
(20)

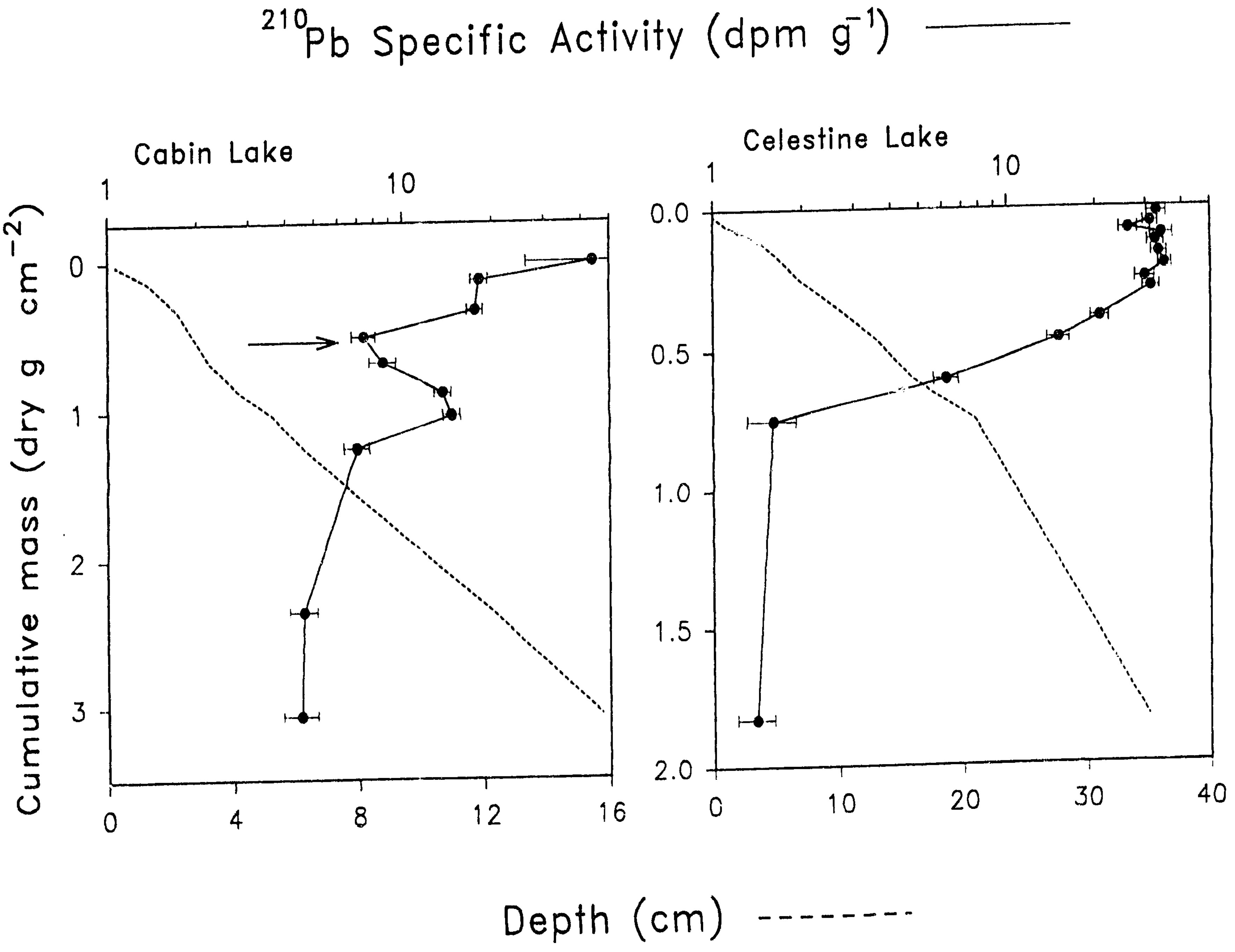
bottom portions of duplicate cores from each lake showed similar patterns in subfossil Chaoborus (Table 2.3).

