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RECONSTRUCTING THE POPULATION HISTORY OF NATIVE WESTSLOPE CUTTHROAT TROUT (*ONCORHYNCHUS CLARKI LEWISI*) IN AVALANCHE LAKE, THROUGH ANALYSIS OF FOSSIL ZOOPLANKTON ASSEMBLAGES IN PROFUNDAL SEDIMENTS (GLACIER NATIONAL PARK, MONTANA).

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Final Report

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EXECUTIVE SUMMARY

Genetically pure populations of native westslope cutthroat trout (*Oncorhynchus clarki lewisi*) in headwater lakes of Glacier National Park could play an important role in the recovery of cutthroat trout in the Lake McDonald basin. Indigenous populations of this trout in the park are thought to have become established at some time during postglacial history through natural dispersive colonization. In the case of the native cutthroat trout in Avalanche Lake, however, natural colonization has been considered uncertain because the high-gradient stream giving access to this lake from Lake McDonald appears to form a significant barrier for naturally dispersing fish, and because other fish species that normally occur in association with the trout are absent.

This study aimed to find out whether the lake-resident native trout in Avalanche Lake really established itself through successful natural colonization, or whether it became established much more recently through an undocumented introduction in the decades prior to the creation of Glacier National Park in 1910. The study design involved examination of fossil zooplankton assemblages contained in the lake's profundal sediments, based on the premise that recent introduction of planktivorous trout to a naturally fishless lake would have caused abrupt changes in the lake's zooplankton community. Visual, size-selective predation by fish typically results in preferential removal of larger prey species and of prey that stay in the upper water column during daytime. In headwater lakes of Glacier Park, there are two groups of zooplankton whose populations are likely to be affected by vertebrate predation, and which also possess exoskeletal elements that preserve well enough for these changes to be traceable in the sedimentary record: the cladoceran microcrustaceans *Daphnia rosea* and *D. middendorffiana*, and the planktonic larvae of three species of phantom midge, *Chaoborus*.

A survey of living zooplankton and surface-sediment death assemblages in eight Glacier Park lakes that do or do not sustain trout populations today demonstrated that predation by fish indeed plays a dominant role in the structuring of local zooplankton communities. Analysis of fossil zooplankton assemblages in a sediment-core profile dated by ^{210}Pb, wildfire records, and a flood event, then allowed reconstruction of zooplankton dynamics in Avalanche Lake from about 1700 AD to the present. The results indicate that predation by fish kept *Daphnia* populations at or below present levels during most of this period and excluded *Chaoborus* from the lake, a pattern indicative for the original and continued presence of cutthroat trout. Paleolimnological evidence for much larger *Daphnia* populations in the 1930's and possibly early 1940's points to a temporary upset of the lake's trophic equilibrium, most probably related, whether directly or indirectly, to the failed attempts between 1915 and 1943 to stock Avalanche Lake with Yellowstone cutthroat trout (*O. clarki bouvieri*).

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INTRODUCTION

In historical times the westslope cutthroat trout (*Oncorhynchus clarki lewisi*) has been severely depleted in drainage basins throughout its native range in the Rocky Mountains of Montana, Idaho, British Columbia and Alberta (Trotter, 1987; Fig. 1). The major reasons for this decline appear to be degradation of spawning streams impacted by catchment disturbance from logging and road construction, and the detrimental effects of former fisheries management practices which promoted introduction of non-native game fish. Because adult westslope cutthroat trout are less piscivorous then other salmonids, its dependence on zooplankton makes the westslope trout particularly vulnerable to competition from other specialized planktivores, and subject to predation by more piscivorous salmonids. In Glacier National Park (Montana), where landscape degradation is minimal, the decline in indigenous populations of cutthroat trout must be attributed primarily to predation and competition for zooplankton from non-native fish species. Lake trout (*Salvelinus namaycush*), kokanee (*Oncorhynchus nerka*), and lake whitefish (*Coregonus clupeaformis*) invaded Lake McDonald and several other large glacial lakes within Glacier Park since the 1930's, after they had been introduced by the state of Montana in lakes throughout the Flathead River basin in the park's vicinity. Between as early as 1912 and the early 1970's, numerous headwater lakes in Glacier Park were deliberately stocked with primarily rainbow trout (*Oncorhynchus mykiss*) and Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*), to enhance the native fisheries and so promote recreational harvesting (Marnell, 1988). Non-native trout populations were established in more than a dozen lakes where fish were previously absent, and all but four park lakes known to contain indigenous cutthroat trout were planted at least once with rainbow trout or Yellowstone cutthroat trout, both of which are capable of hybridizing with the westslope

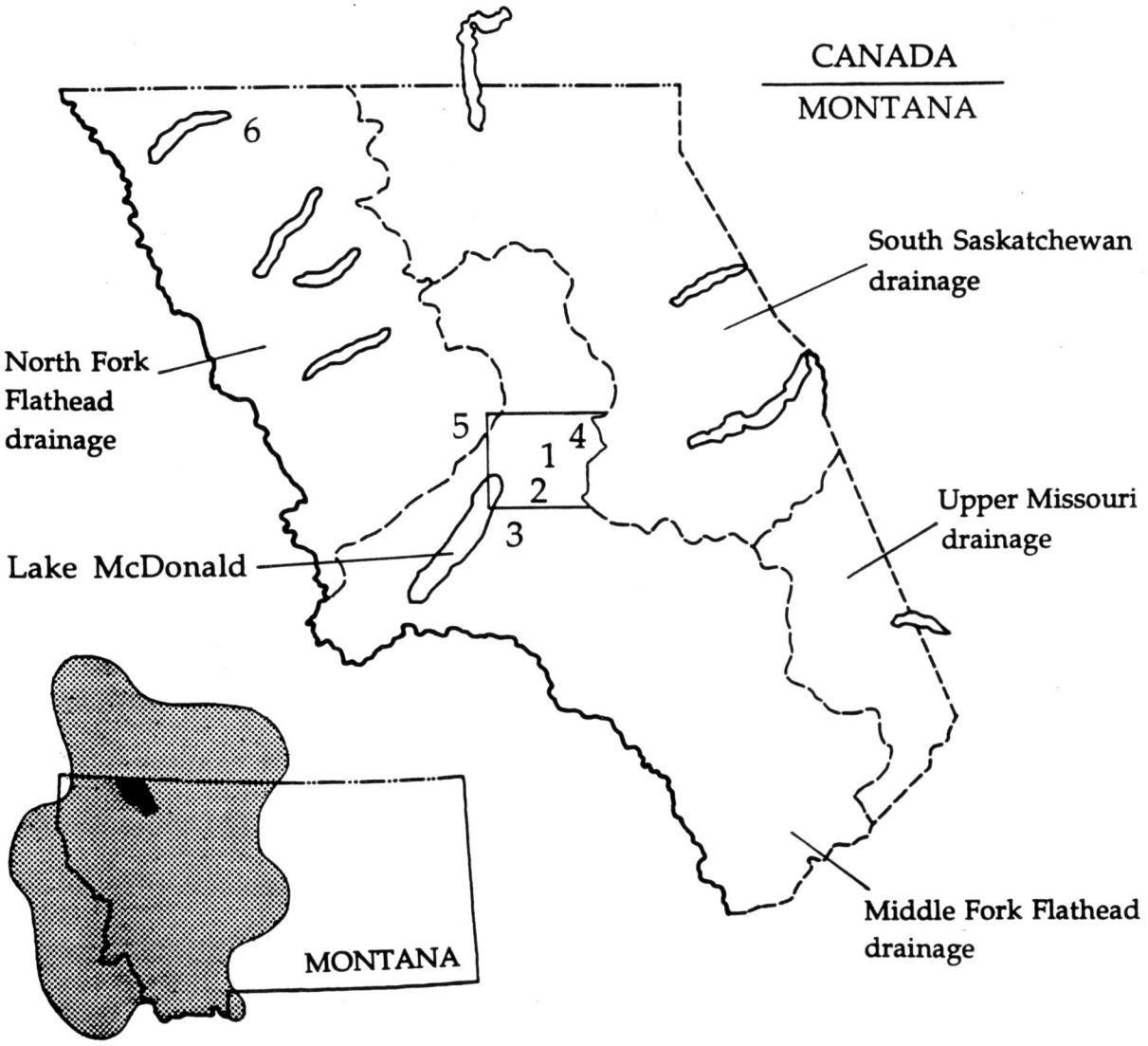


Fig. 1. Historical range of westslope cutthroat trout (stippled; Trotter, 1987), and major drainage basins within Glacier National park, Montana. Numbers refer to headwater lakes mentioned in the text: 1. Avalanche Lake; 2. Snyder Lake and Upper Snyder Lake; 3. Fish Lake; 4. Hidden Lake and 'Hidden Pond' (see text, p.9); 5. Trout Lake; 6. 'Babbe Lake' (see text, p.9). Central part enlarged in Fig. 2.

cutthroat trout. However, despite this widespread stocking of closely related species and subspecies, genetic contamination of the native trout appears to have been minimal. Meristic and electrophoretic analyses (Marnell et al., 1987) revealed that genetically pure westslope cutthroat trout currently survive in 16 Glacier Park lakes, all of which drain to the North and Middle Forks of the Flathead River.

Avalanche Lake, a headwater lake within the Lake McDonald basin of the Middle Fork Flathead River drainage (Fig. 1), contains one of the remaining genetically pure populations of westslope cutthroat trout. Its secure status makes this fishery particularly suitable as the source of hatchery fish in a management program aimed at recovering native trout fisheries throughout the Lake McDonald basin. However, the high gradient and extensive cascading of Avalanche Creek, which gives access to the lake from Lake McDonald and the Flathead River drainage, make it uncertain that the native trout could have arrived in Avalanche Lake by natural, dispersive colonization. Also, other native fish species which co-occur with westslope cutthroat trout in several other Glacier Park lakes (e.g. bull trout, *Salvelinus confluentus*) are absent in Avalanche Lake. Together these observations have raised the suggestion that Avalanche Lake may have been historically fishless, and that the cutthroat trout has been transplanted to it in an undocumented stocking effort (Marnell et al., 1987). Anecdotal accounts indicate that native trout was already present several decades prior to the first hatchery fish introductions of Yellowstone cutthroats in 1915, but also indicate that early entrepreneurs regularly transported native fish between lakes throughout the region in the decades prior to the creation of Glacier National Park in 1910. In view of its possible role in future fisheries management of Glacier Park, we undertook this study to investigate whether or not the Avalanche Lake population of native trout is indigenous to the lake. Evidence for the historical status of the fishery is derived from examination of fossil zooplankton assemblages contained in the lake's

bottom sediments. This approach is based on the premise that recent introduction of zooplanktivorous trout to the previously fishless lake would have caused changes in the zooplankton community that are substantial enough to be detected in the paleolimnological record.

