American Fisheries Society Symposium 37:XXX–XXX, 2003

Hydrologic and Geomorphic Effects of Beaver Dams and Their Influence on Fishes

MICHAEL M. POLLOCK, MORGAN HEIM, AND DANIELLE WERNER

National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center
2725 Montlake Boulevard E., Seattle, Washington 98112, USA

Abstract.—Beaver dams alter the hydrology and geomorphology of stream systems and affect habitat for fishes. Beaver dams measurably affect the rates of groundwater recharge and stream discharge, retain enough sediment to cause measurable changes in valley floor morphology, and generally enhance stream habitat quality for many fishes. Historically, beaver dams were frequent in small streams throughout most of the Northern Hemisphere. The cumulative loss of millions of beaver dams has dramatically affected the hydrology and sediment dynamics of stream systems. Assessing the cumulative hydrologic and geomorphic effects of depleting these millions of wood structures from small and medium-sized streams is urgently needed. This is particularly important in semiarid climates, where the widespread removal of beaver dams may have exacerbated effects of other land use changes, such as livestock grazing, to accelerate incision and the subsequent lowering of groundwater levels and ephemeralization of streams.

Introduction

In most of the temperate Northern Hemisphere, beaver historically altered low-gradient, small-stream ecosystems by constructing millions of dams made primarily of wood. Almost every northern temperate ecosystem that had trees or shrubs growing along streams also once had beaver dams. In Eurasia, evidence of beaver has been found in streams as far south as Iraq and Turkey, in the Arctic, and stretching from Scotland in the west to Kamchatka in the east (Figure 1; Halley and Rosell 2002). In North America, beaver were once found far south into the arid environments of Arizona and northern Mexico along rivers such as the San Pedro, Colorado, and the Rio Grande (Pattie 1833; Leopold 1972; Fredlake 1997) and occupied all biomes north of the border from coast to coast, except for the Arctic, peninsular Florida, and the dry Great Basin and desert country of Nevada and southern California (Figure 1; Jenkins 1979).

Historically, beaver dams created streams systems with slow, deep water and floodplain wetlands dominated by emergent vegetation and shrubs. Geomorphology and plant communities of small low-gradient streams were much changed throughout much of the Northern Hemisphere after reduction of beaver populations (Rea 1983; Naiman et al. 1988). In both Eurasia and North America, beaver populations have generally declined as human populations have increased. In both continents, only small populations survived by the end of the 19th century (Naiman et al. 1988; MacDonald et al. 1995; Nolet and Rosell 1998; Halley and Rosell 2002). The primary reasons for the declines were that people trapped beavers either because they were resources for fur or oil or competitors for productive valley bottom lands (MacDonald et al. 1995; Mackie 1997; Halley and Rosell 2002). More recently, however, there has been widespread recognition that beaver dams play a vital role in maintaining and diversifying stream and riparian habitat (Naiman et al. 1988; Pollock et al. 1994; Gurnell 1998; Collen and Gibson 2001). In the past century, land managers throughout the Northern Hemisphere have attempted to reintroduce beaver in areas where they have been extirpated. Today, beaver populations are rebounding throughout North America, with the population estimated to be about 10 million and reoccupying most of its former range (Naiman et al. 1988). Throughout Eurasia, recovery has been slower, with the Eurasian beaver population be-

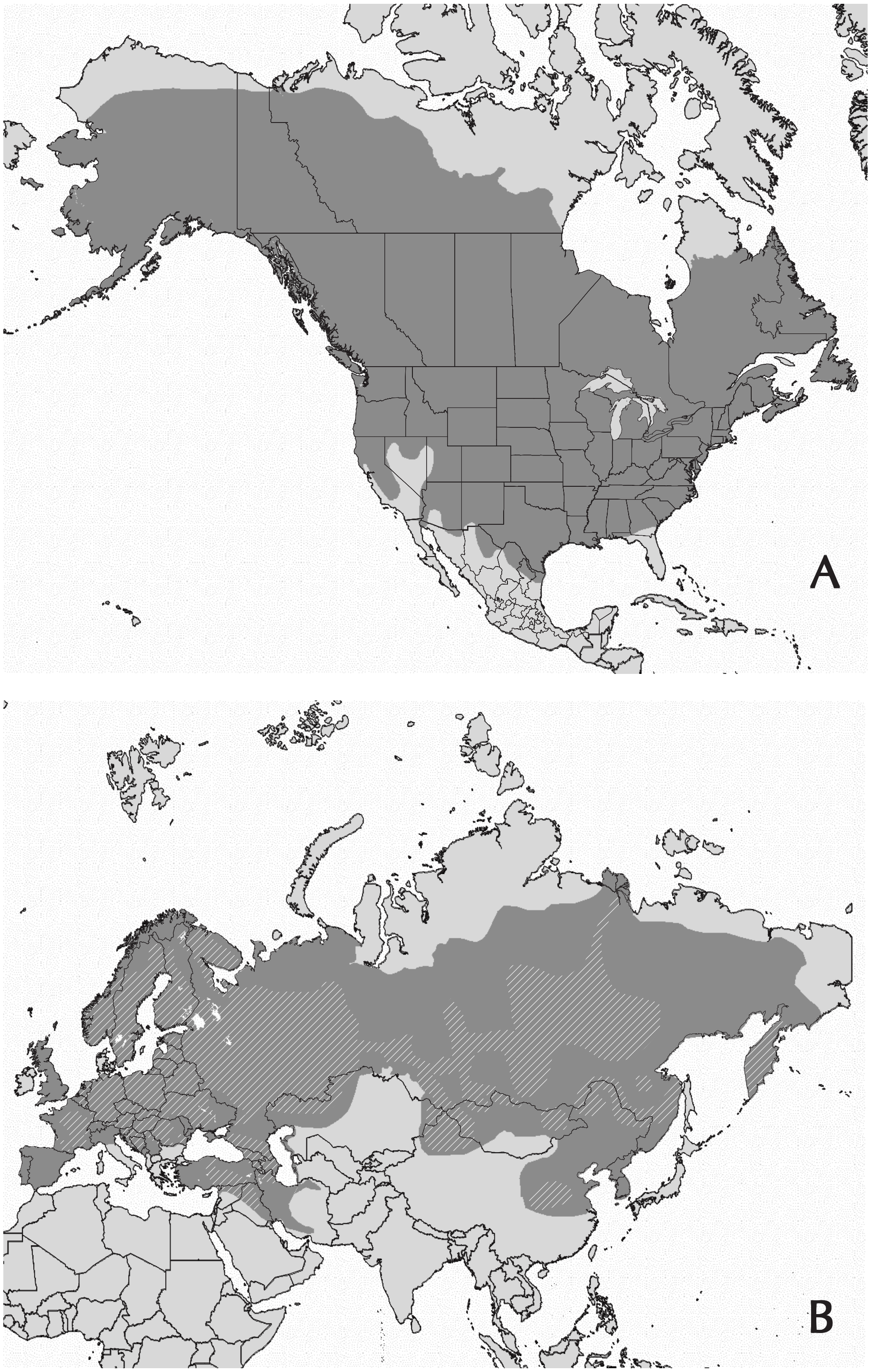

FIGURE 1. Estimated current and historic distribution of beaver in North America (A) and Eurasia (B). Isolated populations in peninsular Florida and Southern California are not shown. In Eurasia, cross hatching delineates current distribution. In North America, the current and historic distributions are approximately coincidental. (Based on Jenkins 1979; Halley and Rosell 2002; MacDonald et al. 1995).

tween a half to one million, with large geographic areas where no beaver are present or where the current status is unknown (Halley and Rosell 2002).

North American beaver have also become established in regions outside their geographic range, such as the Tierra del Fuego region of Argentina and Chile where they are spreading rapidly (Jaksic et al. 2002). The current beaver population in Tierra del Fuego is estimated to be around 70,000 (Jaksic et al. 2002). Several North American beaver populations have also been established in Europe prior to the recognition of the Eurasian and North American beavers as separate species (Figure 1; Nolet and Rosell 1998; Halley and Rosell 2002). In such areas, beaver are exotic species and may have undesirable impacts on native species and ecosystem processes.

The primary instream habitat value of beaver dams is that they impound water to form large pools and ponds. These impoundments trap sediment, help to create productive and diverse wetland environments on adjacent floodplains, improve water quality, and facilitate groundwater recharge. All these functions are ultimately the result of the dams reducing stream velocities and spreading water over a large surface area.

Here, we review how beaver dams have altered stream hydrology and morphology, both in the past when dams were much more abundant and under current conditions. We estimate the historic abundance and location of beaver dams in watersheds throughout the Northern Hemisphere, assess the cumulative hydrologic effects of multiple beaver dams, evaluate the geomorphic consequences of those effects, and examine what influence these physical effects have on fishes. Most of the scientific literature on the ecological effects of beaver dams come from studies of the North American beaver while literature on the ecological effects of the Eurasian beaver dams are rarer, if for no other reason than that the Eurasian beaver itself is still quite rare throughout much of its former range. However, available studies indicate that the two species are quite similar in most respects, though some evidence suggests the Eurasian beaver builds fewer dams and lodges and has a lower reproductive rate (Danilov and Kan'shiev 1983; Collen and Gibson 2001; Halley and Rosell 2002). Studies of the hydrologic and geomorphic effects of North American beaver dams should be applicable to Eurasian beaver, but studies of the effects on fishes may not be directly applicable, depending on what fish species were studied. Reviews of the many additional ecosystem impacts of beaver that are not directly related to their dams, such as their effects on riparian communities, can be found elsewhere (Naiman et al. 1988, 1994; Pollock et al. 1994; Gurnell 1998; Collen and Gibson 2001).

The Historical Abundance of Beaver Dams

Contemporary studies of protected or remote beaver populations support the contention that, historically, dams were very common in most small, low-gradient streams, throughout North America and Eurasia, but that the frequency of these dams varied considerably. Where beaver populations are undisturbed, localized dam frequencies range from 7.5 per km to as high as 74 per km, with frequencies of around 10 dams per km being more typical in low-gradient streams (Table 1; Warren 1926; Scheffer 1938). Frequencies may decrease when larger areas are considered. Two studies examining dam occurrence across entire, multiple watersheds found frequencies of 2.5 per km for the 750 km^2 Kabetogama Peninsula in Minnesota and 9.6 dams per km for an 85 km^2 area encompassing two watersheds in Wyoming (Skinner et al. 1984; Johnston and Naiman 1990b).