A combination of ^{210}Pb profiles and known sediment markers were used to date the cores. In cores from Cabin Lake a debris band, mostly coarse sand, was visible between 2.5 and 3 cm. Presumably, this band indicates the building of the dike at the lake outlet in the 1940's. This band is also coincidental with a sharp decrease in the ^{210}Pb activity of the sediments (Fig. 2.6). Most likely, the erosion of the lake margin caused by the rise in water level produced an influx of ^{210}Pb-poor material to the sediments (Oldfield and Appleby 1984). Due to the disruption of the ^{210}Pb record, we were unable to date the Cabin Lake core precisely. Based on the sediment accumulation rate obtained from the position of the debris band and from the depth at which unsupported ^{210}Pb became undetectable, the loss of the Chaoborus fauna occurred early this century. In Celestine Lake, the ^{210}Pb profile showed a more typical log-linear decrease in activity, with some evidence of mixing (Fig. 2.6). Based on the ^{210}Pb sediment accumulation rate, the Chaoborus species change occurred during the period of the first recorded fish stocking. No dating was available for the Caledonia Lake core. Based on the sedimentation rates obtained from Cabin and Celestine lakes ($\approx$1 mm$\cdot$yr^{-1}), the Caledonia core represents about 150 years of record.

Table 2.3. Number of *Chaoborus* mandibles retrieved from the deep portion of a duplicate sediment core from Cabin, Caledonia and Celestine lakes.

Lake	Depth (cm)	Volume of sediments (mL)	*C. americanus*	*C. trivittatus*	*C. flavicans*
Cabin	14-16	12	3	5	0
Celestine	20-24	8	12	0	0
Caledonia	20-24	16	0	0	6

Fig. 2.6. ^{210}Pb specific activity profiles in Cabin and Celestine lakes relative to the cumulative dry mass of sediments in the cores. The arrow represents the position of the debris band in the Cabin Lake core (ca. 1945). Error bars represent one standard deviation.


^{210}Pb Specific Activity (dpm g^{-1})
Cabin Lake
Celestine Lake
1
10
Cumulative mass (dry g cm^{-2})
0
1
2
3
0.0
0.5
1.0
1.5
2.0
0
4
8
12
16
10
20
30
40
Depth (cm)

Discussion

The combination of contemporary *Chaoborus*/fisheries surveys with subfossil mandible analysis provides new information about the historical status of fish populations in lakes of Jasper National Park. In both lakes, *C. americanus* used to be a dominant species but was eliminated early this century, most likely by the stocking of fish. As a result I conclude that Cabin and Celestine lakes were fishless prior to this century. The presence of *C. flavicans* throughout the Caledonia Lake core indicates that planktivorous fish were present in the lake prior to this century. The survey of lakes from the mountain parks did not include any lake solely inhabited by cyprinids. However, planktivorous minnows like lake chub (Neave and Bajkov 1929, Scott and Crossman 1973) have been shown to be strong predators of *Chaoborus* (von Ende 1979, Kitchell and Carpenter 1988). Therefore, it is unlikely that either trout or lake chub were historically present in Cabin and Celestine lakes.

Subfossil *Chaoborus* mandibles give no information about the species composition of past fish populations besides the presence of planktivores. Based on the earliest records of the fishes of Caledonia Lake, I speculate that the most likely fish species present would have been native Athabasca rainbow trout (*O. mykiss* v. *athabascae*). Bajkov (1927) sampled the fishes of Caledonia Lake in 1926, five years after the only prior stocking. Bajkov described two morphs of rainbow trout from Caledonia Lake and elsewhere in Jasper National Park based on detailed morphometric and meristic characteristics (Plate 2). It is possible that one

Plate 2. Photograph of the two rainbow trout morphs found in Jasper National Park by Bajkov (1927, Plate Ia). Top: "*Salmo* *irideus* morpha *argentatus*" (3 years old female). Bottom: "*Salmo* *irideus* Gib. typical morph" (3 years old female). The "typical" morph from Jasper National Park could have been what is now known as the Athabasca rainbow trout, a proposed subspecies endemic to the headwaters of the Athabasca River. Among differences observed between morphs, the "typical" one grew slower, had X or C-shaped spots instead of round ones, kept its parr marks even as adults, had rectangular scales instead of round ones, and was more darkly colored (Bajkov 1927).

morph was representative of the stocked rainbow trout and the other of a native rainbow trout population (Mayhood 1992a). Native rainbow trout populations can still be found in areas adjacent to Jasper National Park (Nelson and Paetz 1992), but whether they presently occur in Caledonia Lake or elsewhere in the park is undetermined (Mayhood 1992a).