Numerous studies have demonstrated the impact of size-selective predation by fish since it was first documented by Hrbacek et al. (1961), Brooks and Dodson (1965) and Galbraith (1967); the latter study described the elimination of the large crustacean zooplankter *Daphnia pulex* that resulted from stocking two Michigan lakes with rainbow trout. In three fishless alpine lakes of the Canadian Rocky Mountains, calanoid copepods and large *Daphnia* spp. dominated the zooplankton until they where eliminated between 2 and 6 years after stocking the lakes with rainbow trout, brook trout (*Salvelinus fontinalis*) and cutthroat trout (Anderson, 1972). In its simplest formulation, the principle of size-selective predation holds that fish will eat more of the larger available prey because these have the greatest probability of being detected, leaving less vulnerable smaller prey to dominate the zooplankton (O'Brien, 1979). Size-selective predation is now one of the best understood mechanisms governing the community structure of zooplankton (Kerfoot and Sih, 1987), and several paleolimnological studies (e.g. Brugam and Speziale, 1983; Kitchell and Kitchell 1980; Kerfoot, 1981; Leavitt et al., 1989; Salo et al., 1989) have confirmed its role as major causative agent in local extinction, dominance shifts and permanent reduction of body-size in species assemblages of crustacean zooplankton.

Large *Daphnia* are among the prey most susceptible to visual predation by fish. In fall, females engage in sexual reproduction and then form a protective capsule, the ephippium, to enclose their overwintering diapause eggs. When dead ephippial females become buried in the bottom sediments, these capsules preserve much better than fragments of the fragile exoskeleton. *Daphnia* ephippia are

recovered in abundance from ancient lake deposits (Frey, 1964) and can often be identified to species. Postabdominal claws are the only other body fragment of *Daphnia* that can be found at depth in lake sediments, and they also can be used in reconstructions of zooplankton history (see e.g. Kitchell and Kitchell, 1980).

A second group of zooplankton which likely would have been adversely affected by the recent addition of planktivorous fish to a fishless Avalanche Lake, and whose buried remains preserve well enough to trace these changes in the sedimentary record, are the planktonic larvae of *Chaoborus*, the phantom midges. Larvae of *Chaoborus* commonly occur in the limnetic zone of lakes, where they function as predators on smaller zooplankton (Uutala, 1990). The various species in the genus differ in size, coloration, and their distribution in the water column, all factors which affect their susceptibility to predation by fish (von Ende, 1978; Stenson, 1980; Borkent, 1981). *Chaoborus americanus* lacks the habit of daily vertical migration, and by staying in the upper water column during daytime it is particularly vulnerable to visual predation by fish (Fedorenko and Swift, 1972; Stenson, 1978). Consequently, it is normally found only in fishless lakes. *C. americanus* and its European counterpart *C. obscuripes* have been eliminated in lakes to which fish were experimentally introduced (Northcote et al., 1978; Evans, 1989), and have colonized recently acidified lakes from which fish had disappeared (Johnson et al., 1990). *C. trivittatus* and *C. flavicans*, on the other hand, migrate into the poorly illuminated hypolimnion during the day and are therefore able to coexist with zooplanktivorous fish, at least in sufficiently deep lakes (Borkent, 1981). Still numbers of *C. trivittatus* were drastically reduced when cutthroat trout was introduced to the historically fishless Lake Eunice in British Columbia (Northcote et al., 1978). Luecke (1988) found that the impact of cutthroat trout on *C. flavicans* in Lake Lenore, Washington, depends on seasonal water temperature. Cutthroat trout prey most heavily on the pupae of *Chaoborus*, which like the larvae reside in the

bottom sediment during the day and ascend to the surface at night. Increasing surface water temperatures from 16.2 °C in May to 19.6 °C in June shortened duration of the pupal stage from 8.9 to 2.4 days, which reduced exposure to the trout and so favored successful emergence of the midges. In alpine and subalpine lakes of Glacier Park, summer water temperatures remaining below 16 °C may drastically increase the vulnerability of migrating *Chaoborus* species such as *C. flavicans* to fish predation.

Subfossil mandibles of *Chaoborus* are commonly found in lake sediments (Frey, 1964), and can be identified to species (Uutala, 1990). In this study we concentrate on sedimentary remains of both *Chaoborus* and *Daphnia* to assess the historical status of cutthroat trout in Avalanche Lake by reconstructing the history its zooplankton community. Our conclusions will be supported by the results of a comparative survey on the species composition of living zooplankton and surface-sediment death assemblages in eight Glacier Park lakes that do or do not sustain cutthroat trout today.

2. STUDY AREA

Avalanche Lake (48°39'23"N/113°47'05"W) is a clear 23-ha headwater lake situated in a tributary cirque drainage of the glacier-widened McDonald Creek valley (Fig. 2). At 1190 m a.s.l. it occupies the floor of an elongated basin immediately downstream from the cirque of Sperry Glacier, from which it receives meltwater via a series of steeply cascading streams and waterfalls, the Monument Falls. Most bedrock exposed in the Avalanche Lake catchment are metamorphic siltites and argillites of the Grinnell Formation, while the Sperry Glacier cirque is carved out of limestone/dolomitic quartzites to argillites of the overlying Empire and Helena

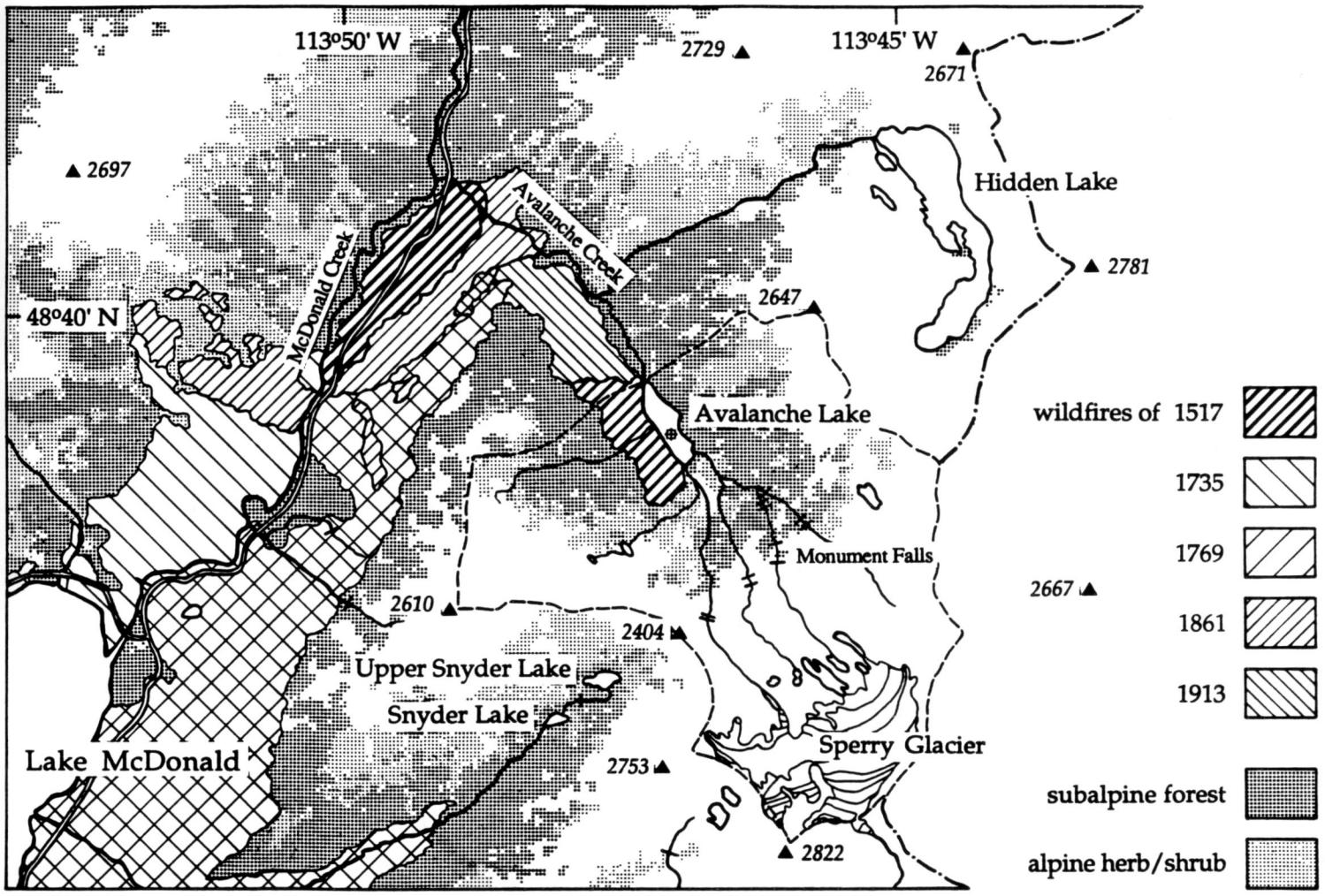


Fig. 2. The Avalanche Lake catchment (within the dashed line) and surrounding areas on the western side of the Continental Divide, in the Middle Fork Flathead River drainage. Core locality indicated by the crossed-circle symbol. Extent of areas burned by historical wildfires has been determined by fire-scar data from surviving trees (Carl Key, Glacier National Park, unpublished).

Formations (Raup et al., 1983). Apart from the barren headwall at its upstream end, the lake is surrounded by subalpine forest with Douglas-fir (*Pseudotsuga menziesii glauca*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*), grading into alpine meadows with huckleberry shrub (*Vaccinium globulare*) at higher elevations. The Avalanche Lake basin has never been logged and the last major fire within the lake's catchment area occurred in 1517 AD, as dated by dendrochronology (Carl Key, Glacier National Park, unpublished data). The lake is inhabited by a genetically pure, unhybridized population of native westslope cutthroat trout, despite at least seven attempts between 1915 and 1943 to introduce non-native Yellowstone cutthroat trout. Like many interior populations of native cutthroat trout in isolated lakes of Glacier Park, adult trout in Avalanche Lake are lake-resident. They spend their adult life in the lake and use gravelly bottoms of the nearby inlet or outlet streams for spawning (Marnell et al., 1987).

3. FIELD COLLECTION AND METHODS

Two short cores (Core AL91.1: 74 cm; Core AL91.2: 60 cm) with undisturbed sediment/water interface were recovered by single-drive piston coring (Digerfeldt, 1978) from the profundal bottom of Avalanche Lake, at a near-deepest central locality in 19.80 m of water (Fig. 2). In upright position and with the piston still in the core tube, the cores were carried to a field station on the shore of Lake McDonald, where they were extruded and sectioned in 1-cm increments. The mud slices were packed individually in Whirl-Pack bags for transport to Minneapolis.