Estimates of historic dam densities over large geographical areas can be calculated if colony densities are known and the average dams built per colony can be estimated. Reported colony densities of remote or protected populations show a trend of lower densities in subarctic regions and higher densities in more temperate regions, with an overall average of a little less than 0.5 colonies per km^2 (Table 2). Johnston and Naiman (1990b) used remote sensing on the Kabetogama Peninsula and estimated a colony density of 0.92 km^2 and a beaver pond density of 2.96 km^2, which gives an average of 3.2 dams per colony. Recognizing both the high spatial variation and uncertainty of estimates of both colony density and dams per colony, these studies suggest that, before the arrival of Europeans, at least 25 million beaver dams spanned small to medium-sized streams throughout the 15.5×10^6 km^2 of the North American continent where beaver once existed (Figure 1; Jenkins 1979). Historic dam densities were probably similar throughout Eurasia, though there is some evidence to suggest that the remnant Eurasian beaver build fewer dams than their North American counterparts (Danilov and Kan'shiev 1983).

TABLE 1. Beaver dam density reported in the literature for pristine, remote, or protected areas.

Source	Dams /km	Range dams/km	Surveyed length/km	Location	Gradient	Comments
(Naiman et al. 1986)	10.6	8.6–16.0	4.3	Quebec	low	Pristine
(Smith 1950)	12.0	n/a	4.4	Colorado	1–3%	Remote
(Smith 1950)	19.1	n/a	4.4	Colorado	1–3%	Includes inactive dams
(Warren 1926)	73.7	n/a	0.3	Colorado	12.5%	Pristine
(Warren 1926)	41.6	n/a	1.2	Colorado	3.5%	Pristine
(Scheffer 1938)	7.5	n/a	8.0	Washington	low	Transplanted population
(Scheffer 1938)	35.4	n/a	0.6	Washington	low	Transplanted population
(Skinner et al. 1984)	9.6	2.9–41.1	43.3	Wyoming	85 km^2 area	Remote
(Woo and Waddington 1990)	14.3	5-19	n/a	Ontario	low	Remote, pristine
(Naiman et al. 1988)	2.5	2.0–2.9	n/a	Minnesota	750 km^2 area	Protected population
(Hering et al. 2001)	27.8	n/a	0.9	W. Germany	n/a	Recovering population
(Hering et al. 2001)	12.3	n/a	1.3	S. Germany	n/a	Recovering population
(Medwecka-Kornas and Hawro 1993)	20.0	n/a	1.0	Poland	n/a	Recovering population

Using Collen and Gibson's (2001) estimated overall mean of 5.2 individuals per colony of North American beaver, and using a continental mean of 0.5 colonies per km^2 (based on Table 2), provides an historic population estimate of North American lodge-building beaver of around 40 million individuals. Only about 75% of beaver live in lodges, and the rest burrow into banks (Danilov and Kan'shiev 1983); we estimate a total historic population of around 55 million. This estimate is on the low end of, but not inconsistent with, Seton's (1929) often cited population estimate of 60–400 million, which was derived primarily from the qualitative data. However, we will never be certain whether current estimates of individuals per colony or colony densities are applicable to historic populations. Because colony density is affected by habitat quality, it is not unreasonable to assume that, historically, overall colony densities were much higher, and thus populations much greater, when the entire vast, productive lowland river bottom habitat throughout North America had not yet been altered by humans and was available for beavers

TABLE 2. Colony density estimates for North American and Eurasian beaver for protected, unprotected, and recovering populations.

Source	Location	Density km^2	Status
(Howard and Larson 1985)	Massachusetts	0.92	Protected
(Johnston and Naiman 1990a)	Minnesota	0.92	Protected
(McCall et al. 1996)	Maine	0.15–0.32	Managed
(Voigt et al. 1976)	Ontario	0.38–0.76 (3.0)	Remote
(Bergerud and Miller 1977)	Newfoundland	0.2–0.3 (4.2)	Remote
(Aleksiuk 1970)	Northwest Territories	0.38	Remote
(MacDonald et al. 1995)	Latvia	0.37	Recovering
(Hartman 1994)	Sweden	0.25	Recovering
(Zurowski and Kasperczyk 1986)	Poland	0.15	Recovering
(Jaksic et al. 2002)	Argentina	1.9	Introduced

to use. The Eurasian beaver has a slower reproductive rate and a lower average colony size (3.8); so, historic estimates of populations and densities cannot be directly extrapolated from studies of the North American beaver (Danilov and Kan'shiev 1983). However, recovering populations of European beaver suggest that high densities may be achievable in the long term if management authorities desire such a goal (Halley and Rosell 2002).

Location of Dams in Watersheds

Beaver prefer to dam small, low-gradient streams with unconfined valleys, but they can also dam both large and high-gradient streams. Retzer et al. (1956) studied 365 reaches in 61 streams throughout Colorado to determine the physical factors determining beaver pond location. Beaver built dams on 82% of all the low-gradient (1–3%) streams surveyed, 73% of reaches with 4–6% gradients, and 61% of reaches with 7–9% gradients (Figure 2). Use of streams with a slope greater than 9% dropped off dramatically. On streams with gradients greater than 15%, just one active dam was found on a 16% stream slope and one abandoned dam was found on a 21% stream slope. Beaver overwhelmingly preferred to dam streams in valleys wider than 46 m (150 ft); they used 85% of such streams, but only 35% of streams with narrower valleys, regardless of their slope. These results are confounded because wide valleys tend to have low-gradient streams.

Consistent with these results, Pollock and Pess (1998) studied 341 beaver ponds in the 1,741 km^2 Stillaguamish watershed, Washington and found that 91% were in low-gradient (≤4%) streams with unconfined (>4 channel widths) valleys, and almost all of them were in watersheds less than 15 km^2. In this study, 16% was the steepest gradient where a beaver pond was found. Similarly, Suzuki and McComb (1998) studied 170 beaver dams in the Drift Creek basin, Oregon and consistent with these results found that more than 90% were on stream gradients of less than 6%. Beier and Barrett (1987) also found that geomorphic and hydrologic conditions were the best predictors of dam-site suitability, with gradient, stream depth, and stream width the most important factors. They found that biological factors, such as food availability, did not provide additional explanatory power as to the location of dam sites.

The maximum size of streams that beaver can dam is not well documented, and it will certainly vary from region to region, depending on hydrologic conditions. In Washington, historic

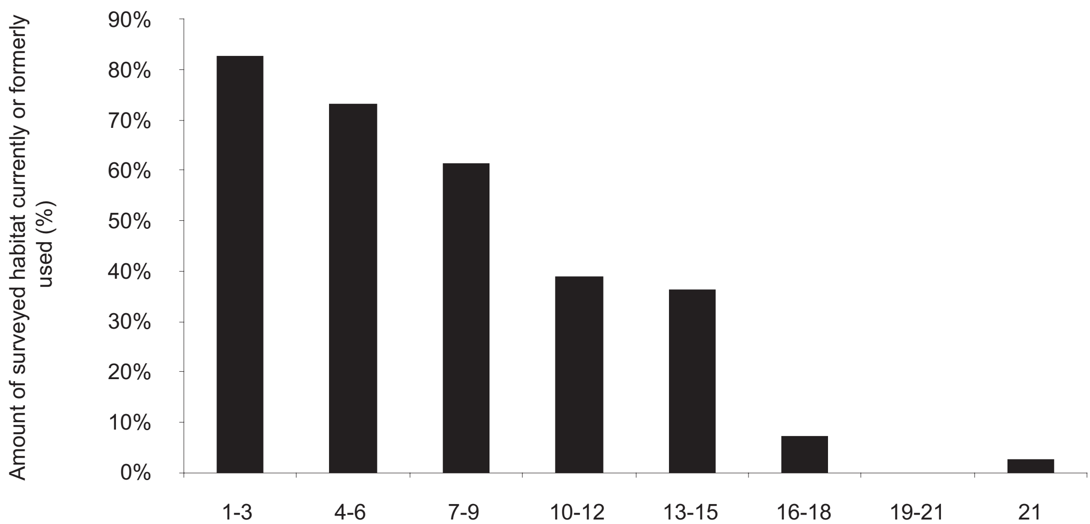

FIGURE 2. Beaver–dam frequency based on stream gradient from a survey of 356 stream reaches in the mountainous regions of Colorado, showing that beaver strongly prefer to dam low-gradient streams (adapted from Retzer et al. 1956).

records note a beaver dam on a stream with a drainage area of 107 km^2. Naiman et al. (1984) report seasonal dams being built on the lower reaches of the 207 km^2 Muskrat River watershed, Quebec. In 1998, one of us (Pollock) noted a stable beaver dam crossing the entire South Fork of the Little Colorado River with an upstream drainage area of 280 km^2. We suspect that unreported dams exist on larger and more powerful streams, but stream size or drainage area are generally not reported in the literature. The size of streams and rivers that could be dammed by the bear-sized Pleistocene beaver is a matter of interesting speculation (Mai 1978). We are not aware of any published literature that has identified prehistoric beaver dams.

Effects of Beaver Dams on Stream Hydrology

Even the casual observer notices that beaver dams retain water and thus slow its downstream movement. What is surprising is how few studies have attempted to quantify what happens to the water retained by beaver dams and what the hydrologic effects are. The limited available evidence suggests that key hydrologic functions of beaver dams are to dissipate stream energy, attenuate peak flows, and increase groundwater recharge and retention, which increases summer low flows and elevates groundwater levels in stream valleys, thus expanding the extent of riparian vegetation (Stabler 1985; Lowry 1993).

Beaver dams slow the velocity of water, thereby reducing energy and increasing retention time. During floods, energy is dissipated as the water works its way through a tortuous path of small branches on the downstream side of the dam. Finally, energy is further dissipated by floodplain vegetation below the dam that must be overcome as the water works its way back to the stream channel (Li and Shen 1973; Woo and Waddington 1990; Dunaway et al. 1994).

Because beaver dams slow stream velocity, they should also attenuate flood peaks. Research on the effects of wood dams in small (third-order) streams suggests that they can retain water at least 50% longer than streams where such dams are absent (Ehrman and Lamberti 1992). Given the much lower permeability of beaver dams compared to large wood jams, it is reasonable to expect them to retain water for much longer periods of time (Hering et al. 2001).