Chaoborus Distribution and Lake Temperature

Although lakes colder than 16°C were not included in our survey, due to marginal temperatures and perhaps low lake productivity, even fish-tolerant *Chaoborus* may be frequently eliminated by fish predation in montane lakes (Fig. 2.4). The developmental rate of *Chaoborus* larvae is dependent on water temperature (Swift 1976, Giguère 1980, Büns and Ratte 1991). Slower developmental rates can result in increased predation by fish on vulnerable life-stages such as pupae (Luecke 1988). *C. americanus* and *C. flavicans* are in the same subgenus (*Chaoborus*) and have been shown to have a similar distribution relative to lake temperature in Jasper and Banff national parks (Chapter 1). Therefore, it is unlikely that the changes in species observed in the cores were due to variation in lake temperature.

Implications and Future Studies

For management purposes, the fish populations of Cabin and Celestine lakes should be considered non-native to Jasper National Park and require no special status other than regulations already in place. The possibility that a native stock of rainbow trout still occurs within the Caledonia Lake drainage basin should be investigated. Detailed morphometric and molecular genetic studies of the rainbow trout of Caledonia Lake and its tributaries may provide indications whether native rainbow trout are still present. Enzyme electrophoresis studies in progress have shown that the Athabasca rainbow trout has some unique allelic frequencies among black-spotted trouts that could be used as genetic markers (L. Carl, Ontario Ministry of Natural Resources, Research Section, Fisheries Policy Branch, P.O. Box 5000, Maple, Ontario L6A 1S9, Canada, pers. comm.). Similar work is under way using restriction enzymes on mitochondrial DNA to distinguished between stocked and native rainbow trout populations in areas adjacent to Jasper National Park (R. Vitic, Department of Zoology, University of Alberta, Edmonton AB, T6G 2E9, pers. comm.)

Paleolimnological analysis could be used to determine whether or not fish were originally present in other lakes of the mountain parks where there are no early fish records. Other paleolimnological markers of changes in food-web structure could be used to supplement the information gathered from Chaoborus mandibles, especially for high elevations lakes where Chaoborus do not occur. In whole-lake experiments, cladoceran remains and fossil pigments have accurately recorded changes in the food-web brought by the manipulation of planktivore and piscivore populations (Kitchell and Kitchell 1980, Leavitt et al. 1989). Because the analysis of complete cores is time-consuming, partial analysis ('top-bottom') could be an alternative in surveys of large number of lakes (Cumming et al. 1992).

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General Discussion

I will use this section to summarize some preliminary work and opportunities for future studies, both on the use of paleolimnology relative to fisheries problems and on the ecology of invertebrates along the temperature gradient of mountain lakes.