Core AL91.1 was used for dating, sediment analyses, and study of fossil zooplankton assemblages. Sediment composition, bulk density (dry weight per cm^3 of wet sediment) and porosity were determined with standard loss-on-ignition

methods (Bengtsson and Enell, 1986) at 1-cm (0-25 cm and 63-70 cm core depth) or 2-cm (25-63 cm and 70-74 cm depth) intervals (Appendix 1). Excess ^{210}Pb-activity was measured at 15 depth levels in the upper 45 cm of the core to determine sediment age and accumulation rates for the past 120 years. ^{210}Pb was measured through its grand-daughter product ^{210}Po, with ^{208}Po added as an internal yield tracer. Sample preparation was modified from Eakins and Morrison (1978), and activity was measured in an alpha spectroscopy system. Asymptotic activity at depth (lower 3 samples) yielded an estimate of supported ^{210}Pb-activity of 1.79 ± 0.04 $pCi.g^{-1}$ (Appendix 2). Unsupported ^{210}Pb was obtained by subtracting supported activity from the total activity measured at each level. Dates and sedimentation rates were determined according to the c.r.s. (constant rate of supply) model (Appleby and Oldfield, 1978), with confidence intervals calculated by first-order error analysis of counting uncertainty (Binford, 1990).

For the comparative survey of local zooplankton community structure, seven other lakes in the Flathead River drainage of Glacier Park were selected on the basis of accessibility and, ideally, similarity to Avalanche Lake in elevation and trophic state. Four lakes (Fish, Snyder, Trout, and Hidden lakes; Fig. 1 and Table 1) contain indigenous or introduced populations of westslope and/or Yellowstone cutthroat trout (Marnell et al., 1987); the three other lakes (Upper Snyder Lake, 'Hidden Pond', and 'Babbe Lake') are fishless. 'Babbe Lake' is an unnamed small lake in the Kintla basin of the North Fork Flathead drainage. It is surrounded by subalpine forest at the foot of a talus slope, and lacks a permanent outlet. Upper Snyder Lake and 'Hidden Pond', an unnamed pond connected to the outlet stream of Hidden Lake, are too shallow (2.0 m and 1.5 m, respectively) for resident fish populations to survive winter freeze-over.

At offshore locations in each of these seven lakes and Avalanche Lake, surface sediment was collected with a modified Hongve gravity corer (Wright, 1990),

Table 1. Selected lakes and ponds in Glacier National Park

Lake Name	Elev. (m a.s.l.)	Area (ha)	Fish[2]	Outlet	Access[3]	Flathead River drainage	Sampling date	Temp.[4] (°C)	Depth (m)
Avalanche Lake	1191	23	WCT	+	(+)	Middle Fork	09/18/91	10.1	19.80
Trout Lake	1190	86	WCT	+	+	North Fork	09/23/91	13.5	20.10
Snyder Lake	1585	2	WCT	+	(+)	Middle Fork	09/22/91	8.3	0.55[(5)]
Hidden Lake	1944	110	YCT	+	-	Middle Fork	09/24/91	9.5	20.10
Fish Lake	1265	3	WCTxYCT	(+)	(+)	Middle Fork	09/20/91	15.7	7.20
Upper Snyder Lake	1699	4	absent	+	-	Middle Fork	09/22/91	8.1	2.00
'Babbe Lake'[1]	1309	2	absent	-	-	North Fork	09/25/91	13.5	12.55
'Hidden Pond'[1]	1944	1	absent	+	-	Middle Fork	09/24/91	10.6	1.55

Footnotes. 1: both are unnamed; see text. 2: fishery data from Marnell et al. (1987); WCT = Westslope Cutthroat Trout (*Oncorhynchus clarki lewisi*), YCT = Yellowstone Cutthroat Trout (*O. clarki bouvieri*), WCTxYCT = hybrid population. 3: access to a lake for dispersing trout implies the presence of a surface outlet and absence of significant barriers such as falls. 4: surface water temperature at the date of sampling. 5: the surface-sediment sample in Snyder lake was collected nearshore.

and living late-summer limnetic zooplankton was sampled qualitatively by vertical tows with a 85-µm mesh plankton-net. In the laboratory, volumetric subsamples of the 1-cm slices of both the Hongve surface samples and core AL91.1 from Avalanche Lake were processed for extraction of *Daphnia* ephippia and *Chaoborus* mandibles, following standard methods described in Frey (1986) and Uutala (1990). Sieves used to separate the appropriate size fractions had 250 µm and 105 µm mesh sizes, respectively. Retained residues were diluted to 100 ml and scanned in full at 16X under a dissecting microscope. Living and subfossil *Chaoborus* spp. were identified at 25-100X with reference to Cook (1956), Saether (1970) and Uutala (1990); *Daphnia* spp. and other Cladocera were identified using keys in Brooks (1959) and Pennak (1991). Ephippia of the two *Daphnia* species present in the samples were distinguished mainly on the basis of a row of fine spinules, present along the dorsal margin of ephippia of *D. middendorffiana* and absent in *D. rosea*. However, these spinules are less resistant to breakage after burial than the ephippial capsule, so that older ephippia of *D. middendorffiana* become difficult to distinguish from those of *D. rosea*. We decided not to search for post-abdominal claws of *Daphnia*, because when zooplankton densities are naturally low and large volumes of sediment need to be scanned, visual obstruction of the claws by fine organic particles makes sample processing prohibitively time-consuming.

To allow between-lake comparison of the abundance of various zooplankton taxa in the surface-sediment death assemblages, a fixed criterion must be adopted to make the analyzed volumes of mud equivalent among lakes. Large variation of surface-sediment porosity in the sampled Glacier Park lakes (Appendix 3) would bias simple volumetric analysis in favor of lakes with low-porosity surface sediments. Equivalency based on dry mass, on the other hand, disfavors lakes with high clastic mineral input such as Avalanche Lake and Upper Snyder Lake. On the assumption that, in the absence of fish predation, zooplankton densities and secondary

productivity would be roughly proportional to primary productivity, surface-sediment sample volumes were normalized with respect to organic content. This measure allowed analysis of larger samples for the more oligotrophic lakes, which would otherwise have been numerically disfavored. Samples from the seven reference lakes were chosen to correspond to 5 ml (for *Chaoborus*) and 25 ml (for *Daphnia*) wet surface sediment from Avalanche Lake (Appendix 3 and Table 2).

The relationship between ephippium length and bodysize of *Daphnia* in Glacier Park waters was established using intact ephippial females from the collections of modern late-summer zooplankton in the reference lakes (Appendix 4). This relationship was found to be linear within the size range covered (Fig. 3). We note that bodysize estimates for modern and fossil *Daphnia* populations based on ephippial females is probably proportional to but not identical with the actual mean bodysize of all adult *Daphnia* in these populations.

4. SEDIMENT COMPOSITION AND CHRONOLOGY

Profundal sediments in Avalanche Lake are composed of low-organic clays, containing between 8 and 19 % carbonate (Fig. 4). The sediment is mostly allogenic, derived from fine-grained debris carved by the Sperry Glacier in limestone/ dolomitic argillites and siltites of the Empire Formation. This 'glacial flour' is released from underneath the retreating glacier (Johnson, 1980) and flushed to Avalanche Lake via the Monument Falls. The sedimentary profile of the core is quite uniform both in dry-sediment composition and visual appearance (Fig. 4). Slight color changes correspond with minor variation in content of organic matter, the only obvious color change paralleling a slight increase in organic content from 2.5-3.5 % to 3.5-6.5 % at about 25 cm depth. Two narrow horizons with coarse plant

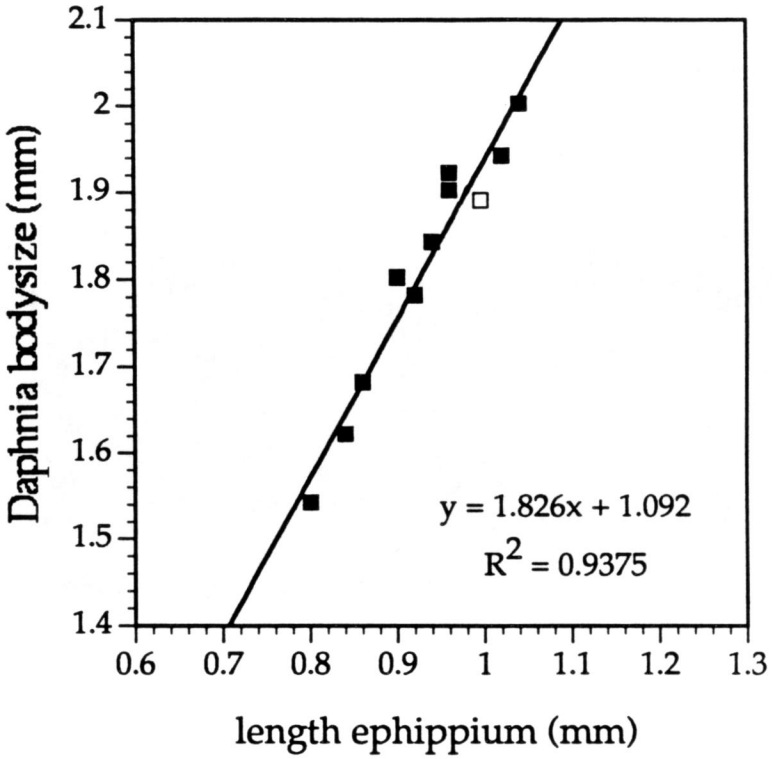


Fig. 3. Regression of *Daphnia* bodysize (crest of head to base of tailspine) on ephippium length, based on modern ephippial females from Trout, Fish, Snyder and Upper Snyder Lakes (*D. rosea*, filled squares), and 'Hidden Pond' (*D. middendorffiana*, open square). Analytical error is 0.02 mm.