Beedle (1991) used the dimensional characteristics of beaver dams in the glacially carved valleys on a southeastern Alaska island to evaluate the hydrologic effects of these structures on peak flows. Using simulated peak-flow routing, Beedle estimated that a single full beaver pond reduced peak flows by more than 5%, but that a series of five large ponds in series could reduce peak flows of a 2-year event by 14% and peak flows of a 50-year event by 4%. The simulation also suggested that beaver dams did not greatly alter the shape of outflow hydrographs, resulting in a 10–15-min delay in the peak and a slight increase in flood duration. Beedle's simulation assumed that all ponds were at full storage capacity before the storm and that water pouring over dams instantly returned to the channel. Although these assumptions were necessary for the simulation, under natural conditions, where dams are not filled to capacity and flood water pouring over dams is spread out across the floodplain, peak flows could likely be further reduced. Because many streams may have dozens of dams, expecting stronger cumulative effects is reasonable (Scheffer 1938; Smith 1950; Naiman et al. 1986).

Effects of Beaver Dams on Aquifer Recharge and Low Flow Discharges

Some researchers have suggested that beaver dams and other instream obstructions that retain water contribute to groundwater recharge and thus help to increase summer low flows. Anecdotal reports in the literature support this contention, though few quantitative data exist. In Massachusetts, Wilen et al. (1975) compared changes in summer low flows caused by beaver dams when beaver colonized one of their study sites. In a paired stream study, beaver dams and large wood were removed from one stream, and the other stream was retained as a control. During the first year of the experiment, both streams remained perennial, but the undisturbed stream had more flow. In spring of the next year, beaver recolonized the experimental reach, building a series of dams. That summer, the experimental stream remained perennial below the newly built dams, but the "control" stream with no beaver dams went dry.

Tappe (1942) noted summer flows in several streams in northern California increased after beaver colonized upstream reaches. In Missouri, Dalke (1947, cited in Stabler 1985) reported that the return of beaver to small streams restored perennially flowing water that could support fish. Likewise, Finley (1937) reported that stream flow in Silver Creek, in the Ochoco National Forest of eastern Oregon, decreased substantially after the loss of beaver dams. Trappers removed about 600 beaver from the headwaters of Silver Creek, and several creeks dried up in following years as water levels dropped. According to Finley, groundwater levels dropped sufficiently that pastures near streams could no longer support grass, resulting in an annual loss of approximately 15,000 tons of pasturage. Further downstream, water was no longer available to irrigate farmland, resulting in additional economic losses.

In eastern Oregon, groundwater levels in the floodplain near a beaver dam substantially increased as compared to a reach lacking any dams, suggesting that dams do help increase water availability to riparian areas at least 50 m from the pond (Lowry 1993). Additionally, Lowry estimated that about 90 m^3 of groundwater could be obtained if the beaver dam was breached.

Human-built structures have yielded analogous results. Brown (1963), studying a conservation program in Flat Top Ranch, Texas noted that small lakes and ponds created in sandy soils allowed for rapid infiltration of stormwater and helped to convert all major drainages from intermittent to perennial streams. In coastal British Columbia, a small check dam no larger than a beaver dam was used to retain stormwater in a 27-ha pond and ensure that the stream flowed throughout the summer (Wood 1997).

In Alkali Creek, Colorado, Heede and DeBano (1984) observed that perennial flow developed in downstream reaches 7 years after installation of 132 small check dams in ephemeral, gullied streams. Old beaver dams were observed in the gully walls while the check dams were being built, and 14 years after the project began, beaver have begun recolonizing some of the reaches with perennial flow (Stabler 1985). Stabler also noted the work of Jester and McKirdy (1966) who installed check dams in Taos Creek, New Mexico. Within 10 years, they obtained perennial flow that could sustain trout populations. Similarly, Ponce and Lindquist (1990) noted that perennial flow was an unexpected result of a small (5-m) dam built to retain sediment on Sheep Creek, Utah.

Lowry's (1993) study suggests that the water storage value of beaver dams does not lie solely in the water stored behind the dam because 90 m^3 is only enough water to keep even a small stream flowing for a very short period. If, as the previous examples suggest, beaver dams change stream hydrology so streams that formerly went dry in the summer now flow year round, their ability to recharge groundwater must be substantial. Simple calculations indicate that recharge from the dams of even a few beaver colonies can contribute substantially to summer low flows. As an example, a small stream flowing at a modest 0.1 m^3/s over a period of 100 d (the approximate length of summer in much of the western United States) will need about 8.64×10^5 m^3 of water above and beyond what is lost to evapotranspiration. Assuming that a series of beaver dams provides 1×10^5 m^2 of pond surface area (20 dams, assuming that a typical pond has 5×10^4 m^2 of surface area), aquifer hydraulic conductivities of about 4×10^{-7} m/s are needed to accept this much water during the other 265 d of the year. Because 4×10^{-7} m/s is well within the range of hydraulic conductivities typical of the silts and sands that would be found at the bottom of beaver ponds and fine-grained alluvial deposits (Dunne and Leopold 1978; Lowry 1993), even a small number of beaver impoundments should be able to augment low flow discharges during long periods without rain, provided an aquifer is present to accept the recharge.

A stream may remain perennial if the amount of valley alluvium is sufficient to store waters infiltrating from beaver ponds. Assuming a specific yield of 20%, typical of fine-grained alluvial deposits (Dunne and Leopold 1978; Lowry 1993), an aquifer volume of 4.32×10^6 m^3 is needed to store the 8.64×10^5 m^3 of water needed to maintain flow at 0.01 m^3/s for 100 d. As an example, sustaining this flow would require valley alluvium 150 m wide by 2.4 km long by 12 m deep. By comparison, to retain this much water behind typical beaver dams (0.5 m high on a 1% stream gradient and a 50-m-wide dam, and assuming they are not storing any sediment) would require the impoundment of 35 km of low-gradient streams. Together, these numbers suggest that if beaver impoundments augment summer low flows in small streams, they do so primarily by recharging aquifers, and the direct storage of water behind dams probably plays a minor role in low-flow augmentation.

Whether a series of beaver dams is actually able to recharge an alluvial aquifer, and whether that water is ultimately available to augment streamflows in the summer, depends upon the geometry and hydraulic properties of the aquifer. Aquifer geometry determines the size of the aquifer. Hydraulic properties, such as hydraulic conductivity and the coefficient of storage, control the rate of recharge and discharge, which determines whether an aquifer will drain throughout the summer. For example, a highly porous aquifer may quickly recharge but also quickly discharge, thereby precluding the slow release of water throughout the summer.

Effects of Beaver Dams on Valley Floor Morphology

The slow velocity of water behind beaver dams creates extensive depositional areas for sediment and organic material transported from upstream reaches. The shallow waters behind the dams allow highly productive emergent vegetation to grow, allowing in situ development of organic material, much of which is ultimately deposited on the (submerged) valley floor. Together, the onsite creation of organic material and the deposition of sediment and organic material from upstream raise the surface of the stream bed and inundate the adjacent valley floor. Sediment storage behind beaver dams can be substantial.

In a boreal forest ecosystem, Naiman et al. (1986) found that sediment storage behind beaver dams ranged from 35 to 6,500 m^3, yet they found no relation between dam size and sediment retained. Butler and Malanson (1995) studied sediment deposition behind five young (<6 years) and three "old" (>10 years) beaver dams in Glacier National Park, Montana. They found more sediment stored behind the older ponds. Sediment volumes behind the more recent dams ranged from 9 to 165 m^3 (average = 56 m^3); while behind the older dams, sediment storage ranged from 77 to 267 m^3 (average = 203 m^3). In parts of the arid western United States, beaver dams have been used to trap sediment in eroding streams with good results (Scheffer 1938; Apple 1985). In Mission Creek, Washington, beaver were successfully "employed" to control sediment losses resulting from poor land-use practices. In just 2 years, 4,863 m^3 of sediment were trapped behind 22 dams along a 622-m reach for an average of 7.8 m^3 of sediment stored per linear meter of stream (Scheffer 1938). The average sediment retention behind beaver dams was 221 m^3 and ranged from 34 m^3 to 586 m^3. A reanalysis of Scheffer's data shows a significant relationship between the surface area of the dam face and the amount of sediment stored ($r^2 = 0.30$, $p < 0.001$, $n = 22$). Removing the three statistical outliers greatly increases the strength of the correlation ($r^2 = 0.82$, $p < 0.001$, $n = 19$; Figure 3). These data suggest a general trend of increasing sediment storage with increasing dam size, with some notable exceptions. These exceptions could be explained by the age of the dams or the recent failure of a dam upstream.

These studies indicate that sedimentation rates behind beaver dams vary widely. Factors influencing sedimentation rates include growth rates of the emergent vegetation (which itself is determined by species composition, climate, and site productivity), upstream sediment loads (which is determined by geology, watershed land-use history, and disturbance history), the number of beaver dams upstream, and the frequency of dam failure for both the dam in question and any upstream dams. Given the high spatial and temporal variation for all of these factors, general predictions of sedimentation rates will be inaccurate and site-specific measurements will be required.

Sediment behind beaver dams is often a combination of fluvially transported material and organic material produced by the emergent vegetation growing on the pond edge. As ponds fill in with sediment, emergent vegetation is able to grow towards the pond center, helping to trap more sediment and producing more organic material, thereby accelerating the rate of filling. Before being completely filled, most ponds are abandoned, and dams often breach (Pastor et al. 1993), thus ending the accumulation of sediment. Although inorganic sediment accumulation may cease, however, wetland graminoids (sedges, rushes, grasses) colonize the exposed sediments on the pond edges, typically turning the former pond into a highly productive wet meadow and creating and depositing yet more organic matter on the former pond floor.

The observation that beaver dams trap sediment have led some scientists to conclude that the accumulation of such sediment over long periods can cause permanent changes in valley floor morphology. Rudemann and Schoonmaker (1938), Ives (1942), and Rutten (1967) argued that the numerous small, broad, relatively level surfaces at the bottom of recently deglaciated, U-shaped valleys were the result of sediment accumulation behind the numerous beaver dams built and maintained since the last glacial recession.