Opportunities for Recent Paleolimnology in Rocky Mountain Lakes

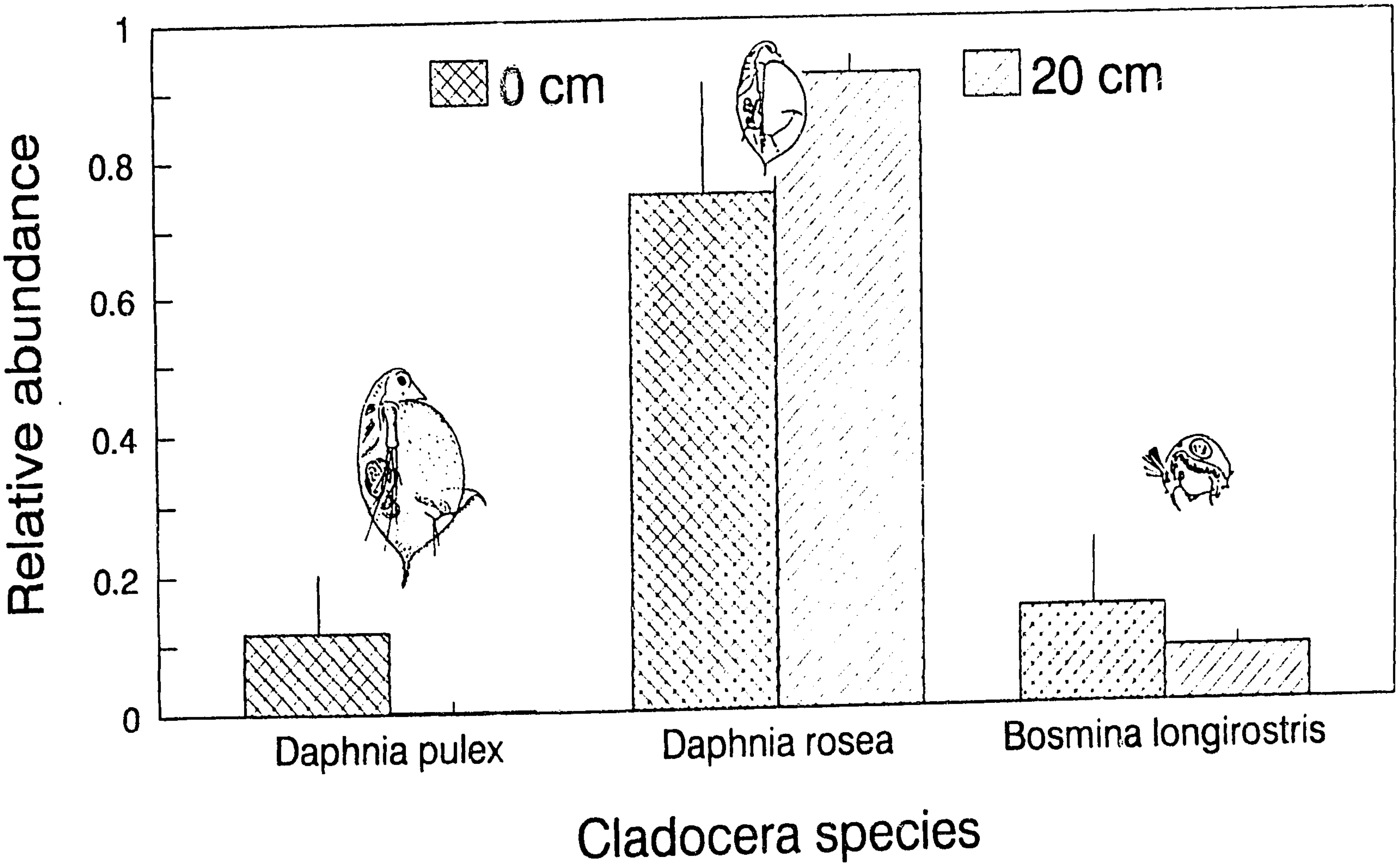
The use of invertebrates subfossils can be difficult in mountain lakes due to their low productivity and sometimes high sedimentation of inorganic matter. This appears to be particularly true in high alpine areas, where productivity is lowest. I was not able to use invertebrate remains (cladocerans and chironomids) to infer the impact of fisheries manipulation in Snowflake Lake, Banff National Park, at an elevation of 2 200 m. Invertebrate remains were so scarce that it was not possible to obtain statistically-significant samples at close temporal intervals (i.e., I found a total of 4 Daphnia claws). On the other hand, in Snowflake Lake, it was possible to follow the changes in the food-web brought by the stocking of fish using fossil pigments (P. Leavitt pers. comm.). The use of diatom or chrysophycean fossils has not been investigated. In brief, further investigation of paleoecological applications is needed, but its use may be restricted to lower trophic levels, particularly in high alpine sediments.

It is also possible that different techniques, such as density gradient centrifugation or treatments with strong acids, would be able to concentrate fossils from larger amounts of sediments (Frey 1986, Walker and Mathewes 1989). However, the appropriate methodology will need to be developed and tested prior to practical use, and large sediment samples would be needed in order to get acceptable temporal resolution. My own efforts at using techniques such as suspension of fossils in heavy liquids (sucrose solutions, $ZnCl_2$) have met with limited success (see also Berglund and Ralska-Jasiewiczowa 1986).