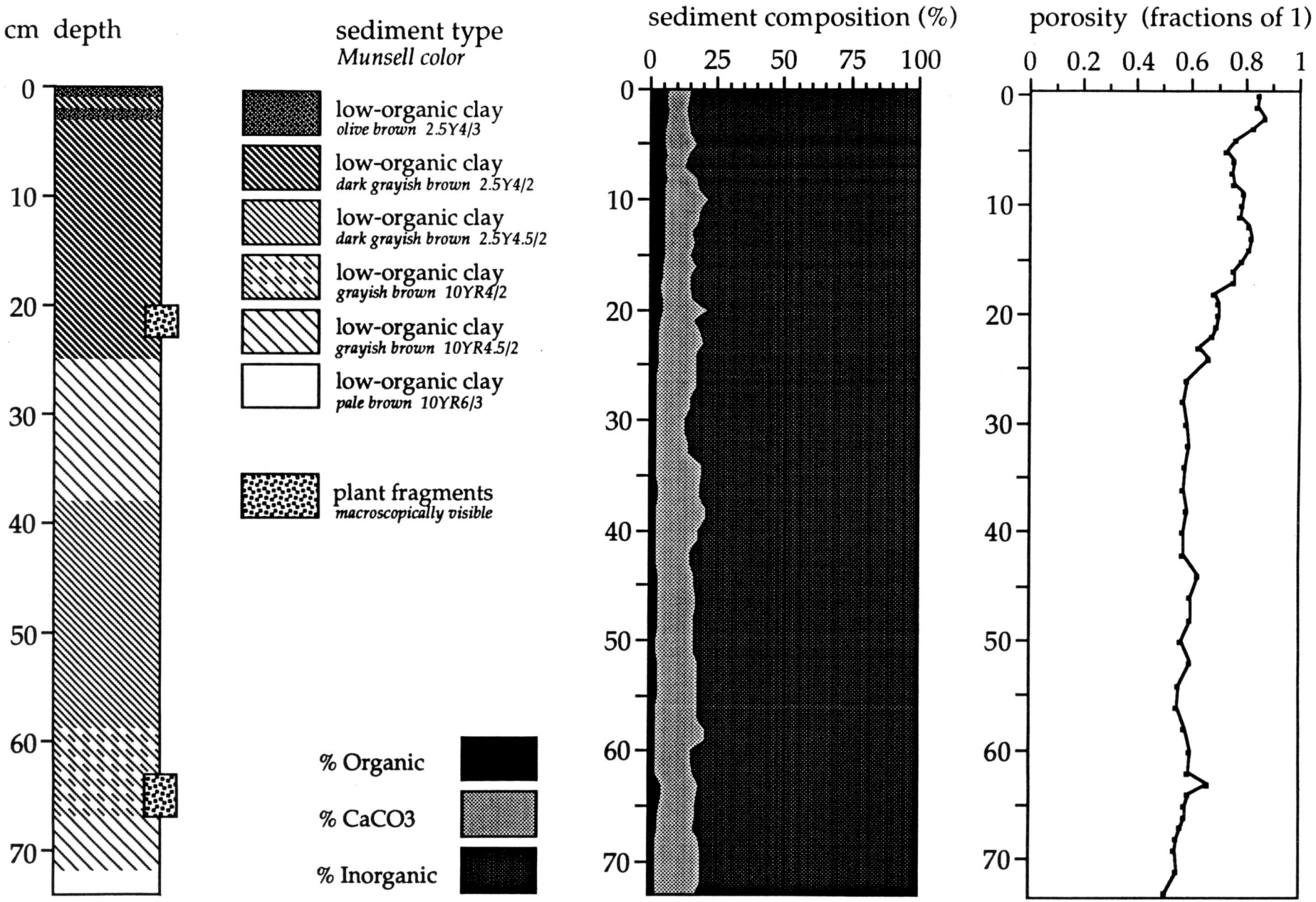


Fig. 4. Visual stratigraphy, dry-sediment composition and porosity of Avalanche
L ore AL91.1.

fragments around 65 cm and 21 cm depth are hardly discernible as peaks in the loss-on-ignition profile. The sediment is dense, with dry weight increasing from 0.4 g ml^{-1} at the surface to more than 1.2 g ml^{-1} below 27 cm depth. The porosity profile shows a subsurface minimum at 5-9 cm sediment depth, not accompanied with any significant change in lithology.

The logarithmic plot of ^{210}Pb-activity versus cumulative dry mass (Fig. 5a) is essentially straight, except for two large kinks. In the c.r.s. (constant rate of supply) model of ^{210}Pb-dating (Appleby and Oldfield, 1978), changes in slope of this plot represent shifts in sediment accumulation. Hence the general form of the activity plot suggests that the rate of sedimentation in Avalanche Lake has remained more or less constant over the past 100 years, except for two periods of significantly increased sedimentation. The plot of accumulation rate versus time (Fig. 5b) shows these relatively short periods to peak around 1910 and in the mid-1960's. The only human activity which may potentially affect runoff from forest soils near Avalanche Lake is the establishment and maintenance of park trails. There is no indication, however, that this activity could have significantly increased sedimentation rates in profundal areas of the lake. Quite probably the more recent peak in sedimentation rate relates to the catastrophic spring flood of 1964, when an unusually heavy winter snow pack was assaulted by warm rain during a June storm. Meltwater turned steep tributary creeks in all major valleys of Glacier National Park into "...raging torrents which tore away banks and spread over the countryside" (Williams, 1986). In sediments of Avalanche Lake deposited around and shortly after that time, there is apart from the subsurface porosity minimum no indication that the 1964 flood-water carried forest-floor detritus or other materials different from normal stream input. This observation is consistent with the notion that at all times most inorganic sedimentation in Avalanche Lake derives from the glacial debris that is continually melted out at the terminus of Sperry Glacier, rather than

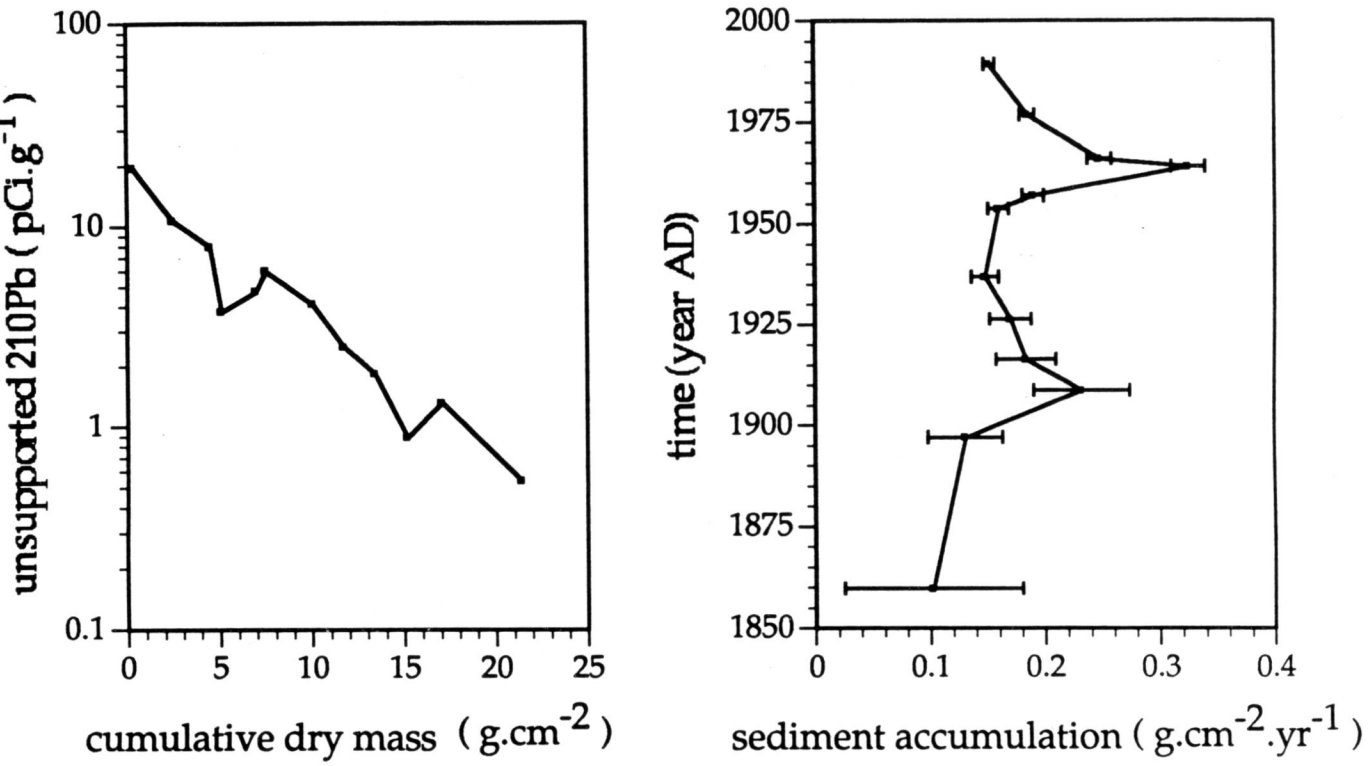


Fig. 5. a (left): Unsupported ^{210}Pb activity versus cumulative dry mass for core AL91.1; counting errors are generally smaller than the plotted symbols and are not shown. b (right): Dry-sediment accumulation rate versus time; error bars represent 1 SD propagated from counting uncertainty.

from forest soil around the lake. L. B. Sperry first suggested in 1894 that the slight milkiness of the water in Avalanche Lake must come from a then-undiscovered glacier (A. L. Sperry, 1938). Sperry Glacier has shrunk considerably since it was first mapped in 1901 (Johnson, 1980). Although the average annual recession and decrease in total area slowed after the mid-1940's, the overall recession of the glacier terminus in this century (ca. 700 m between 1913 and 1969) has allowed shallow pro-glacial lakes to form on the central deglaciated plain of the cirque, just upstream from Avalanche Lake (Fig. 2). We speculate that flushing of fine-grained glacial flour, which through the years had accumulated in these lakes, contributed significantly to peak sedimentation in Avalanche Lake during the 1964 flood. The origin of the peak in sedimentation which occurred earlier this century is unclear. It appears most likely that this peak too is caused by a temporary increase in sediment discharge from the Sperry Glacier, due to a similar flushing event or a change in sediment flux released from the glacier.

Lead-210 dating produced a continuous chronology for the upper portion of core AL91.1 (Fig. 7). Sediment deposition during this century totals 25.0 cm, corresponding to a mean annual accumulation of 2.72 mm wet sediment for the past 91 years. The Avalanche Lake sediment chronology is further constrained by historical wildfires. Fires burning forest in the Avalanche Lake basin can be expected to have left detectable sedimentary horizons with charcoal particles and mineral indicators of increased surface runoff and soil erosion. However, fires directly affecting the forest within the lake's catchment area have not occurred since 1517 AD (Fig. 2; Carl Key, Glacier National park, unpublished data). Dendro-chronology did document a series of forest fires that have occurred since that time in the Lake McDonald valley downstream from Avalanche Lake, within a few km from the lake. The high frequency with which wildfires burn forested slopes both within and in the vicinity of Glacier Park may result in a nearly continuous

atmospheric input of microscopic charcoal to Avalanche Lake sediments (cf. Tolonen, 1986). Depending on wind direction and strength, wildfires may also deliver airborne charred plant fragments as large as several centimeters to nearby lakes (Schaefer, 1976). Burzynski (1982) demonstrated that fragments larger than 237 μm can be easily distributed at least 800 m from the place of the fire. However, sieved organic residues of the Avalanche Lake sediment samples used for analysis of fossil zooplankton did not appear to contain much charcoal or charred particles larger than 105 μm. On the other hand, the fraction of organic material (by weight percentage) in these residues consisting of particles larger than 250 μm shows a downcore profile with two pronounced maxima and several minor ones (Fig. 6). The two largest peaks in the profile (20.5 % at 65 cm and 14.0 % at 21 cm depth, respectively; Appendix 4) correspond with the two horizons containing macroscopically visible plant fragments shown in Fig. 4. Coarse organic particles in the maxima are flaky fragments of terrestrial plants, with no obvious evidence of charring or burning. However, downcore extrapolation of the ^{210}Pb-derived average accumulation rate for this century strongly suggest that the maxima correlate with the documented fires of 1735 and 1913, which burned portions of the lower Avalanche Creek gorge just downstream from the lake, or nearby portions of the Lake McDonald valley (Fig. 2). The lack of an erosional signal in the sedimentary matrix suggests that the event did not affect the lake's catchment directly, and absence of evidence of charring suggests that the particles in the sediment were not airborne from the direction of a fire. We therefore resort to the speculation that the particles are derived from forest-floor detritus blown into Avalanche Lake from high-elevation areas of its catchment, dispersed by the strong draft winds that were channeled through the steep Avalanche Creek gorge to provide oxygen for a blazing wildfire nearby. Alternatively, production and wind-dispersal of forest-floor detritus in those years may have been unrelated to the fires itself, but due to