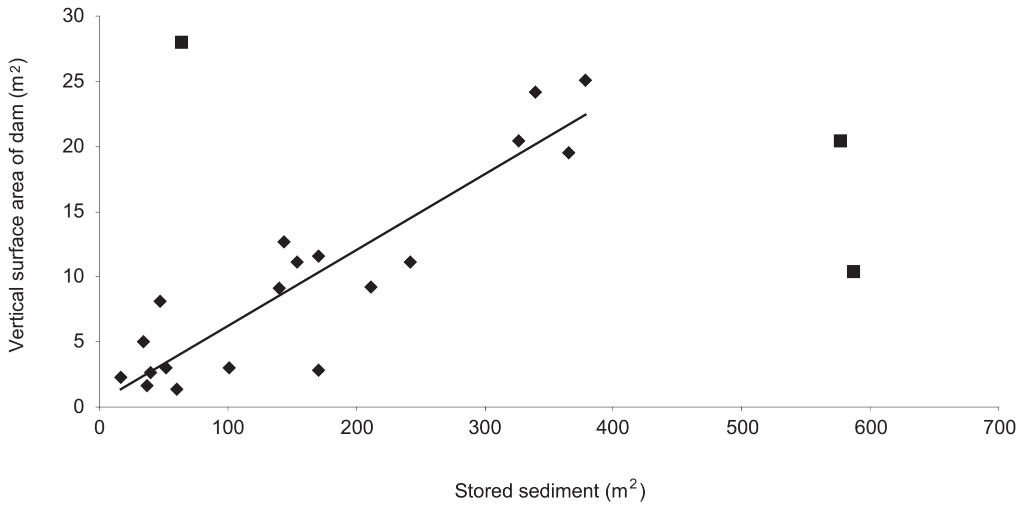

FIGURE 3. The relation between sediment stored and vertical dam face area is weak but significant ($r^2 = 0.30$, $p < 0.01$, $n = 22$). With three statistical outliers removed (large square symbols), the relation becomes much more apparent ($r^2 = 0.83$, $p < 0.01$, $n = 19$) (adapted from Scheffer 1938).

Ives observed that a competing hypothesis, that postglacial lake deposits formed the bottoms, was unlikely because the valleys were, in fact, gently sloping over long distances. Ives also dismissed the hypothesis that the flatness of the valleys was the result of the meandering of postglacial braided rivers on the grounds that such action would have left a more uneven topography because braided reaches differentially incise and because the valley fill was fine-textured, suggesting a depositional environment rather than the coarse-textured sediment that would be typical of a braided river transporting glacial outwash. Finally, Ives observed slight steps in some valley floors coincidental with the presence of abundant buried wood similar in size and shape to the wood of beaver dams.

Others, such as Rutherford (1964), have argued that although beaver dams have contributed to the accumulation of fine sediments on valley floors, the presence of underlying geologic features, such as glacial moraine or dykes, are the underlying control that allows flat valleys to form. We believe that both hypotheses have merit and are not mutually exclusive. However, the extent to which beaver dams control valley floor morphology (e.g., slope) over long periods is still largely unknown.

Over short periods in small reaches, beaver dams create a stair-step valley and stream profile consisting of flat areas with abrupt gradient changes at dam sites. We suggest that, over long periods, beaver dams can change the longitudinal profile of streams such that they effectively change valley slope over long distances. This change could be accomplished if beaver dams at the mouth of a valley were consistently built higher or were more closely spaced to act as a series of step dams. Although the total gradient would stay the same, most of the valley would be gently sloping, with a steeply graded but stepped gradient near the mouth. Simple calculations suggest that, over long periods, significant morphological changes are possible.

Geometric relations can be used to estimate maximum potential sediment storage behind beaver dams:

$$V_m = 0.5H^2W/S \ ,$$

where V_m = maximum sediment storage volume, H = dam height, W = dam width, and S = stream slope. Thus, as an example, a dam rising 1.0 m above a 50-m-wide valley floor with a slope of 0.01 could store a maximum of 2,500 m^3 of sediment, or about 25 m^3/m of stream length, which on average would elevate the valley floor 0.5 m. Assuming that on average beaver build 1.0-m-high dams and that they are half filled every 50 years, a valley floor could be raised at a rate of 0.5 cm/year, or accumulate about 12 m (vertical) of sediment and organic material, over a period of 10,000 years. Measured sediment accumulation rates behind dams range from 4 to 30 cm/year over short time frames and from 0.25 to 6.5 cm/

year over decadal time scales (Scheffer 1938; Devito and Dillon 1993; Butler and Malanson 1995), suggesting that our calculations are conservative. On the other hand, sediment will compact under the weight of additional sediment, and a certain amount of sediment behind abandoned dams is exported if the stream incises into the deposits behind the former dam. Also, the cycle of beaver habitat colonization and abandonment can be at shorter intervals than 50 years (Warren 1932; Neff 1959). As a rough approximation, however, these calculations illustrate the theoretical capacity of beaver dams to substantially raise valley floor elevations over long periods. Studies of the cumulative geomorphic effects of beaver dams (and their widespread removal) would be worthwhile. Observations of meters-thick accumulations of compressed organic material exposed on the valley walls of incised streams, where beaver dams are known to have existed until recently, provide additional physical evidence to support the idea that a series of beaver dams built over long periods can raise valley floors (Pattie 1833, Fredlake 1997; Pollock, author's personal observation).

Other researchers have observed streams that historically contained beaver and well-vegetated floodplains and are now incised in many places (Winegar 1977; Parker et al. 1985; Elmore and Beschta 1987). The rapid incision that has occurred throughout much of the western United States and other parts of the world in recent centuries suggests that base elevations were not controlled by hard geological features, such as bedrock, but by "soft" grade-control structures like beaver dams, large wood, or the dense roots of streamside vegetation (e.g., Zierholz et al. 2001). In the western United States, the coincidence of widespread incision with the arrival of the first white settlers suggests that one of their early land-use activities may have been the causal agent. Removal of beaver by trappers was one of the first major land-use changes to occur in the United States following European settlement (Mackie 1997). Rapidly removing millions of beaver resulted in the loss of millions of functioning dams throughout the West. For small streams, this loss must have resulted in a series of catastrophic floods, as dams ruptured during high flows and destroyed downstream dams that were acting as "roughness elements" (sensu Lisle 1982) slowing stream velocities and dissipating energy.

The effects of catastrophic beaver dam failures are documented (Butler 1989; Stock and Schlosser 1991). Often channel incision occurs just downstream of the dam and fine sediment is deposited farther downstream, along with uprooted plant material and organic matter. Large wood from streams has also resulted in the loss of sediment and the rapid downcutting of channel beds (Smith et al. 1993). Recent restoration efforts using large wood have elevated the base of streambeds (Slaney and Zaldokas 1997).

These studies taken as a whole suggest that beaver dams can substantially elevate and maintain wide, low-gradient valley floors over long periods and that these geomorphic features should persist as long as healthy populations of beaver are available to maintain the dams. The available evidence also suggests that the repeated building of beaver dams, the subsequent backfilling with sediment and organic matter, and the building of new dams on top of old fill can create valley and stream-slope elevational profiles that differ from the underlying slope.

Whether the widespread elimination of beaver dams is the ultimate cause of the recent incision that has occurred in many streams in the western United States has not been determined. But this hypothesis is consistent with available information: indirect support for it comes from the work of land managers who are using beaver dams—or small artificial dams—as a tool to aggrade incised streams.

In Wyoming, Apple et al. (1983) provided cut cottonwood branches to recently relocated beaver who subsequently built dams that aggraded incised channels. The initial dams quickly backfilled with sediment, and the beaver continued to build additional structures upstream. In Mission Creek, Washington, relocated beaver built dams and trapped thousands of cubic meters of sediment in just a few years (Scheffer 1938). Similar human-built structures have also yielded good results. In Sheep Creek, Utah, a 5-m-high retaining dam with a storage volume of 1.09×10^5 m^3 of sediment was built in 1961 and filled up in just 1 year. The dam continues to cause aggradation upstream of the storage area and, by 1984, had retained a total volume of 4.39×10^5 m^3 of sediment (Haveren et al. 1987). A formerly incised xeric valley is now supporting abundant riparian vegetation on a gently sloping valley floor.

On a smaller scale, in Alkali Creek, Colorado, Heede (1978) built small concrete "check" dams on small ephemeral streams containing no riparian vegetation. The barriers quickly filled with sediment and now support substantial amounts of riparian vegetation because the dams create localized areas of groundwater recharge. The vegetation itself helps to trap additional sediment, thus creating a positive feedback of valley aggradation. Together, these studies suggest that, where small dams exist, whether built by beavers or people, they can cause localized aggradation of valley floors and infilling of incised valleys, provided a sufficient supply of sediment is upstream. Additional studies to determine the feasibility of using beaver dams to initiate aggradation of incised valleys would be useful.

Beaver Dams and Fish

Effect of dams on communities and populations

When beaver impound streams by building dams, they substantially alter stream hydraulics that may benefit many fish species (Murphy et al. 1989; Snodgrass and Meffe 1998). More than 80 North American fishes have been documented in beaver ponds, with 48 species commonly using them (Table 3). Fish use of beaver ponds in Eurasia is not as well documented. In Sweden, Hagglund and Sjoberg (1999) observed that minnow *Phoxinus phoxinus* and brown trout *Salmo trutta* used beaver ponds, while burbot *Lota lota* and northern pike *Esox lucius* were found in the ponds occasionally. In general however, studies of the effects of the Eurasian beaver on fish populations are not common, and data are often extrapolated from studies of the North American beaver (e.g., see Collen and Gibson 2001). Because beaver ponds usually have slow current velocities and large edge-to-surface-area ratios, they provide extensive cover to fish and a productive environment for both vegetation and aquatic invertebrates, affording fish foraging opportunities not found in unimpounded stream habitat (Hanson and Campbell 1963; Keast and Fox 1990). Fish expend less energy when foraging in slow water. Thus sections of streams impounded by beaver dams are often more productive than unim-pounded reaches in both the number and size of fish (e.g., Gard 1961b; Hanson and Campbell 1963; Murphy et al. 1989; Leidholt Bruner et al. 1992; Schlosser 1995). Fish are not the only beneficiaries of beaver dams. Relative to unimpounded reaches, increases in either biomass or diversity have also been observed for a wide range of taxa, including birds, mammals, amphibians, plants, and insects in areas affected by beaver (see reviews in Naiman et al. 1988; Pollock et al. 1994).

The physical components of beaver dams affect a variety of fish species. Much of the research on beaver–fish interactions has been concerned with how salmonids are affected by beaver ponds, primarily brook trout *Salvelinus fontinalis* and juvenile coho salmon *Oncorhynchus kisutch* (however, see Hanson and Campbell 1963; Keast and Fox 1990; Schlosser 1995; Snodgrass and Meffe 1999). Some early observations of the increased siltation in beaver ponds, along with increased temperatures caused by the loss of shade-producing vegetation, led some to conclude that beaver ponds could be detrimental to salmonid populations (Salyer 1935; Reid 1952; Knudsen 1962). These opinions were based on subjective observations and assumptions that fine sediment deposited behind beaver dams smothered redds and decreased benthic invertebrate production, that higher summer temperatures found in ponds were detrimental, and that the flooding of vegetation led to water quality problems such as low dissolved oxygen levels.