Cladoceran remains are potential indicators of past fisheries manipulations (Kitchell and Kitchell 1980, Leavitt *et al*. 1989, Miskimmin and Schindler in press) and could be used to supplement the information gathered with *Chaoborus* to deduce more clearly the changes to mountain lake communities caused by fish stocking. Size-selective predation by planktivorous fishes favours small zooplankters (Brooks and Dodson 1965, Carpenter *et al*. 1985, McQueen *et al*. 1986). Therefore, there should be a shift towards smaller species of cladocerans when fishless lakes are stocked with planktivorous fish. The usefulness of cladocerans may be limited by the low productivity and low species diversity of alpine lakes. For example, usually only one pelagic cladoceran, *Daphnia middendorfianna*, is found in alpine lakes whereas several species are found at montane elevations (*Bosmina longirostris*, *Daphnia pulex*, *D. rosea*) In alpine lakes, when *D. middendorfianna* is eliminated it is not replaced by smaller bodied cladocerans like *Bosmina longirostris* or *Daphnia rosea*, which are better able at withstanding fish predation (Anderson 1980). Therefore, in alpine lakes enough sediments will need to be processed to accurately follow changes in density and average size of D. middendorfianna, instead of relative change in abundance of different cladoceran species (Kitchell and Kitchell 1980, Leavitt et al. 1989). In Caledonia Lake, preliminary work with fossil cladocerans supported the findings made with Chaoborus mandibles (Fig. 3.1). The present zooplankton community is dominated by the medium-sized D. rosea, as was the fossil community approximately 120 years ago, suggesting that fish were also present at that time.

Wabasso Lake in Jasper National Park could be a site for further studies with subfossil Chaoborus mandibles (Appendix 2). This lake was sampled by Bajkov (1927) in 1925-26 and, as for Caledonia Lake, he collected two morphs of rainbow trout from this lake (Plate 2). It is possible that native rainbow trout still occur within this drainage (D. Donald, Environment Canada, 1901 Victoria Ave, Regina, Sask. S4P 3R4, pers. comm.).

Fig. 3.1. Comparison of the relative abundance of cladoceran remains at the top and bottom of a core from Caledonia Lake, Jasper National Park. Error bars represent two standard errors. The surface sample represents the recent fauna, while bottom sample (20 cm) represents the fauna approximately 120 years ago. Past and present communities are dominated by the medium size _D. rosea_, which suggests that fish were also present 120 years ago (Anderson 1980).



Caledonia lake

Top - Bottom comparison

Ecology of Invertebrates in Mountain Lakes

Mountain lakes over a range in elevation offer a tremendous opportunity to study the response of invertebrate populations to lake temperature and productivity. In this study, simple measures such as lake elevation and mid-summer surface water temperature were successful at predicting the distribution of *Chaoborus*, and other invertebrates (Anderson 1974, Donald and Anderson 1977, S. Lamontagne unpubl. data). The next step is to build a more mechanistically oriented degree-days model predicting the rate of development of life-stages of species such as *Chaoborus*. These models would require two basic components: a temperature of activation (i.e. minimum temperature for degree-days to start accumulating) and cumulative degree-days above the temperature of activation (Danks 1971, Danks and Oliver 1972, Büns and Ratte 1991). These may require intensive data collection.

Temperatures of activation will probably be difficult to define but are important because they may be the major difference between cold and warm adapted species (Danks and Oliver 1972, Walker 1991). It is likely that organisms will have to be reared under controlled conditions to define this parameter. Hopefully, temperatures of activation will be relatively similar between different life-stages of a given organism. A survey of the literature could be made to see how other workers have dealt with this problem.

Degree-days budgets could be defined and compared between populations of a given organism along a climatic gradient. For Chaoborus, I would use populations of a given species from 5 or 6 lakes along a gradient from the Edmonton region to some of the highest lakes where Chaoborus are found near Jasper, Jasper National Park. Assuming that we know or can estimate the temperature of activation, it would be possible to define how many degree-days are necessary to go through each step of development (i.e. hatching, instars I-IV, pupation). Under marginal climatic conditions, Chaoborus will likely need to lengthen their life-cycle to complete their development (Downes 1964, Danks 1971).

There is evidence that some Chaoborus populations have two years life-cycle at high elevations near Jasper, whereas at lower elevations it is probably one year. Chaoborids usually overwinter as fourth instars larvae and hatch the following spring. In populations with two-years life-cycles, the fourth instar goes through a second summer of growth and is distinctly more pigmented than 'young' fourth instars (Fedorenko and Swift 1972, Borkent 1979). 'Jet-black' C. americanus larvae have been collected in some high elevation lakes in Jasper National Park (R.S. Anderson pers. comm.). If these populations indeed have two years life-cycles, it would be interesting to define the threshold in the heat budget where Chaoborus switch to a longer life-cycle. Food availability also has an impact on Chaoborus developmental rates (Neill 1988, Büns and Ratte 1991). Food addition experiments in mesocosms could be used to test the effect of increased or reduced food supplies on Chaoborus developmental rates. Overwinter mortality can be an important factor limiting population size when food is in short supply (Neill 1988).