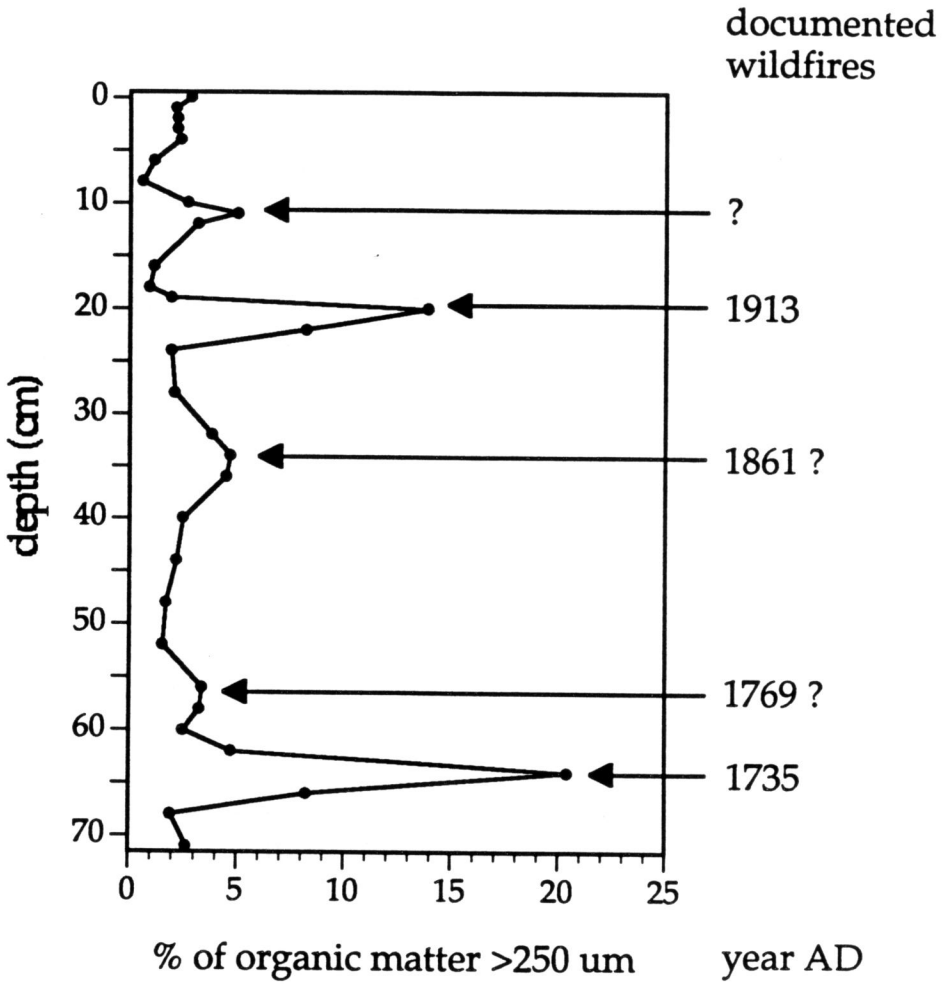


Fig. 6. Percentage of coarse (> 250 μm) plant fragments in the organic fraction of Avalanche Lake sediments, and correlation of the profile with documented wildfires.

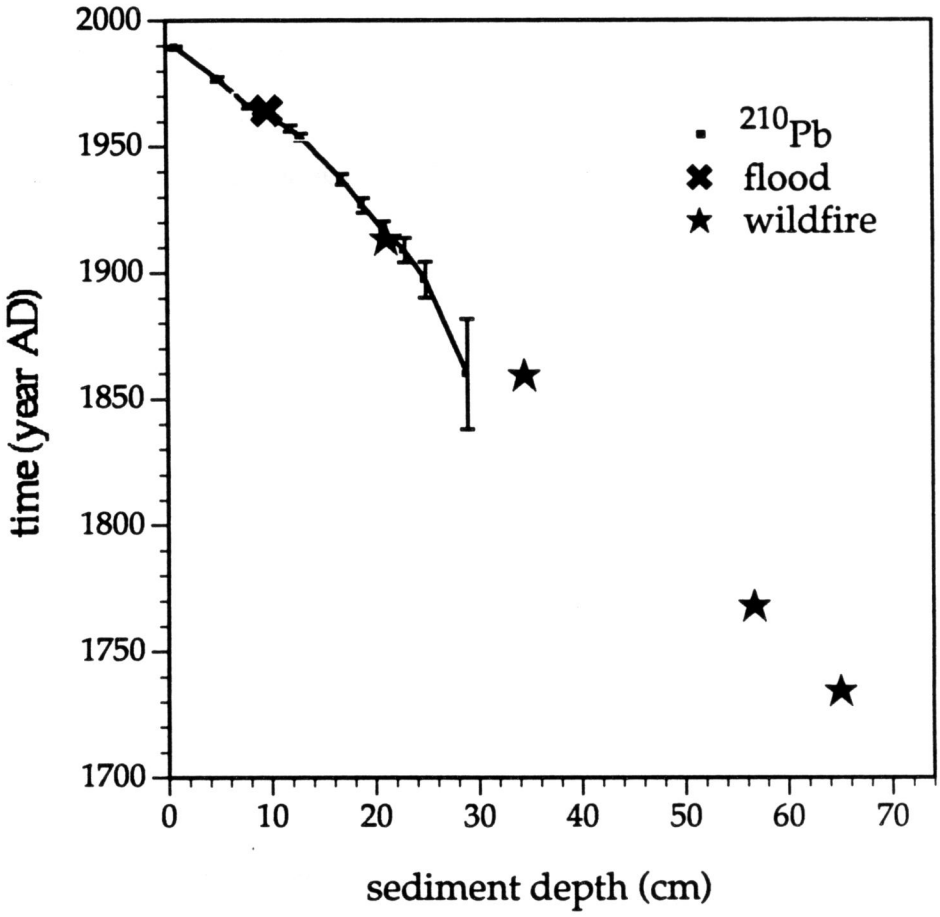


Fig. 7. Composite sediment chronology for core AL91.1, based on ^{210}Pb-dating, wildfire records, and a flood event.

conditions of exceptional summer drought which also makes the forest prone to burning. Two smaller highpoints in the curve (3.4 % at 57 cm and 4.7 % at 35 cm) are tentatively related to the fires of 1769 and 1861. A fifth maximum (5.0 % at 12 cm) could not be related to any of the known wildfires.

The ^{210}Pb-, flood-, and wildfire-chronologies are combined in a general sediment chronology for Avalanche Lake (Fig. 7). Extrapolation below 65 cm suggests that core AL91.1 covers lake history since about 1700 AD. Sedimentation rates in the profundal of Avalanche Lake appear to have remained fairly stable for the past three centuries, with an overall mean accumulation of 2.54 mm wet sediment per year.

5. IMPACT OF PREDATION BY CUTTHROAT TROUT ON ZOOPLANKTON COMMUNITY STRUCTURE IN GLACIER NATIONAL PARK

Interpretation of the Avalanche Lake record of fossil zooplankton in terms of trout population history assumes that vertebrate predation is the dominant factor structuring the lake's zooplankton community. Notwithstanding the numerous case studies and field experiments that demonstrate the pervasive importance of presence or absence of zooplanktivorous fish (cf. above), a large geographic survey in alpine and subalpine lakes of the Canadian Rocky Mountains (Anderson, 1974, 1980) suggests that the situation is more complex. For instance, although *Chaoborus* and large *Daphnia* spp. are both vulnerable to vertebrate predation, juveniles of the *Daphnia* may also be vulnerable to invertebrate predation by *Chaoborus* or predatory copepods. Persistence of *Daphnia* may thus depend on the particular combination of vertebrate and invertebrate predators present, including the trout, calanoid copepods, certain cyclopoid copepods, and *Chaoborus*, as well as the

availability of small cladocerans such as *Ceriodaphnia* and *Bosmina* as alternative prey for the trout. Anderson (1980) recognized several patterns and correlations in the co-occurrence or mutual exclusion of specific zooplankton groups in his large set of mountain lakes. Most notably, he observed that in the cutthroat trout lakes (in contrast with lakes occupied by brook trout, rainbow trout or Dolly Varden char, *Salvelinus malma*), large *Daphnia* spp. were almost as common in lakes with fish as in lakes without fish. However, Anderson only discussed correlations among the various biota, and did not systematically investigate the role of factors such as lake trophy and water transparency on zooplankton community structure. We have noticed in Glacier Park (Verschuren, unpublished) that the abundance of large *Daphnia* in cutthroat trout lakes is correlated with the existence of a sizable predation refuge (Shapiro, 1990). Vulnerable *Daphnia* and other large-bodied zooplankters can escape visual predation by fish if they stay below the illuminated zone of the upper water column (Zaret and Suffern, 1976; Wright et al., 1980). In deep, oligotrophic mountain lakes the size of this refuge is proportional to the relative depth of the well-oxygenated but poorly illuminated lower water column. We conclude, therefore, that the impact of predation by trout on *Daphnia* and *Chaoborus* in any particular lake may depend both on the composition of the remainder of the zooplankton and on certain characteristics of the lake's physical limnology. Consequently, if we want to interpret the Avalanche Lake record of fossil zooplankton in terms of trout population history, we need additional assurance that presence or absence of cutthroat trout is the overriding force in structuring zooplankton communities in headwater lakes of Glacier Park.