Although these researchers expressed concern that beaver dams are harmful to trout, no study has ever demonstrated a detrimental population-level effect of dams on salmonids, nor has a study shown that beaver dams are more than a seasonal barrier to fish movement. On the contrary, most studies support the contention that the pond habitat formed by beaver dams is highly beneficial to many fishes and that species regularly cross dams in both upstream and downstream directions (Rupp 1954; Huey and Wolfrum 1956; Gard 1961b; Hanson and Campbell 1963; Call 1970; Bustard and Narver 1975; Swales et al. 1988; Murphy et al. 1989; Keast and Fox 1990; Leidholt Bruner et al. 1992; Schlosser 1995; Snodgrass and Meffe 1998, 1999).

Comparing salmonid productivity in stream reaches above beaver dams with reaches where beaver dams are absent generally demonstrate that the reaches above beaver dams produce either more fish or larger fish or both. In a detailed study of the effects of beaver dams on trout in Sagehen Creek in the Sierra Nevada of California, Gard (1961b) found that the number of trout (brook, rainbow *O. mykiss*, and brown) were about the same over a 3-year period for a dam-affected reach and a “control” reach of a similar length (67 m), but that the size of the trout in the reach above the beaver dam were much larger.

TABLE 3. Common and scientific names of fish species known to use beaver ponds. The relevant scientific papers are also noted.

Species	Common name	Abundance[a]	References[b]
Aphredoderus sayanus	Pirate perch	C	1
Campostomus anomalum	Central stoneroller	C	2
Catostomus commersoni	White sucker	C	2,7,9
Centrarchus macropterus	Flier	C	1
Phoxinus eos	Northern redbelly dace	C	3,4,7,15
Culaea inconstans	Brook stickleback	C	3,4
Enneacanthus chaetodon	Blackbanded sunfish	C	1
Enneacanthus gloriosus	Bluespotted sunfish	C	1
Erimyzon oblongus	Creek chubsucker	C	1
Esox americanus americanus	Redfin pickerel	C	1
Esox niger	Chain pickerel	C	1
Etheostoma serrifer	Sawcheek darter	C	1
Fundulus diaphanus	Banded killifish	C	3
Fundulus lineolatus	Lined topminnow	C	1
Gambusia holbrooki	Eastern mosquitofish	C	1
Hybognathus hankinsoni	Brassy minnow	C	4
Ameirus melas	Black bullhead	C	2,4,5
Lepomis auritus	Redbreast sunfish	C	1
Lepomis cyanellus	Green sunfish	C	2
Lepomis gibbosus	Pumpkinseed sunfish	C	3,4
Lepomis gulosus	Warmouth	C	1
Lepomis marginatus	Dollar sunfish	C	1
Lepomis punctatus	Spotted sunfish	C	1
Notropis cummingsae	Dusky shiner	C	1
Notropis heterodon	Blackchin shiner	C	3,4
Notropis lutipinnis	Yellowfin shiner	C	1
Luxilus umbratilis	Redfin shiner	C	2
Oncorhynchus clarkii	Cutthroat trout	C	6, 9
Oncorhynchus kisutch	Coho salmon	C	6, 10,12,13[c]
Oncorhynchus nerka	Sockeye salmon	C	6
Phoxinus neogaeus	Finescale dace	C	4
Phoxinus phoxinus	Minnow	C	16
Pimephales promelas	Fathead minnow	C	2,3,4,16
Pungitius pungitius	Ninespine stickleback	C	7,15
Salmo trutta	Brown trout	C	8,17
Salvelinus fontanilus	Brook trout	C	8,9,12,16[c]
Salvelinus malma	Dolly Varden char	C	6,10,12
Semotilus atromaculatus	Creek chub	C	1,2,4,5,7,16
Semotilus coporalis	Fallfish	C	7
Cottus spp.	Sculpins	LC	6
Esox lucius	Northern pike	LC	4,14,17
Gasterosteus aculeatus	Threespine stickleback	LC	6, 12
Micropterus salmoides	Largemouth bass	LC	1,2,4,5
Notemigonus crysoleucas	Golden shiner	LC	1,2,3,16
Luxilus cornutus	Common shiner	LC	2,4
Notropis heterolepis	Blacknose shiner	LC	4
Notropis topeka	Topeka shiner	LC	2
Perca flavescens	Yellow perch	LC	3,4,16
Prosopium spp.	Whitefish	LC	6
Ameiurus natalis	Yellow bullhead	U	1,2

TABLE 3. Common and scientific names of fish species known to use beaver ponds. The relevant scientific papers are also noted.

Species	Common name	Abundance[a]	References[b]
Ameiurus platycephalus	Flat bullhead	U	1
Acantharchus pomotis	Mud sunfish	U	1
Ictalurus nebulosus	Brown bullhead	U	3
Lepomis humilis	Orangespotted sunfish	U	2
Lota lota	Burbot	C	16
Cyprinella lutrensis	Red shiner	U	2
Noturus leptacanthus	Speckled madtom	U	1
Notropis petersoni	Coastal shiner	U	1
Oncorhynchus mykiss	Steelhead	U	6, 10
Oncorhynchus mykiss	Rainbow trout	U	8, 9
Oncorhynchus tshawytscha	Chinook salmon	U	6, 10
Pimephales notatus	Bluntnose minnow	U	2,3
Prosopium williamsoni	Mountain whitefish	U	10
Margariscus margarita	Pearl dace	O	16
Amia calva	Bowfin	O	1
Anguilla rostrata	American eel	O	1
Elassoma zonatum	Banded pygmy sunfish	O	1
Etheostoma exile	Iowa darter	O	3
Etheostoma fricksium	Savannah darter	O	1
Etheostoma fusiforme	Swamp darter	O	1
Etheostoma nigrum	Johnny darter	O	2
Etheostoma olmstedi	Tessellated darter	O	1
Etheostoma spectabile	Orangethroat darter	O	2
Lepomis macrochirus	Bluegill	O	2
Minytrema melanops	Spotted sucker	O	1
Nocomis leptocephalus	Bluehead chub	O	1
Notropis dorsalis	Bigmouth shiner	O	2
Noturus gyrinus	Tadpole madtom	O	1
Oncorhynchus gorbuscha	Chum salmon	O	6
Percina caprodes	Logperch	O	2
Umbra limi	Central mudminnow	O	3
Umbra pygmaea	Eastern mudminnow	O	1

[a] Species sorted by frequency of use: C = common, LC = locally common, U = uncommon, O = occasional.
[b] Reference key: 1 = Snodgrasss and Meffee 1998; 2 = Hanson and Campbell 1963; 3 = Keast and Fox; 1990, 4 = Schlosser 1995; 5 = Stock & Shlosser 1991; 6 = Murphy et al. 1989; 7 = Rupp 1954; 8 = Gard 1961a, 1961b; 9 = Huey and Wolfrum 1956; 10 = Swales et al. 1988; 11 = Bryant 1983; 12 = Call 1970; 13 = Bustard and Narver 1975; 14 = Knudsen 1962; 15 = Rupp 1954; 16 = Balon and Chadwick 1979; Hagglund and Sjoberg 1999.
[c] For brook trout and coho salmon use, there is an abundance of additional literature, referenced in the text.

The average length in the dam-affected reach was 147 mm, and the average weight was 117 g; trout lengths in the control reach averaged 110 mm, and their average weight was 22 g. The brook trout and brown trout generally benefited more from the beaver ponds because they could feed on the pond's bottom fauna. After floods destroyed the dams, the brown trout population crashed and rainbow trout became the dominant species (Gard and Seegrist 1972).

Similarly, Huey and Wolfrum (1956) compared summer trout populations in three stream reaches upstream of beaver dams with three control reaches in the upper Red River, New Mexico and found that the dam reaches contained many more trout (mostly cutthroat *O. clarki* and brook trout, but some rainbow). Average trout populations in the three control reaches ranged from 12 to 80 (mean = 40) and, in the dam reaches, ranged from 131 to 218 (mean = 167). All the reaches were about 46 m long. Other studies have noted the abundance of trout upstream of beaver dams but did not directly compare them with unimpounded reaches. Call (1970), studying the effects of beaver on headwater streams in Wyoming, noted that beaver created trout habitat, where previously none existed, by damming very small streams and seeps, substantially increasing available brook trout habitat and allowing for the development of a productive fishery. Similarly, Gard (1961a) built small artificial dams to mimic beaver dams in the headwaters of Sagehen Creek, California and created a productive brook trout fishery where none had previously existed. Some of the increased salmonid productivity may be a result of the increased numbers of forage fish in beaver ponds. Rupp (1954) observed in a beaver pond in Maine that increased numbers of small fish, primarily three-spine stickleback *Gasterosteus aculeatus* and northern redbelly dace *Phoxinus eos*, were used as forage by brook trout.

Beaver ponds may be particularly important habitat for overwintering resident char and trout. Both Chisholm et al. (1987) and Cunjak (1996) observed that brook trout had a strong tendency to move into the slow water habitat of beaver ponds to overwinter. Likewise, Jakober (1995) observed that, in Montana streams, bull trout *Salvelinus confluentus* and cutthroat trout aggregated in large numbers to overwinter in beaver ponds. As temperatures drop in the autumn, other fishes appear to aggregate and seek out slow water habitat in which to overwinter, but it is not clear whether or not they utilize or prefer beaver ponds (Craig 1978; Paragamian 1981).