Initially, chaoborids inhabiting fishless lakes (C. americanus, C. trivittatus) may be easier to study because of the potential confounding effect of fish predation. Also, Chaoborus tend to be more abundant in fishless lakes and the ecology of these species is relatively well-known. Lakes could be sampled weekly or every other week during the ice-free season, and perhaps a few time over the winter. Minimum-Maximum thermometers would be an inexpensive and reliable method of recording heat budgets for the epilimnions (Danks 1971, Donald and Anderson 1977).

orus could be used as a model organism to test whether invertebrate populations are more sensitive to fish predation when lake temperature is low. It is probable that fish predation will have a greater impact on invertebrate populations having longer life-cycles (i.e. lower turnover rates), as seems to be the case for chaoborids and other invertebrates in mountain lakes (Anderson 1980).

Although my study mainly oriented to Chaoborus, many ecologically important invertebrates could be studied in a similar fashion (Gammarus lacustris, Hesperodiaptomus arcticus). Preliminary data suggest that G. lacustris in Snowflake Lake have a two year life-cycle (S. Lamontagne, unpubl. data). This species has a one year life cycle in prairie lakes and two generation a year in warmer lakes (Menon 1966, Sarviro 1980). Invertebrates are the top predators in most alpine lakes of the

Rockies, yet we know little about their basic ecology. A better understanding of the alpine lake ecosystem could be gained by studying the adaptations of organisms to harsh environmental conditions such as low temperature and high UV radiation (Thomasson 1956). Because small changes in environmental conditions may affect alpine communities greatly, alpine ecosystems could become a good reference environment to follow the impacts created by disturbances such as climate warming (Luckman 1990) or the depletion of the ozone layer.

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Appendix 1. Data used in the analysis of Chaoborus distribution. Fish species acronyms: RT - rainbow trout (Oncorhynchus mykiss), LC - lake chub (Couesius plumbeus), BT - brook trout (Salvelinus fontinalis), LS - longnose sucker (Catostomus catostomus), B - bull trout (Salvelinus confluentus), LT - lake trout (Salvelinus namaycush), BU - burbot (Lota lota), CT - cutthroat trout (O. clarki), S - splake (S. fontinalis X S. namaycush), MW - mountain whitefish (Prosopium williamsoni), LD - longnose dace (Rhinichthys cataractae). Chaoborus acronyms: A - C. americanus, F - C. flavicans, T - C. trivittatus and P - C. punctipennis. Chaoborus acronyms in brackets represent species found in recent sediments. Fish and Chaoborus species present represents conditions in the 1970's; present conditions may be different in some lakes.

Lake	Park	Elevation (m above sea level)	Mid-Summer Surface Water Temperature (°C)	Maximum Depth (m)	Lake Area (ha)	Fish spp.	Chaoborus spp.
Bench	Jasper	1355	19	5.8	1.8	None	A
Cabin		1217	18	20.5	32.2	RT,LC	(F,A,T)
Caledonia		1161	17.5	11	13	RT,BT,LC	F
Christine		1338	20	8.0	7.0	BT	F
Cutt		1445	17.5	7.5	15.5	CT	F
Dorothy		1336	19	14.6	25.1	RT,LC,LS	F
Golden		1485	17	10.3	13.4	RT	F
Hibernia		1198	20	8.5	9.6	RT	A,F
Hidden		1258	21	6.0	2.6	BT	A
High #1		1455	20	6.0	1.0	None	A