Qualitative analysis of modern late-summer zooplankton in Avalanche Lake and seven other headwater lakes in the Flathead River drainage of Glacier Park indicates that copepods dominate the majority of lakes sampled (Table 2). Copepods cannot be employed for the purpose of this study, however, because their remains

Table 2. Composition of late-summer zooplankton in selected lakes and ponds of Glacier National park

Lake	Avalanche	Trout	Snyder	Hidden	Fish	Upper Snyder	'Babbe'	'Hidden Pond'
Surface temperature (°C)	10.1	13.5	8.3	9.5	15.7	8.1	13.5	10.6
Sediment depth (cm)	0-1	1-3	1-3	0-2	3-5	1-3	1-3	1-3
Volume *Chaoborus* (ml)	5.00	4.13	4.39	10.61	5.02	5.88	5.94	6.41
Volume *Daphnia* (ml)	25.00	20.65	21.95	20.28	25.01	29.4	28.23	32.05
Trout fishery	Yes	Yes	Yes	Yes	Yes	No	No	No
Calanoida	+	a		a	c	+	a	a
Cyclopoida	a	+	+		+	+	+	+
Holopedium gibberum					c			
Daphnia rosea	**+ (1.4)**	**c (19)**	**+**		**c (99)**	**c (29)**	**+ (6)**	
D. middendorffiana	**+ (0.4)**		**+**					**c (20)**
Scapholeberis kingi			c					
Chaoborus americanus					**(21)**	**(1)**	**+ (5)**	
C. trivittatus					**(37)**	**(26)**		
C. flavicans					**+ (4)**			

Code: + = present, c = common, a = abundant in living late-summer zooplankton. Numbers in parentheses are the densities of remains of *Daphnia* spp. and *Chaoborus* spp. in surface-sediment death assemblages, expressed as the total number found in sample volumes as indicated in column 1.

do not survive well in the sediment record (Frey, 1964). Therefore detailed analysis of zooplankton composition inclusive of copepods is not considered pertinent to this study. Compared to copepods, cladocerans were rather scarce in the reference lakes. They were common in only three, and only in Upper Snyder Lake did they outnumber copepods. Apart from *Holopedium gibberum*, which is common in Fish Lake, and some *Scapholeberis kingi* in the littoral of Snyder Lake, *Daphnia* spp. were the only cladocerans present (Table 2). *D. rosea* occurs as the only species of its genus in Trout, Upper Snyder, Fish, and 'Babbe' lakes, *D. middendorffiana* is the only species in 'Hidden Pond', and both species were found in Avalanche and Snyder lakes. *Daphnia* ephippia were recovered in surface-sediment death assemblages in proportion to their abundance in the modern zooplankton (Table 2), with the exception of Snyder Lake, where *Daphnia* is rare and no ephippia were found. Remains of three species of *Chaoborus* were collected in the surface-sediment samples: *C. americanus* in Fish, Upper Snyder, and 'Babbe' lakes, *C. trivittatus* in Fish and Upper Snyder lakes, and *C. flavicans* in Fish Lake.

On the basis of abundance of *Daphnia* and *Chaoborus* remains in the modern death assemblages (Fig. 8), there appears to be a clear distinction between lakes with cutthroat trout and lakes without cutthroat trout, except for Fish Lake where trout are present but the zooplankton appears more typical of fish absence. Fish Lake is quite unlike any of the other reference lakes in being warm (surface temperature 15.7 °C in September 1991) and fringed by a quaking bog of *Sphagnum* and sedges along its northwestern shore. At present, Fish Lake is inhabited by a hybrid trout population (Marnell et al., 1987; Table 1). In view of the lack of a permanent inlet stream, it is hypothesized that the hybrid population is sustained by spawning activity in the lake itself, presumably near subsurface seepage inlets where detritus-free gravel beds may locally occur. On the other hand, fry and juvenile trout have not been observed in recent years (L. Marnell, Glacier National Park, pers.comm.).

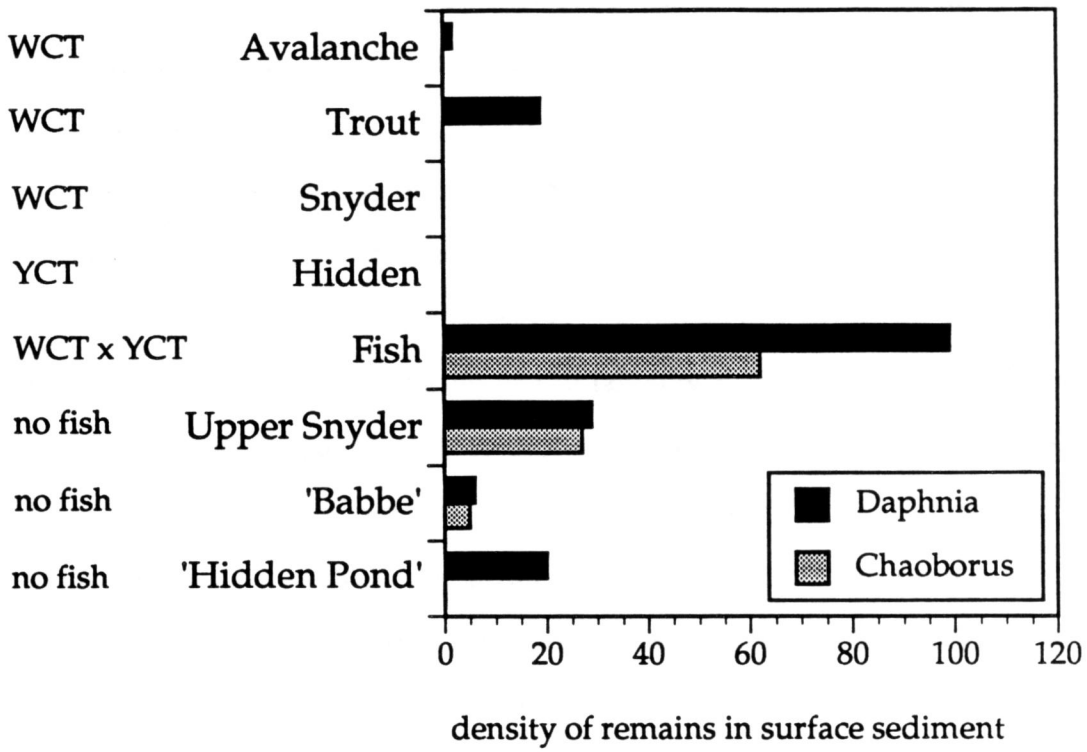


Fig. 8. Density of *Daphnia* ephippia (black columns) and *Chaoborus* mandibles (stippled columns) in the surface sediment of Avalanche lake and seven reference lakes in Glacier Park. See text for information on equivalency among samples.

Also, it seems possible that unlike the situation in colder, less productive headwater lakes, adult cutthroat trout in Fish Lake preys on aquatic insect larvae rather than on zooplankton. The composition of the modern zooplankton, and the abundance of *Chaoborus* and *Daphnia* remains in the sediment (Fig. 8), certainly suggest that predation pressure is minimal. If it is true that the trout in Fish Lake does not depend on zooplankton, then Fish Lake must be considered fishless for the purpose of this study. With this qualification, the distinction between reference lakes with trout and those without trout is more tenable and statistically significant at the 5% level (Kruskal-Wallis one-way AOV: $p = 0.0421$). *Chaoborus* occurs in three out of four fishless lakes, but in none of the lakes with fish; *Daphnia* occurs in all four of the fishless lakes, but in only two of the lakes with fish, and then in fairly low numbers (Table 2). Co-occurrence of *Daphnia* with trout in these lakes can be explained by variation in the potential size of a predation refuge, which in the deep lakes is inversely correlated with water transparency (thickness of the euphotic zone) and increases in the sequence Hidden Lake - Avalanche Lake - Trout Lake. Overall, the results of this comparative study suggest that predation by trout constitutes a major and possibly the most important factor structuring zooplankton communities in alpine and subalpine headwater lakes of Glacier Park. Consequently, any changes in the historical status of the cutthroat trout fishery in Avalanche Lake are likely to have resulted in significant changes in composition of the zooplankton, and these changes can be traced through analysis of fossil zooplankton assemblages in the sediment record.

6. HISTORY OF THE ZOOPLANKTON, AND IMPLICATIONS FOR THE STATUS OF CUTTHROAT TROUT IN AVALANCHE LAKE

Remains of *Chaoborus* were absent in the surface sediments of Avalanche Lake and nine deeper levels spaced evenly along the core profile. Because the volume of sediment analyzed at each level had been made equivalent to the volume of the surface-sediment samples in the comparative study (Appendix 5), we must conclude that *Chaoborus* probably has not occurred for any prolonged period in Avalanche Lake since at least 1700 AD. Thirty-six sediment samples in the core profile were scanned for ephippia of planktonic Cladocera. Apart from a single ephippium of *Simocephalus vetulus* (at 3 cm depth), only *Daphnia* were found. Ephippia of *D. rosea* and *D. middendorffiana* were recovered from 13 levels, mostly concentrated near the sediment surface and in a narrow horizon at 14-19 cm depth (Fig. 9). *D. rosea* is most common in the subsurface samples, while *D. middendorffiana* appears to have dominated the earlier peak population. The maximum count of 127 ephippia at 16 cm depth corresponds to an annual flux (calculated with a 2.5 mm yr^{-1} wet sedimentation rate) of 17,000 preserved ephippia per m^2. In comparison, the modern flux is about 1,200 ephippia m^{-2} yr^{-1}. No ephippia were recovered from any level below 19 cm depth. We cannot exclude the possibility that the sudden appearance of ephippia at 19 cm depth would be due to a temporal shift in sedimentation conditions prevailing near the coring site at the time the ephippia were buried. We consider this unlikely, because a shifting sedimentation pattern would likely have been accompanied by concurrent changes in other components of the stratigraphy, and also would have concentrated other organic particles of similar weight together with the ephippia, which is not the case (cf. Fig. 4). The increase in ephippia from none at 7 cm depth to 9 in the surface sample may reflect a slight but real increase in *Daphnia* in the last two decades. Alternatively, the downward