In anadromous-fish streams along the west coast of North America, comparisons of the growth and survival of juvenile coho salmon and other salmonids between reaches upstream of beaver dams and nonimpounded reaches have yielded similar results. Swales et al. (1988) compared populations of juvenile coho, chinook *O. tshawytscha*, and steelhead *O. mykiss* in side-channels impounded by beaver with the mainstem of the Coldwater River in British Columbia and found that the side channels upstream of beaver dams were heavily used by overwintering coho, but less so by chinook and steelhead. Over the course of 3 years, these researchers captured and measured coho in both habitats monthly and found that the coho upstream of the beaver dam were consistently larger, more abundant, and grew faster than those downtream. Juvenile coho were not only using the ponds for overwintering habitat, but as important refuge and rearing areas throughout the year. Murphy et al. (1989) studied summer use of mainstem and off-channel habitat in the valley floor of the Taku River, Alaska and found the highest densities of juvenile coho in reaches upstream of beaver dams (0.59 per m^2) and virtually all the larger coho were in beaver ponds (Figure 4). These reaches accounted for just 0.7% of the total available habitat; yet, 34% of all the juvenile coho were found there. Consistent with other studies, the coho in these reaches were longer than coho found in other habitat types. Murphy et al. also found that juvenile sockeye used reaches upstream of beaver dams, averaging 0.48 per m^2, and that these fish too were larger and grew faster than fish using other instream habitats. Similarly, Leidholt-Bruner et al. (1992) found that summertime densities of juvenile coho in "pools" upstream of beaver dams (0.34 per m^2) were higher than in pools formed by other obstructions (0.26 per m^2). Studying three small coastal streams in the islands of southeast Alaska, Bryant (1983) found that populations of coho juveniles in summer were significantly greater in impounded reaches compared with reaches just upstream and downstream, but that the densities in the impounded reach were lower because the beaver dams had greatly expanded the surface area of the stream. The highest population of Dolly Varden *Salvelinus malma* char was found in one of the impounded reaches, but no consistent pattern among all streams was found. In Carnation Creek, British Columbia, Bustard and Narver (1975) found that survival rate of overwintering juvenile coho in old beaver ponds was about twice as high as the 35% estimated for the entire stream system.

Other studies have found that many fish species, besides salmonids, are abundant in beaver ponds. Hanson and Campbell (1963), in a study of headwater streams in north Missouri, determined that the presence of beaver dams greatly increased the productivity of fishes compared to unimpounded reaches. They used rotenone to sample three beaver ponds and one "natural" pool to determine biomass and species composition for each of the habitats. The three beaver ponds had an average biomass of 2.8 g/m^2, and the natural pool had a biomass of 1.1 g/m^2. Hanson and Campbell also found 21 species in

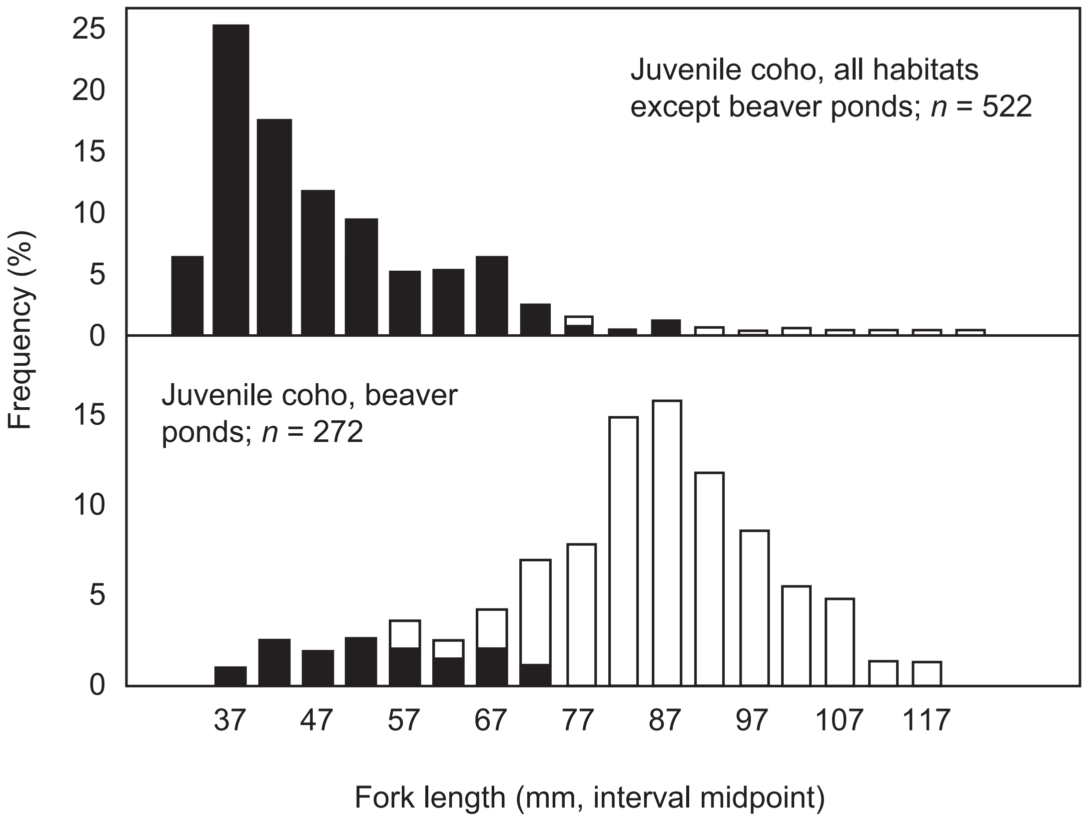

FIGURE 4. Size-frequency distribution of juvenile coho in main channel and off-channel habitat in the Taku River, southeast Alaska, showing that larger coho (age-1 light columns, age-0 dark columns) overwhelmingly prefer beaver ponds over any other habitat. Beaver ponds account for just 0.7% of the total instream habitat area in the Taku River floodplain (adapted from Murphy et al. 1989).

the beaver ponds, a 50% increase in number over the 14 species they found in an unimpounded reach nearby.

Snodgrass and Meffe (1998), in a study of fish community use of beaver ponds in the southeastern United States, found that beaver dams in first- and second-order streams had higher fish diversity (32 and 38 species, respectively), than in third-order streams (26 species). They concluded that, by creating pool habitat in small headwater streams where it is generally absent, beaver dams increase fish diversity. They also concluded that the generally positive relation observed between species richness and drainage area is a recent phenomenon resulting from the extirpation of beavers from their historical range. Finally, they found that headwater stream reaches upstream of beaver dams tended to be dominated by a few predators, suggesting that the deeper, more open water created more predation opportunities.

Schlosser (1995) concluded that beaver ponds in a headwater stream in northern Minnesota provided a source for fish populations, while adjacent stream environments acted as "sinks." Keast and Fox (1990) found a high amount of habitat and dietary specialization among the common fish species observed in an Ontario beaver pond. For example, Iowa darters were found only over bare (unsilted) substrate; one of the preferred habitats of the blackchin shiner *Notropis heterodon* was the open, silted area near the pond inlet; and fathead minnows *Pimephales promelas* were generally found in the old creek channel. They also determined that fish species richness and body size were smaller in a beaver pond relative to more permanent lentic water bodies in the area.

Impact of beaver dams on spawning

A number of observers have speculated that beaver dams can affect fish populations by covering spawning sites with silt or deep, slow water or by blocking access to upstream spawning grounds (Knudsen 1962; Call 1970; Swanston 1991; Cunjak and Therrien 1998). While beaver dams have led to the siltation of spawning habitat and probably restrict access to spawning grounds for some species, there is little evidence of negative population-level effects. Because beaver ponds trap sediments and dampen floods, siltation and scouring of spawning gravels further downstream may be reduced, making determination of an overall negative population effect problematic (Scheffer 1938; Beedle 1991; Dunaway et al. 1994; Butler and Malanson 1995; Hering et al. 2001). Further, some species that require clean spawning gravels, such as brook trout, cutthroat trout, and coho salmon, extensively use beaver ponds as rearing habitat (Gard 1961b; Call 1970; Murphy et al. 1989). However, where spawning habitat is limiting, beaver ponds may affect fish populations. As an example, Rabe (1970) found that beaver ponds with little accessible spawning sites nearby contained fewer, larger brook trout than those ponds where nearby spawning habitat was abundant. Similarly, Balon and Chadwick (1979) observed that three lithophilic fish species, two *Semotilus* species, and brook trout, creek chub *Semotilus atromaculatus*, and *Semotilus margarita*, needing gravel or rock substrate for their early development (e.g., spawning and egg incubation), did not reproduce in an Ontario lake after construction of a beaver dam that raised the lake level. Three other species, yellow perch *Perca flavescens*, fathead minnow, and golden shiner *Notemigonus crysoleucas*, were not lithophilic and were able to successfully reproduce.

Beaver dams as a barrier to fish movement

Studies examining the permeability of beaver dams to fish passage suggested that many species are able to gain passage, but they are seasonally restricted by low flows. Gard (1961b) found that all three species that they studied (brown, brook, and rainbow trout) were able to move both upstream and downstream across a series of 14 dams. Brown trout crossed dams more frequently than the others; rainbow trout showed greater ability to cross a series of dams, with some crossing an entire series of 14 dams. Movement upstream and downstream was equal for all species. In a less detailed study, Rupp (1954) monitored the movement of brook trout in a series of five beaver dams in the Sunkhaze Stream, Maine. Rupp set up two monitoring stations, one above all the dams and one below, and found substantial movement across the entire dam series. In contrast to Gard, Rupp found more downstream movement than upstream movement, and he could not correlate movement with streamflow. In Gould Creek, Minnesota, Schlosser (1995) studied the movement of a 12-species fish assemblage in beaver ponds and observed that downstream movement of fish was weakly correlated with elevated stream flows that coincided with the approximate stage at which water began moving over and around a dam. Upstream movement, however, was not correlated with streamflow, and fish moved up over dams across a broad range of flow conditions.

On the west coast of North America, the question of whether beaver dams are a barrier to anadromous salmonid movement has long been debated, and even today, some natural resource agencies remove beaver dams to "enhance" salmonid habitat. Personal observations and published literature suggest that both adults and juveniles of coho, steelhead, sea-run cutthroat, Dolly Varden, and sockeye are able to cross beaver dams (Bryant 1983; Swales et al. 1988; Murphy et al. 1989). In a study of out-migration from a floodplain beaver pond on the Coldwater River, British Columbia, Swales et al. (1988) monitored 1,257 coho salmon smolts, 62 steelhead trout (mean length = 129 mm), and 3 Dolly Varden char moving downstream over a period of 2.5 months in the spring. Bryant (1983) found abundant populations of young-of-the-year and age-one coho juveniles in the slow water areas behind beaver-dammed streams in southeast Alaska. He concluded that the abundance of young of the year indicated that adult coho were able to cross the dams (including one dam 2.1 m high), on the presumption that such small fish (<52 mm) do not move upstream across beaver dams in great numbers. Little information has been published about whether the adults of chum salmon are able to cross beaver dams, but the general consensus among salmon fisheries managers is that beaver dams can be an obstacle to upstream chum salmon movement. Anecdotal evidence also suggests that beaver dams can be an obstacle to the upstream movement of adult Atlantic salmon *Salmo salar* (Cunjak and Therrien 1998).