High #2		1459	20	1.5	1.5	None	A
High #3		1479	19	1.0	1.7	None	A
High #4		1515	17	2.0	1.6	None	A
High #5		1570	16	2.0	1.2	None	A
High #6		1535	18	1.3	2.0	None	A
High #7		1495	18.5	7.5	2.9	BT	F
Marjorie		1143	18	8.0	7.3	RT,BT	F
Mina		1214	20	13.2	8.3	RT,LC	F
Minnow		1415	17.5	3.3	6.1	BT,LC	F
Rathlin		1298	20	4.3	2.2	None	A
Riley		1175	18.5	10.5	4.6	RT,LC	F
Saturday Night		1418	18	8.3	9.7	RT,BT,LC	F
Virl		1305	17	6.0	3.5	BT	A,F
Upper Colfair		1355	19.5	7.5	2.9	RT	F
Edwards		1228	14.5	10	0.5	RT	None
Chalet		1976	8.5	0.9	1.5	BT	None
Fryatt		1710	-	7.0	13.1	None	None
Lower Geraldine		1600	11	6.0	17.7	BT,RT	None
Geraldine #2		1690	9	4.0	0.6	RT	None

Geraldine #3		1855	10.5	31	50.7	RT	None
Geraldine #4		1970	10	5.5	5.7	None	None
Geraldine #5		1995	-	25	26.5	None	None
Honeymoon		1405	21.5	7.0	18.4	RT	F
Little Honeymoon		1310	23	4.0	1.0	None	A
Hostel Pond		1560	12.5	4.0	4.9	BT	None
Kerkeslin		1743	7.5	4.5	33.9	B	None
Leach		1237	18	11	13.1	RT	F
Lectern		1515	18	14	1.9	RT	F
Long		1357	16	3.0	5.1	BT	None
Mile 16½		1174	24	6.0	9	BT	None
Mitchell		1783	6	14	29.9	None	None
Moab		1204	16.5	18	23.9	RT,LT,B+	F,T
Amethyst		1967	13	25	470	RT,BT	None
Moat		1945	14	10.5	35	RT	None
Beaver		1498	19	2.0	31	BT	None
Maligne		1675	13	96	2066	RT,BT	None
Medecine		1442	15	17.5	516	RT	None
Mona		1750	17	11.5	11.5	BT	None

Annette		1024	19	23	28.6	BT,LC,RT	None
Beauvert		1030	15	25	32.3	LC,LS,BU, RT	None
Edith		1024	17	18	50	RT,LC	None
Horseshoe		1230	14	31.5	8.93	RT	None
Patricia		1180	17	40	69	LC,LS,BU, RT,BT,LT	None
Pyramid		1186	18	19	127	LT,BT,RT, MW,LS,LC	None
Beaton		1646	-	2.5	1.1	BT	None
Lower Caribou		1767	14	18	46.3	RT	None
Upper Caribou		1788	10.5	29	43.2	RT	None
Celestine		1260	16	14	39	RT,BU,LC	F,(A)
Dolly		1555	14	5.5	7.7	B,RT	None
Harvey		1617	10	21	58	RT	None
Kidney		1375	20	12	24.1	LT,LC	None
Miette		1864	11	6.5	7.2	B	None
O'Beirne #1		2133	9	25	5.6	None	None
O'Beirne #2		2027	11	33	10.8	None	None
O'Beirne #3		2120	7.5	23.5	8.9	None	None

O'Beirne #4		2027	12	32	6.8	None	None
Rink		1793	10.5	5	13.8	None	T?
Sassenach #2		1851	14	16	8.1	LT	None
Topaz		1773	15	28	128.5	RT	None
Twintree		1558	12.5	51	320.1	RT	None
Phalarope		2220	-	6	1.5	-	None
Outer Rink		2027	-	18	9.5	-	None
Upper Cairn		2180	-	27	20	-	None
Medecine Tent		2138	-	34	45	-	None
Edna		1000	-	2.0	25	-	None
Lily Pond		1323	-	4.0	0.8	-	A
Tekarra		1098	-	1.5	0.2	-	A
Cold Sulfur		1006	-	1.5	0.4	-	A
E.Henry Pond		2105	-	4.5	3.5	-	T
Leach Pond #2		1200	-	1.0	1.0	-	A
Palisades		1027	-	1.0	0.4	-	A
Brachinecta		2270	-	2.5	0.5	-	None
North Summit		1540	-	3.0	12	-	None
South Summit		1540	-	3.0	14	-	None