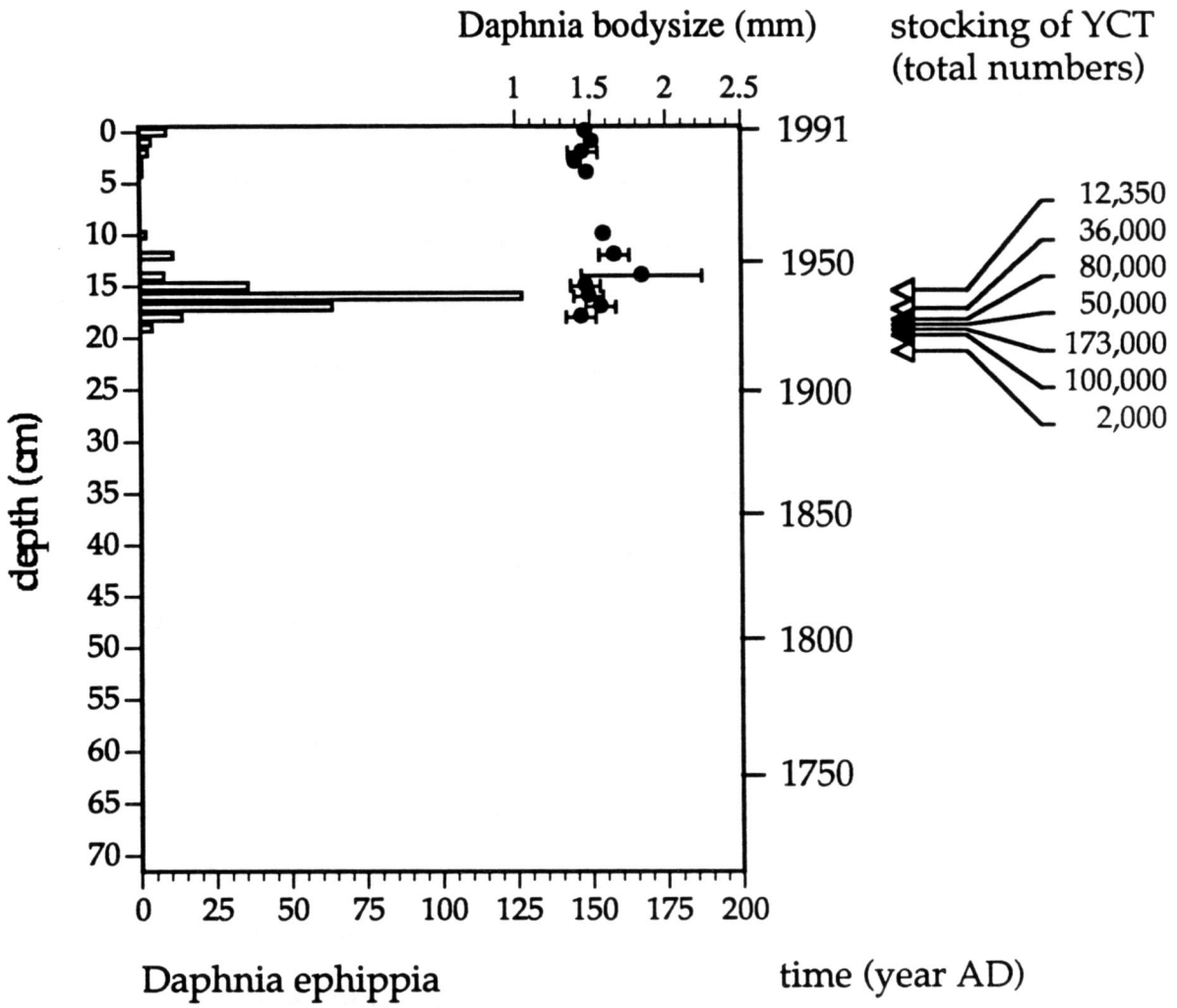


Fig. 9. Density of *Daphnia* ephippia in Avalanche Lake sediments, evolution in average size of ephippial females since the late 1920's, and stocking record of non-native Yellowstone cutthroat trout.

decrease in preserved ephippia may represent the natural breakdown and loss of buried ephippia through shredding by benthic invertebrates. The latter explanation would suggest that much higher numbers of ephippia must be deposited in order for a significant fraction to escape consumption. Taking the possibility of post-burial loss into account, we conclude that populations of *Daphnia* in Avalanche Lake have remained at or below present low densities through most of the lake's history since about 1700 AD, indicative for the original and continued presence of cutthroat trout.

Several hypotheses can be entertained to explain the peak in ephippia at 19-14 cm depth, which suggests explosive development of *Daphnia* populations in the 1930's and (possibly) early 1940's. The peak in ephippia may to some extent have been spread vertically in the sediment profile due to downmixing caused by bioturbation. However, the ^{210}Pb-profile near the sediment surface does not show evidence of the mixed layer that would result if such reworking was occurring in Avalanche Lake today. One scenario links the relatively short period of abundant *Daphnia* to a hypothetical forest fire, through nutrient enrichment of surface waters by airborne ash particles; such temporary enrichment has been observed in Glacier Park streams draining forested areas burned in the 1988 Red Bench fire (Spencer and Hauer, 1990). This enrichment would have boosted primary production in Avalanche Lake, which in turn would have promoted zooplankton development. The trout population would adjust to this higher food availability only several years later, allowing *Daphnia* to maintain high densities for several consecutive years. However, at least 10 years lapsed between the last major fire of 1913 (particulate peak at 20 cm depth) and the *Daphnia* maximum (peak at 16 cm), by which time any possible enrichment would already long have returned to background levels (Schindler et al., 1980; Tarapchak and Wright, 1986). This scenario also does not explain why similar enrichment effects on zooplankton did not occur after any of the other major fires recorded in the Avalanche Lake sediments.

Accepting the conclusion reached above that *Daphnia* populations in Glacier Park headwater lakes are primarily regulated by zooplanktivory of resident trout, it appears most likely that their peak development in Avalanche Lake during the 1930's must be related to temporary relaxation of predation pressure normally exercised by the native trout. There is no indication that this relaxation also resulted in a larger average bodysize in *Daphnia* (Fig. 7), which was observed by Kitchell and Kitchell (1980) in a similar case of reduced predation. The bodysize value obtained at 14 cm depth is suspect because of large variability in a small sample (n = 2; Appendix 6), and the value obtained from the more reliable sample at 13 cm depth is not significantly different from the overall mean of 1.47 mm. Thus *Daphnia* body size has remained fairly stable in Avalanche Lake since at least the 1920's, before the population explosion.

A first possibility is relaxation of predation pressure during the summer following a severe winterkill of the planktivorous fish (Shapiro, 1980). In the deep, oligotrophic and well-oxygenated Avalanche Lake, however, a winterkill eliminating the resident cutthroat trout can be excluded. A second possibility is temporary overharvesting by sport fishing. However, although the repeated stocking of non-native Yellowstone cutthroat trout in Glacier Park lakes was intended to promote sport fishing by enhancing the local stocks, there is no indication that fish stocking caused any substantial increase in fishing pressure, nor that the trout in Avalanche Lake were overexploited at any time since the creation of Glacier National Park in 1910 (L. Marnell, pers. comm.). Still, the development of a large *Daphnia* population coincident with and directly following the extended period of stocking (Fig. 7), and not at any other time in the last three centuries, strongly suggests a causal link.

Between 1915 and 1943, a total of about 450,000 juvenile Yellowstone cutthroat trout were added to the Avalanche Lake fishery. Almost 90 % of this

number were planted in just four consecutive years between 1927 and 1931 (Fig. 9). Close analysis of the sediment record reveals that, within the timing uncertainty of ± 2.5 years inherent to the ^{210}Pb-derived chronology, the explosive development of *Daphnia* started immediately following this series of four large stocking efforts. Also, the population density of *Daphnia* was brought back to the historic (i.e. pre-stocking) level within only a few years after the stocking attempts were terminated in 1943. Apparently, the massive stocking with zooplanktivorous juvenile trout caused a temporary upset of the lake's trophic equilibrium, setting in motion a chain of events that eventually allowed *Daphnia* to expand.

Considering the apparent complexity of interactions between salmonids and the various groups of carnivorous and herbivorous zooplankton in headwater lakes (Anderson, 1980), it seems plausible that the addition of trout was beneficial for *Daphnia* through selective removal by the trout of a specialized invertebrate predator on *Daphnia*. This scenario would require that the hypothetical predator is more susceptible to fish predation than *Daphnia*. Northcote et al. (1978) provided evidence that removal of *Chaoborus* by cutthroat trout may lead to increased abundance of crustacean macrozooplankton such as *Daphnia*. However, the complete absence of *Chaoborus* from the Avalanche Lake record indicates that it has always been excluded from the lake through predation by the native trout. Therefore, *Chaoborus* cannot have played a role in the events which followed the addition of non-native trout. Predatory copepods, on the other hand, are less susceptible to fish predation than *Daphnia*, due to their superior escape ability (Confer and Blades, 1975).

We speculate that the *Daphnia* expansion is a direct response to temporary relaxation of vertebrate predation. The lack of hybridization of native westslope cutthroat with the introduced Yellowstone cutthroat (Marnell et al., 1987), despite massive stocking, indicates that most if not all of the stocked trout left Avalanche

Lake by downstream migration before reaching sexual maturity (L. Marnell, pers. comm.). Yet in the few years that juvenile non-native trout roamed the lake, their intensive grazing on zooplankton may have depleted the local food base, daphnids as well as cyclopoid and calanoid copepods, on which the native trout depends. Repetition of this process after each of the massive plantings between 1927 and 1931 may have resulted in a crash or at least severe depression of the native fishery in the early 1930's (L. Marnell, pers. comm.), hence allowing large zooplankters such as *Daphnia* to expand and reach densities similar to those found in fishless lakes. With the ending of resource competition in the years after 1943, gradual recovery of the native trout population over the next decade resulted in reduction of *Daphnia* back to its historical level, in equilibrium with a secure low-density fishery of westslope cutthroat trout. In this context, the occurrence of ephippia in isolated horizons at 10 and 12 cm, which correspond to the early 1950's, may reflect the uneven age structure of the trout population at an early stage of its recovery.

A more detailed analysis of the evidence for resource competition, which roots in differences in life history and behavioral biology of the two trout subspecies, is outside the scope of this report, and the real course of events may only be elucidated by directed fisheries research. We note, however, that the immediate and significant response of *Daphnia* to relaxation of predation pressure subscribes our main conclusion that native trout have played a distinct role in structuring the zooplankton community of Avalanche lake since at least 1700 AD, indicative of the indigenous nature of this population of westslope cutthroat trout.

8. CONCLUSION AND SUGGESTIONS FOR A FOLLOW-UP STUDY

Based on the difficult access to Avalanche Lake for naturally dispersing fish and on the absence of other native fish species, Marnell et al. (1987) speculated that the trout which now inhabits the lake, although native to the area, might have been planted there by early entrepreneurs sometime in the late 1800's or early 1900's. These authors further identified four other isolated headwater lakes in Glacier Park where native trout was suspected to be non-indigenous (i.e. introduced): Upper and Lower Howe Lakes, Snyder Lake, and Fish Lake. In this study we have employed paleolimnological techniques specifically to assess the historical status of the trout fishery in Avalanche Lake. The main conclusion reached is that the native cutthroat trout has most probably inhabited the lake for the past three centuries, and is therefore likely to be indigenous. Application of paleolimnology to the fishery histories of a set of headwater lakes in variable degree of isolation would yield new insight in the dispersal capacity of salmonids and frequency of ingression to hydrologically remote lakes in mountainous regions.

Notwithstanding the additional support derived from the comparative survey of Glacier Park lakes with or without fish, we stress here that the results of this study are partly based on the absence of key organisms, which constitutes negative evidence. In view of possible application to other problems of historical ecology of trout fisheries, it would be worthwhile to pursue validation of this unique paleolimnological method as a fisheries research technique, by reconstructing the history of zooplankton populations in lakes where the stocking history is already known. Hidden Lake in the Middle Fork Flathead River drainage, and Red Eagle Lake in the Upper Missouri River drainage are at present considered in that respect.