Conclusions

The widespread removal of beaver dams across small and medium-sized streams throughout most of the Northern Hemisphere has caused substantial changes to stream hydrology and geomorphology, resulting in dramatic shifts in the composition of communities. Because beaver build dams on small streams, their presence creates slow water pool habitat in a portion of the network where such habitat is often uncommon or nonexistent. This allows fish depending on pool habitat to move farther up the system, sometimes to reaches previously inhospitable. The presence of beaver dams often, though not always, creates fish habitat with higher productivity or diversity. Certain species, such as brook trout and juvenile coho salmon, rely heavily on beaver ponds, and the loss of such habitat has undoubtedly affected populations.

Some studies suggest that beaver dams can restore perennial flow to intermittent streams, but the conditions under which such a transformation can be expected have not been well described. Our calculations suggest that the ability of beaver dams to increase aquifer recharge depends largely on the hydraulic and geometric characteristics of the aquifer. Manmade structures similar in size to beaver dams that have been shown to improve stream flow lend support to our contention that beaver dams can also increase stream flows. Based on our observations of stream systems in the western United States, it is likely that many intermittent streams could have perennial flow restored if beaver colonize them.

Observations of extensive sediment accumulation behind beaver dams lend support to the hypothesis that beaver, acting over long periods, can significantly change valley floor morphology. The potential for sediment accumulation behind beaver dams over the course of millennia is tremendous, especially considering that, until recently, few checks existed on their population outside of habitat or food limitations. There is some evidence to suggest that much of the recent stream incision throughout the western United States is at least partially a result of the widespread loss or removal of beaver dams. The historical records and the banks of incised streams provide evidence that beaver inhabited many of these streams at one time. The cause of this recent incision is still unclear, but the hypothesis that it might be the cumulative result of removing millions of beaver dams is at least consistent with available scientific information about the timing, location, and extent of incision. Studies of incision and the possible use of beaver in restoring incised streams in other arid parts of the beaver's former range, such as in southern Europe and parts of Asia, would be useful.

For all the scientific studies of beaver, very few have addressed the cumulative effects of the widespread dam-removal "experiment" conducted across North America over the past few centuries and across Eurasia over the past millennium. It is likely that the hydrologic, geomorphologic, and biological cumulative effects are, and continue to be, substantial. Watershed-scale experiments to assess the effects of restoring beaver dams to move historical numbers would greatly aid our understanding of how stream systems historically functioned and perhaps lead to innovative large-scale stream-restoration strategies.

References

Aleksiuk, M. 1970. The seasonal food regime of arctic beavers. Ecology 51:264–270.

Apple, L. L. 1985. Riparian habitat restoration and beavers. In Riparian ecosystems and their management: reconciling conflicting uses. USDA Forest Service, Rocky Mountain Forest & Range Experiment Station, General Technical Report RM-120, Fort Collins, Colorado.

Apple, L. L., B. H. Smith, J. D. Dunder, and B. W. Baker. 1983. The use of beavers for riparian/aquatic habitat restoration of cold desert, gully-cut stream systems in southwestern Wyoming. Pages 123–130 *in* Annual proceedings of the American Fisheries Society/Wildlife Society joint chapter meeting, February 8–10, Logan, Utah.

Balon, E. K., and E. M. P. Chadwick. 1979. Reclamation of a perch lake: a case study using density estimates and the guild concept. Archiv fuer Hydrobiologie 85.

Beedle, D. 1991. Physical dimensions and hydrologic effects of beaver ponds on Kuiu Island in southeast Alaska. Master's thesis. Oregon State University, Corvallis.

Beier, P., and R. H. Barrett. 1987. Beaver habitat use and impact in Truckee River basin. California Journal of Wildlife Management 51:794–799.

Bergerud, A. T., and D. R. Miller. 1977. Population dynamics of Newfoundland beaver. Canadian Journal of Zoology 55:1480–1492.

Brown, J. B. 1963. The role of geology in a unified conservation program, Flat Top Ranch, Bosque

County, Texas. Baylor Geological Studies Bulletin 5:1–29.

Bryant, M. D. 1983. The role of beaver dams as coho salmon habitat in southeast Alaska streams. Pages 183–192 *in* J. M. Walton and D. B. Houston, editors. Proceedings of the Olympic Wild Fish Conference. Olympic Wild Fish Conference, Port Angeles, Washington.

Bustard, D. R., and D. W. Narver. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Resource Board of Canada 32:667–680.

Butler, D. R. 1989. The failure of beaver dams and resulting outburst flooding: a geomorphic hazard of the southeastern Piedmont. Geographical Bulletin 31:29–38.

Butler, D. R., and G. P. Malanson. 1995. Sedimentation rates and patterns in beaver ponds in a mountain environment. Geomorphology 13(1–4):255–269.

Call, M. W. 1970. Beaver pond ecology and beaver-trout relationships in southeastern Wyoming. Doctoral dissertation. University of Wyoming, Laramie.

Chisholm, I. M., W. A. Hubert, and T. A. Wesche. 1987. Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. Transactions of the American Fisheries Society 116:176–184.

Collen, P., and R. J. Gibson. 2001. The general ecology of beavers (*Castor* spp.) as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish - a review. Reviews in Fish Biology and Fisheries 10:439–461.

Craig, P. C. 1978. Movements of stream resident and anadromous arctic char (*Salvelinus alpinus*) in a perennial spring of the Canning River, Alaska. Journal of the Fisheries Resource Board of Canada 35:48–52.

Cunjak, R. A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. Canadian Journal of Fisheries and Aquatic Sciences 53:267–282.

Cunjak, R. A., and J. Therrien. 1998. Inter-stage survival of wild juvenile Atlantic salmon, *Salmo salar* L. Fisheries Management and Ecology 5:209–223.

Dalke, P. D. 1947. The beaver in Missouri. Missouri Conservationist 8:1–3.

Danilov, P. I., and V. Y. Kan'shiev. 1983. The state of populations and ecological characteristics of European (*Castor fiber* L.) and Canadian (*Castor canadensis* Kuhl.) beavers in the northwestern USSR. Acta Zool Fenn. Helsinki: Finnish Zoological Publishing Board 174:95–97.

Devito, K. J., and P. J. Dillon. 1993. Importance of runoff and winter anoxia to the P and N dynamics of a beaver pond. Canadian Journal of Fisheries and Aquatic Sciences 50:2222–2234.

Dunaway, D., S. R. Swanson, J. Wendel, and W. Clary. 1994. The effect of herbaceous plant communities and soil textures on particle erosion of alluvial streambanks. Geomorphology 9:47–56.

Dunne, T., and L. B. Leopold. 1978. Water in environmental planning. Freeman, New York.

Ehrman, T. P., and G. A. Lamberti. 1992. Hydraulic and particulate matter retention in a 3rd-order Indiana stream. Journal of the North American Benthological Society 11:341–349.

Elmore, W., and R. L. Beschta. 1987. Riparian areas: perceptions in management. Rangelands 9:260–265.

Finley, W. L. 1937. Beaver - conserver of soil and water. Transactions of the American Wildlife Conference 2:295–297.

Fredlake, M. 1997. Re-establishment of North American Beaver (*Castor canadensis*) into the San Pedro Riparian National Conservation Area. U.S. Bureau of Land Management, Environmental Assessment EA no. AZ-060–97-004, Tucson, Arizona.

Gard, R. 1961a. Creation of trout habitat by constructing small dams. Journal of Wildlife Management 52:384–390.

Gard, R. 1961b. Effects of beaver on trout in Sagehen Creek, California. Journal of Wildlife Management 25:221–242.

Gard, R., and D. W. Seegrist. 1972. Abundance and harvest of trout in Sagehen Creek, California. Transactions of the American Fisheries Society 3:463–477.

Gurnell, A. M. 1998. The hydrogeomorphological effects of beaver dam-building activity. Progress in Physical Geography 22:167–189.

Hagglund, A., and G. Sjoberg. 1999. Effects of beaver dams on the fish fauna of forest streams. Forest Ecology and Management 115:259–266.

Halley, D. J., and F. Rosell. 2002. The beaver's reconquest of Eurasia: status, population development and management of a conservation success. Mammalian Reviews 32:153–178.

Hanson, W. D., and R. S. Campbell. 1963. The effects of pool size and beaver activity on distribution and abundance of warm-water fishes in a north Missouri stream. American Midland Naturalist 69:137–149.

Hartman, G. 1994. Long-term population development of a reintroduced beaver (*Castor fiber*) population in Sweden. Conservation Biology 8:713–717.

Haveren, B. P., W. L. Jackson, and G. C. Lusby. 1987. Sediment deposition behind Sheep Creek Barrier Dam, southern Utah. Journal of Hydrology (NZ) 26:185–196.

Heede, B. H. 1978. Designing gully control systems for eroding watersheds. Environmental Management 2:509–522.

Heede, B. H., and L. F. DeBano. 1984. Gully rehabilitation–a three-stage process in a sodic soil. Journal of the Soil Society of America 48:1416–1422.

Hering, D., M. Gerhard, E. Kiel, T. Ehlert, and T. Pottgiesser. 2001. Review: study on near-natural conditions of central European mountain streams, with particular reference to debris and beaver dams: results of the REG meeting 2000. Limmologica 31:81–92.

Howard, R. J., and J. S. Larson. 1985. A stream habitat classification system for beaver. Journal of Wildlife Management 49:19–25.

Huey, W. S., and W. H. Wolfrum. 1956. Beaver-trout relations in New Mexico. Progressive Fish-Culturist 18:70–74.

Ives, R. L. 1942. The beaver-meadow complex. Journal of Geomorphology 5:191–203.

Jakober, M. J. 1995. Autumn and winter movement and habitat use of resident bull trout and westslope cutthroat trout in Montana. Master's thesis. Montana State University, Bozeman.

Jaksic, F. M., J. A. Iriarte, J. E. Jimenez, and D. R. Martinez. 2002. Invaders without frontiers: cross-border invasions of exotic animals. Biological Invasions 4:157–173.

Jenkins, S. H. 1979. Castor canadensis. Mammalian Species 120:1–8.

Jester, D. B., and J. H. McKirdy. 1966. Evaluation of trout stream improvement in New Mexico. Annual Conference of the Western Association of State Game and Fish Commissioners 26:79–81.

Johnston, C. A., and R. J. Naiman. 1990a. Aquatic patch creation in relation to beaver population trends. Ecology 71:1617–1621.

Johnston, C. A., and R. J. Naiman. 1990b. The use of a geographic information system to analyze long-term landscape alteration by beaver. Landscape Ecology 4:5–19.