Agnes	Banff	2118	10.5	20.5	6	S?	None
Annette		1996	6	13.7	5.3	None	None
Baker		2210	9	36.4	11.6	BT,CT	None
Little Baker		2240	8	5.0	2.9	BT,CT	None
Boom		1893	13	32	99.6	CT	None
Brachiopod		2271	8	3.0	2.1	None	None
Low.Constellation		1951	5	11.3	14.5	BT,CT	None
Up. Constellation		1951	5	16.2	10.7	BT	None
Eiffel		2271	9.5	13.5	13.5	None	None
Herbert		1600	15.5	13.3	5.7	BT,RT	F
Little Herbert		1570	15.5	8.2	0.6	BT,RT	F
Herbert Pond		1600	17.5	5.0	0.4	None	A
Hidden		2271	7.5	32.3	13.3	CT,BT	None
Island		1570	16	6.4	14.9	None	A
Kingfisher		1539	15	7.2	2	RT	None
Kingfisher Pond		1600	19	6.1	0.5	BT	F
Larch East		2362	6.5	1.5	0.4	None	None
Larch West		2393	5	3.3	0.2	None	None
Louise		1731	13	70	84.5	MW,B,CT	None

McNair		1539	15	3.5	1.7	BT,RT	None
Mirror		2027	12.5	4.5	0.5	None	None
Moraine		1887	6	22.9	41.3	RT,BT,LT	None
Mud		1600	14	7.2	7.3	BT,LD	None
O'Brien		2118	9	20.7	4.6	CT	None
Ptarmigan		2332	10	21.3	27.9	BT,LT	None
Redoubt		2393	8	11	19.1	BT	None
Sentinel		2423	8.5	6.7	2.8	None	None
Taylor		2057	10	43.9	27	CT	None
Temple		2179	10	14	3.1	BT	None
Tilted		2210	10.5	12.2	3.6	BT	None
Bighorn		2347	8	9.2	2.2	BT?	None
Cuthead		2210	9	4.3	3.5	B	None
Grouse		2271	10	-	-	None	None
Harrison		2243	10	10.7	8.4	B	None
Pipit		2217	9	20.6	10.6	RT	None
Snowflake		2320	10	12.5	7.1	BT,RT	None
Wigmore		1996	-	1	2	BT	None
Crescent		2204	-	5.5	4.0	None	None

West Altrude		1628	-	6.1	3.0	None	None
Little Bighorn		2420	-	8.0	0.8	None	None
Dolomite Pond		2385	-	3.0	1.0	None	None
Storm	Kootenay	1213	-	7.5	3.0	None	None
Opabin Pond #3	Yoho	2232	-	1.5	0.3	None	T?
Opabin Pond #4		2232	-	1.4	0.3	None	T?
Peanut	Alberta	730	23	12	30	Present	F,P
Baptiste		725	20	27.5	98	Present	F
Amisk		612	24.5	34	52	Present	F,P
Crooked		617	24	8	-	Present?	P
Ghost		625	22	11	-	Present?	F,P
Jenkins		632	21	15	-	Present?	F,P
Lofty		617	22.5	5.5	-	Present?	A
Halfmoon		617	22	6	4.0	Present?	F
Miquelon		763	20	6	-	Present?	F

Appendix 2. Some of the lakes in the Moutain national parks where paleolimnological analysis could be used to determine the origin of fish populations.

Lake	Park	
Wabasso (Buffalo Prairie)	Jasper	The other lake (with Caledonia) where Bajkov reported native rainbow trout. Small lake (1-2m deep), turbid in summer. Chaoborus may be present.
Pyramid	Jasper	Possibly had lake trout. Chaoborus not found in the lake right now. The fishes of this lake have been extensively manipulated. (reference: D.W. Mayhood)
Dorothy	Jasper	Longnose sucker ? (reference: D.W. Mayhood)
Fifth of five	Jasper	In the valley of five lakes. Possibly had lake chub. Chaoborus present (reference: D.B. Donald).
Upper Altrude	Banff	Cutthroat trout? (reference: D.B. Donald)
Lower Altrude	Banff	Cutthroat trout? (reference: D.B. Donald)
Mystic	Banff	Early records of 'trout' (reference D.B. Donald)
Mud (near Lake Louise)	Banff	Dace ? (reference: D.B. Donald)
Boom	Banff	(Reference: D.B. Donald)
Wapta	Yoho	Lake trout? (reference: D.B. Donald)
Sherbrooke	Yoho	Lake trout? (reference: D.B. Donald)
Osprey	Jasper	Native bull trout? Sediments very inorganic.