8. ACKNOWLEDGMENTS

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Depth	Wet (g/cc)	Dry (g/cc)	Dry/Wet	% Organic	% CaCO3	% Inorg.	Porosity
1	1.2160	0.3662	0.3012	6.50	9.50	84.00	0.8498
2	1.2750	0.4304	0.3376	6.25	8.77	84.98	0.8446
3	1.2502	0.3817	0.3053	6.50	8.10	85.40	0.8685
4	1.2978	0.4718	0.3635	5.91	9.01	85.07	0.8260
5	1.4111	0.6441	0.4565	5.28	10.20	84.52	0.7670
6	1.4298	0.6976	0.4879	5.22	12.81	81.97	0.7322
7	1.4376	0.6832	0.4752	5.65	9.15	85.20	0.7544
8	1.4220	0.6691	0.4705	5.02	8.94	86.04	0.7529
9	1.4229	0.6631	0.4660	5.82	12.21	81.97	0.7598
10	1.3586	0.5648	0.4157	4.92	13.57	81.51	0.7938
11	1.3851	0.6028	0.4352	5.21	17.16	77.63	0.7823
12	1.3676	0.5869	0.4291	5.16	13.87	80.97	0.7807
13	1.3443	0.5337	0.3970	5.10	13.63	81.27	0.8106
14	1.3124	0.4896	0.3731	5.31	11.15	83.54	0.8228
15	1.3276	0.5124	0.3860	5.29	11.80	82.91	0.8152
16	1.3693	0.5835	0.4261	5.18	10.64	84.19	0.7858
17	1.4555	0.6991	0.4803	4.52	13.66	81.82	0.7564
18	1.4423	0.6821	0.4729	4.65	11.10	84.25	0.7602
19	1.5834	0.8992	0.5679	3.71	11.94	84.35	0.6842
20	1.5525	0.8490	0.5469	4.20	11.97	83.82	0.7035
21	1.5357	0.8319	0.5417	4.59	17.63	77.78	0.7038
22	1.5460	0.8548	0.5529	3.85	13.30	82.85	0.6912
23	1.5829	0.9037	0.5709	3.23	16.18	80.59	0.6792
24	1.6574	1.0296	0.6212	3.12	17.27	79.61	0.6278
25	1.6032	0.9387	0.5855	3.42	14.80	81.78	0.6645
27	1.7429	1.1527	0.6614	2.49	15.25	82.26	0.5902
29	1.7553	1.1782	0.6712	2.50	13.57	83.93	0.5771
31	1.7331	1.1380	0.6566	2.50	11.33	86.17	0.5951
33	1.7225	1.1256	0.6535	2.67	12.06	85.26	0.5969
35	1.7405	1.1576	0.6651	2.61	17.09	80.30	0.5829
37	1.7298	1.1563	0.6685	2.77	16.22	81.01	0.5735
39	1.7528	1.1627	0.6633	2.46	18.76	78.78	0.5901
41	1.7640	1.1872	0.6730	2.62	16.13	81.25	0.5768
43	1.7608	1.1848	0.6729	2.64	13.30	84.06	0.5760
45	1.6825	1.0552	0.6272	2.97	13.92	83.11	0.6273
47	1.7201	1.1208	0.6516	2.78	14.79	82.43	0.5993
49	1.6972	1.0932	0.6441	2.92	14.60	82.48	0.6040
51	1.7714	1.2060	0.6808	2.60	14.82	82.58	0.5654
53	1.6848	1.0840	0.6434	3.39	14.98	81.64	0.6008
55	1.7418	1.1816	0.6784	2.90	15.57	81.53	0.5602
57	1.7933	1.2426	0.6929	2.70	16.05	81.25	0.5507
59	1.7574	1.1784	0.6705	2.65	19.07	78.29	0.5790
61	1.7010	1.0988	0.6460	2.65	13.91	83.44	0.6022
63	1.7181	1.1242	0.6543	2.64	14.64	82.71	0.5939
64	1.6148	0.9500	0.5883	4.59	14.70	80.71	0.6648
65	1.6494	1.0506	0.6370	4.18	14.22	81.60	0.5988
66	1.7372	1.1586	0.6669	3.52	14.19	82.29	0.5786
67	1.7507	1.1723	0.6696	3.36	14.84	81.80	0.5784
68	1.8008	1.2330	0.6847	2.94	14.39	82.68	0.5678
69	1.7929	1.2418	0.6926	2.50	16.59	80.91	0.5511
70	1.7956	1.2507	0.6965	2.66	17.22	80.12	0.5449
72	1.8094	1.2597	0.6962	2.48	17.87	79.65	0.5497
74	1.7769	1.2687	0.7140	2.44	15.34	82.22	0.5082

Top of Interval (cm)	Base of Interval (cm)	Cum. Dry Mass (g/cm2)	Unsup. Activity (pCi/g)	Error of Unsup. Act. (±s.d.)	Cum. Act. below Int. (pCi/cm2)	Age: Base of Int. (yr)	Error of Age (±s.d.)	Date A.D.	Sediment Accum. (g/cm2 yr)	Error of Sed. Accum. (±s.d.)
0	1	0.3662	19.3332	0.5420	89.3954	2.45	0.66	1989.3	0.1524	0.00467
4	5	2.5258	10.6902	0.3536	60.6172	14.92	0.80	1976.8	0.1854	0.00640
7	8	4.5081	7.9072	0.2550	43.2306	25.78	1.00	1965.9	0.2477	0.01052
8	9	5.1712	3.7476	0.1594	40.7456	27.68	1.04	1964.0	0.3249	0.01477
11	12	7.0081	4.7345	0.1438	32.6909	34.75	1.24	1957.0	0.1903	0.00933
12	13	7.5418	5.9758	0.2253	29.5016	38.05	1.35	1953.7	0.1602	0.00888
16	17	10.0901	4.0903	0.1795	17.4560	54.90	2.14	1936.8	0.1484	0.01173
18	19	11.7885	2.4931	0.1323	12.6341	65.28	2.89	1926.4	0.1701	0.01799
20	21	13.4860	1.8391	0.1177	9.2411	75.33	3.91	1916.4	0.1838	0.02612
22	23	15.2575	0.8808	0.0931	7.2968	82.91	4.92	1908.8	0.2323	0.04193
24	25	17.1174	1.3121	0.0833	5.0625	94.65	7.04	1897.1	0.1311	0.03250
28	29	21.4710	0.5366	0.0964	1.5836	131.97	21.85	1859.7	0.1028	0.07738

Supported Pb-210: 1.7855 ± 0.0418 pCi/g

Number of Supported Samples: 3

Cum. Unsup. Pb-210: 96.4752 pCi/cm2

Unsup. Pb-210 Flux: 3.0865 pCi/cm2 yr

Taxon	Origin	Ephip L (mm)	Body L (mm)	Ephip/Body
D.rosea	Trout Lake	0.96	1.90	0.505
D.rosea	Trout Lake	0.90	1.80	0.500
D.rosea	Snyder Lake	0.96	1.92	0.500
D.rosea	Fish Lake	0.80	1.54	0.519
D.rosea	Upper Snyder L	1.04	2.00	0.520
D.rosea	Upper Snyder L	1.02	1.94	0.526
D.rosea	Upper Snyder L	0.92	1.78	0.517
D.rosea	Upper Snyder L	0.94	1.84	0.511
D.rosea	Upper Snyder L	0.84	1.62	0.519
D.rosea	Upper Snyder L	0.86	1.68	0.512
D.middendorffiana	Hidden Pond'	1.00	1.88	0.532
Mean		0.93	1.81	0.515

Daphnia	Depth	Wet (g/cc)	Dry (g/cc)	% Org.	Vol. (cc)	Organic (g)	Wet (g)	250um (g)	% Coarse	Depth
9	1	1.2160	0.3662	6.50	**25.00**	**0.5951**	30.40	0.0171	2.87	1
4	2	1.2750	0.4304	6.25	11.06	**0.2975**	14.10	0.0065	2.18	2
3	3	1.2502	0.3817	6.50	23.99	**0.5951**	29.99	0.0132	2.22	3
1	4	1.2978	0.4718	5.91	21.34	**0.5951**	27.70	0.0133	2.23	4
1	5	1.4111	0.6441	5.28	17.50	**0.5951**	24.69	0.0141	2.37	5
0	7	1.4376	0.6832	5.65	7.71	**0.2975**	11.08	0.0034	1.14	7
0	9	1.4229	0.6631	5.82	15.42	**0.5951**	21.94	0.0035	0.59	9
2	11	1.3851	0.6028	5.21	9.47	**0.2975**	13.12	0.0081	2.72	11
0	12	1.3676	0.5869	5.16	9.82	**0.2975**	13.43	0.0150	5.04	12
11	13	1.3443	0.5337	5.10	21.86	**0.5951**	29.39	0.0190	3.19	13
0	14	1.3124	0.4896	5.31	5.72	**0.1488**	7.51			14
8	15	1.3276	0.5124	5.29	5.49	**0.1488**	7.29			15
36	16	1.3693	0.5835	5.18	4.92	**0.1488**	6.74			16
127	17	1.4555	0.6991	4.52	18.83	**0.5951**	27.41	0.0068	1.14	17
64	18	1.4423	0.6821	4.65	4.69	**0.1488**	6.77			18
14	19	1.5834	0.8992	3.71	8.92	**0.2975**	14.12	0.0028	0.94	19
4	20	1.5525	0.8490	4.20	8.34	**0.2975**	12.95	0.0058	1.95	20
0	21	1.5357	0.8319	4.59	15.58	**0.5951**	23.93	0.0829	13.93	21
0	23	1.5829	0.9037	3.23	10.19	**0.2975**	16.13	0.0245	8.24	23
0	25	1.6032	0.9387	3.42	18.54	**0.5951**	29.72	0.0117	1.97	25
0	29	1.7553	1.1782	2.50	20.20	**0.5951**	35.46	0.0126	2.12	29
0	33	1.7225	1.1256	2.67	19.80	**0.5951**	34.11	0.0230	3.86	33
0	35	1.7405	1.1576	2.61	9.85	**0.2975**	17.14	0.0140	4.71	35
0	37	1.7298	1.1563	2.77	18.58	**0.5951**	32.14	0.0269	4.52	37
0	41	1.7640	1.1872	2.62	19.13	**0.5951**	33.75	0.0149	2.50	41
0	45	1.6825	1.0552	2.97	18.99	**0.5951**	31.95	0.0131	2.20	45
0	49	1.6972	1.0932	2.92	18.64	**0.5951**	31.64	0.0101	1.70	49
0	53	1.6848	1.0840	3.39	16.19	**0.5951**	27.28	0.0092	1.55	53
0	57	1.7933	1.2426	2.70	17.74	**0.5951**	31.81	0.0203	3.41	57
0	59	1.7574	1.1784	2.65	9.53	**0.2975**	16.74	0.0098	3.29	59
0	61	1.7010	1.0988	2.65	20.44	**0.5951**	34.76	0.0151	2.54	61
0	63	1.7181	1.1242	2.64	10.02	**0.2975**	17.22	0.0142	4.77	63
0	65	1.6494	1.0506	4.18	13.55	**0.5951**	22.35	0.1217	20.45	65
0	67	1.7505	1.1723	3.36	7.55	**0.2975**	13.22	0.0246	8.27	67
0	69	1.7929	1.2418	2.50	19.17	**0.5951**	34.37	0.0116	1.95	69
0	72	1.8094	1.2597	2.48	19.05	**0.5951**	34.47	0.0159	2.67	72