Keast, A., and M. G. Fox. 1990. Fish community structure, spatial distribution and feeding ecology in a beaver pond. Environmental Biology of Fishes 27:201–214.

Knudsen, G. J. 1962. Relationship of beaver to forests, trout and wildlife in Wisconsin. Wisconsin Department of Natural Resources Technical Bulletin 25:1–50.

Leidholt Bruner, K., D. E. Hibbs, and W. C. McComb. 1992. Beaver dam locations and their effects on distribution and abundance of coho salmon fry in two coastal Oregon streams. Northwest Science 66:218–223.

Leopold, A. S. 1972. Wildlife in Mexico. University of California Press, Berkeley.

Li, R. M., and H. W. Shen. 1973. Effects of tall vegetation on flow and sediment. Journal of the Hydraulics Division, Proceedings of the American Society of Civil Engineers 91:793–814.

Lisle, T. E. 1982. Roughness elements: a key resource to improve anadromous fish habitat. Pages 93–98 *in* T. J. Hassler, editor. Proceedings: Propagation, Enhancement, and Rehabilitation of Anadromous Salmonid Populations and Habitat in the Pacific Northwest Symposium. California Cooperative Fisheries Research Unit, Humboldt State University, Arcata, California.

Lowry, M. M. 1993. Groundwater elevations and temperature adjacent to a beaver pond in central Oregon. Master's thesis. Oregon State University, Corvallis.

MacDonald, D. W., F. H. Tattersall, E. D. Brown, and D. Balharry. 1995. Reintroducing the European beaver to Britain: nostalgic meddling or restoring biodiversity? Mammalian Reviews 25:161–200.

Mackie, R. S. 1997. Trading beyond the mountains. UBC Press, Vancouver.

Mai, H. 1978. Studies on the jaws of the Pleistocene beavers Trogontherium- and Castor- and their stratigraphic classification. Schriften des Naturwissenschaftlichen Vereins fuer Schleswig-Holstein 48:35–39.

McCall, T. C., P. Hodgman, D. R. Diefenbach, and R. B. Owen. 1996. Beaver populations and their relation to wetland habitat and breeding waterfowl in Maine. Wetlands 16:163–172.

Medwecka-Kornas, A., and R. Hawro. 1993. Vegetation on beaver dams in the Ojcow National Park (southern Poland). Phytocoenologia 23:611–618.

Murphy, M. L., J. Heifetz, J. F. Thedinga, S. W. Johnson, and K. V. Koski. 1989. Habitat utilization by juvenile Pacific salmon (*Oncorhynchus*) in the glacial Taku River, southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 46:1677–1685.

Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. Bioscience 38:753–761.

Naiman, R. J., D. M. McDowell, and B. S. Farr. 1984. The influence of beaver (*Castor canadensis*) on the production dynamics of aquatic insects. Proceedings of the Congress of the International Association of Limnology 22:1801–1810.

Naiman, R. J., J. M. Melillo, and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology 67:1254–1269.

Naiman, R. J., G. Pinay, C. A. Johnston, and J. Pastor. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. Ecology 75:905–921.

Neff, D. J. 1959. A seventy-year history of a Colorado beaver colony. Journal of Mammalogy 40:381–387.

Nolet, B. A., and F. Rosell. 1998. Comeback of the beaver *Castor fiber*: an overview of old and new conservation problems. Biological Conservation 83:165–173.

Paragamian, V. L. 1981. Some habitat characteristics that affect abundance and winter survival of smallmouth bass in the Maquoketa River, Iowa. Pages 45–53 *in* L. A. Kruholz, editor. The Warmwater Streams Symposium: a national symposium on fisheries aspects of warmwater streams. American Fisheries Society, Southern Division, Bethesda, Maryland.

Parker, M., F. J. Wood, Jr., B. H. Smith, and R. G. Elder. 1985. Erosional downcutting in lower order riparian ecosystems: have historical changes been caused by removal of beaver? Pages 35–38 *in* R. R. Johnson, editor. Riparian ecosystems and their management: reconciling conflicting uses. USFS, RM GTR 120, Fort Tucson, Arizona.

Pastor, J., J. Bonde, C. Johnson, and R. J. Naiman. 1993. Markovian analysis of the spatially dependent dynamics of beaver ponds. Lectures on Mathematics in the Life Sciences 23:5–27.

Pattie, J. O. 1833. The personal narrative of James Ohio Pattie of Kentucky. Timothy Flint, editor. John H. Wood, Cincinnati.

Pollock, M. M., R. J. Naiman, H. E. Erickson, C. A. Johnston, J. Pastor, and G. Pinay. 1994. Beaver as engineers: influences on biotic and abiotic characteristics of drainage basins. Pages 117–126 *in* C. G. Jones and J. H. Lawton, editors. Linking species to ecosystems. Chapman and Hall, New York.

Pollock, M. M., and G. R. Pess. 1998. The current and historical influence of beaver (*Castor canadensis*) on coho (*Oncorhynchus kisutch*) smolt production in the Stillaguamish River Basin. 10, 000 Years Institute, Seattle.

Ponce, V. M., and D. S. Lindquist. 1990. Management of baseflow augmentation: a review. Water Resources Bulletin 26:259–268.

Rabe, F. W. 1970. Brook trout populations in Colorado beaver ponds. Hydrobiologia 35:431–448.

Rea, A. M. 1983. Once a river: bird life and habitat change on the Middle Gila. University of Arizona Press, Tucson.

Reid, K. A. 1952. The effect of beaver on trout waters. Maryland Conservationist 29:21–23.

Retzer, J. L., H. M. Swope, J. D. Remington, and W. H. Rutherford. 1956. Suitability of physical factors for beaver management in the Rocky Mountains of Colorado. State of Colorado, Department of Game and Fish Technical Bulletin No. 2, Denver.

Rudemann, R., and W. J. Schoonmaker. 1938. Beaver dams as geological agents. Science 88:523–524.

Rupp, R. S. 1954. Beaver-trout relationships in the headwaters of Sunkhaze Stream, Maine. Transactions of the American Fisheries Society 84:75–85.

Rutherford, W. H. 1964. The beaver in Colorado: its biology, ecology, management and economics. Colorado Game, Fish and Parks Department, Technical Publication 17, Denver.

Rutten, M. G. 1967. Flat-bottomed glacial valleys, braided rivers and the beaver. Geologie en Mijnbouw 46:356–360.

Salyer, J. C. 1935. Preliminary report on the beaver trout investigation. American Game 24:6–15.

Scheffer, P. M. 1938. The beaver as an upstream engineer. Soil conservation 3:178–181.

Schlosser, I. J. 1995. Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. Ecology 76:908–925.

Seton, E. T. 1929. Lives of game animals. Doubleday, Doran and Co., Inc., Garden City, New York.

Skinner, Q. D., J. E. Speck, Jr., M. Smith, and J. C. Adams. 1984. Stream water quality as influenced by beavers within grazing systems in Wyoming. Journal of Range Management 37:142–146.

Slaney, P. A., and D. Zaldokas, editors. 1997. Fish habitat rehabilitation procedures. Ministry of the Environment, Lands and Parks, Vancouver.

Smith, A. E. 1950. Effects of water runoff and gradient on beaver in mountain streams. Master's thesis. University of Michigan, Ann Arbor.

Smith, R. D., R. C. Sidle, and P. E. Porter. 1993. Effects on bedload transport of experimental removal of woody debris from a forest gravel-bed stream. Earth Surface Processes and Landforms 18:455–468.

Snodgrass, J. W., and G. K. Meffe. 1998. Influence of beavers on stream fish assemblages: effects of pond age and watershed position. Ecology 79:928–942.

Snodgrass, J. W., and G. K. Meffe. 1999. Habitat use and temporal dynamics of blackwater stream fishes in and adjacent to beaver ponds. Copeia 3:628–639.

Stabler, D. F. 1985. Increasing summer flow in small streams through management of riparian areas and adjacent vegetation - a synthesis. USDA Forest Service General Technical Report RM-120:206–210, Fort Collins, Colorado.

Stock, J. D., and I. J. Schlosser. 1991. Short-term effects of a catastrophic beaver dam collapse on a stream fish community. Environmental Biology of Fishes 31:123–129.

Suzuki, N., and W. C. McComb. 1998. Habitat classification models for beaver (*Castor canadensis*) in the streams of the central Oregon Coast Range. Northwest Science 72:102–110.

Swales, S., F. Caron, J. R. Irvine, and C. D. Levings. 1988. Overwintering habitats of coho salmon (*Oncorhynchus kisutch*) and other juvenile salmonids in the Keogh River system, British Columbia. Canadian Journal of Zoology 66:254–261.

Swanston, D. N. 1991. Natural processes. Pages 139–179 *in* W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.

Tappe, D. T. 1942. The status of beavers in California. State of California Department of Natural Resources Division of Fish and Game. Game Bulletin 3:1–60.

Voigt, D. R., G. B. Kolenosky, and D. H. Pimlott. 1976. Changes in summer food of wolves in central Ontario. Journal of Wildlife Management 40:663–668.

Warren, E. R. 1926. A study of the beaver in the Yancy Region of Yellowstone National Park. Roosevelt Wildlife Annals 1:5–191.

Warren, E. R. 1932. The abandonment and reoccupation of pond sites by beavers. Journal of Mammalogy 13:343–346.

Wilen, B. O., B. P. MacConnell, and D. L. Mader. 1975. The effects of beaver activity on water quality and water quantity. Proceedings of the Society of American Foresters:235–240.

Winegar, H. H. 1977. Camp Creek channel fencing–plant, wildlife, soil and water response. Rangeman's Journal 4:10–12.

Woo, M. K., and J. M. Waddington. 1990. Effects of beaver dams on subarctic wetland hydrology. Arctic 43:223–230.

Wood, J. A. 1997. Augmenting minimum streamflows in sediment deposition reaches. Chapter 14 *in* P. Slaney and D. Zaldokas, editors. Fish habitat rehabilitation procedures. Ministry of Environment, Lands and Parks, Watershed Restoration Program, Vancouver.

Zierholz, C., I. P. Prosser, P. J. Fogarty, and P. Rustomji. 2001. In-stream wetlands and their significance for channel filling and the catchment sediment budget, Jugiong Creek, New South Wales. Geomorphology 38(3–4):221–235.

Zurowski, W., and B. Kasperczyk. 1986. Characteristics of a European beaver population in the Suwalki Lakeland. Acta Theriologica 13:311–325.