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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

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Abstract

The Eurasian and North American beavers are similar in their ecological requirements, and require water deep enough to cover the entrance to their lodge or burrow. A food cache is often built next to the lodge or burrow, except in some southern areas. On small streams (up to fourth order) dams are frequently built to create an impoundment, generally on low gradient streams, although at high population densities dams may be built on steeper gradient streams. On large rivers or in lakes, simply a lodge with its food cache may be built. The beaver is a keystone riparian species in that the landscape can be considerably altered by its activities and a new ecosystem created. The stream above a dam changes from lotic to lentic conditions. There are hydrological, temperature and chemical changes, depending on types of dams and locations. Although the invertebrates may be fewer per unit area, total number of organisms increases, and diversity increases as the pond ages. In cool, small order streams, the impoundments provide better habitat for large trout, possibly creating angling opportunities. However, at sites

where water temperatures rise above their optimum preferenda, salmonids may be replaced by other species, such as cyprinids, catostomids, percids or centrarchids. As the habitat is altered, interactions amongst co-habiting species may change. For example, brown trout or brook trout (charr) may become dominant over Atlantic salmon. In warm water streams there may be a shift from faster water dwellers to pond dwellers. Larger bodied fish, such as centrarchids and esocids may displace smaller bodied fish such as cyprinids, providing better angling. Refugia from high or low water flows, low oxygen or high temperatures, may be provided in adverse conditions in winter or summer. However, in some cases dams are obstructions to upstream migration, and sediment may be deposited in former spawning areas. The practicality and benefits of introducing or restoring beaver populations will vary according to location, and should be considered in conjunction with a management plan to control their densities.

Introduction

The Eurasian beaver (*Castor fiber* L.) and the closely related North American beaver (*Castor canadensis* Kuhl) are semi-aquatic plant eating mammals (Family, Castoridae; Order, Rodentia) (reviews in, Hill, 1982; Novak, 1987; Nolet, 1996). Beavers require access to water with sufficient depth to allow the construction of a winter food cache (except in the more southern regions) and to ensure that the entrance to their lodge or burrow remains underwater. On low gradient, small streams of first to fourth order, beavers frequently build dams to create impoundments. The lodge, in which the family group or colony shelter and rear their young, is built on the bank or on an island in the impoundment. A cache of twigs and branches is prepared adjacent to the lodge to supply winter food. On lakes, a lodge is constructed with an adjacent food pile. The water level may be raised by damming the lake outlet. On rivers which are too large to dam, a lodge is usually constructed, although a beaver colony may live in burrows in the river bank, depending on bank characteristics. Beaver population density is usually expressed in colonies per unit area or per length of stream.

Beavers may alter the riparian landscape considerably. Flooding, as a result of damming activities, kills most woody species and creates wetlands. By felling trees, beavers create open areas in riparian woodlands and can change the species distribution of trees. Positive effects include the creation of habitat for some fish species, and for wildlife favouring ponds and marshes. In some instances beaver activities may have negative effects related to human use such as: flooding of grazing land; flooding of docks and cottages on small lakes; blocking of culverts; obstructing the upstream migration of anadromous or other fish species; and changing the fish composition in the pond to species less desired for angling.

Whether beaver-induced changes of fish populations are beneficial or harmful will depend on the prevailing constraints on local fish species composition and abundance. Lack of information, in some instances, leads many to regard the beaver as a pest and implement removal programmes in ecosystems where hydrological and ecological effects due to the beaver might in fact be positive. Landowners and anglers must know the consequences of proposals to restore beaver populations to areas or countries where the species has been extirpated before such introductions are made (Collen, 1997). This review presents information which will help managers and landowners make informed decisions.

Comparison of Eurasian and North American beavers

Both Eurasian and North American beavers experienced dramatic declines in populations, due to exploitation and habitat loss. Populations have recovered in many areas following conservation and restoration measures. Eurasian beavers were once common in the northern forest belt throughout much of Europe and Asia, but by the 19th century only small residual populations remained (Vernon, 1992). However, beavers from these relic populations have successfully been used for reintroduction programmes and the Eurasian beaver population is now approaching half a million (Nolet and Rosell, 1998). The North American beaver occurs naturally along freshwater bodies over the entire North American continent, except in treeless areas such as the arctic tundra, peninsular Florida and desert lands of the southwest (Jenkins and Busher, 1979; Hill, 1982). It suffered a similar history to the Eurasian beaver: trapping and changes in habitat destroyed many populations. After near extirpation in the US and Canada, management programmes have resulted in the beaver being abundant once again (Novak, 1987). The North American beaver population has recently been estimated to be in the order of 6–12 million (Naiman et al., 1986).

The North American beaver is so similar to the Eurasian beaver that they were originally considered conspecific by some taxonomists (Hill, 1982). However, distinct karyotypes and craniological differences have been demonstrated by Lavrov and Orlov (1973).

Opportunities for comparative studies on these two species have occurred due to the introduction of the North American beaver into parts of the Eurasian beaver's range. During the 1920's and 1930's, North American beaver were released in Poland and Finland (Lahti and Helminen, 1974; Ermala et al., 1989). They were extremely successful in Finland and spread into parts of Russia in the 1950's (Danilov, 1992, 1995). Studies in these countries have allowed researchers to discuss behavioural and ecological differences between the two species.

The North American beaver is reported to indulge in greater building activity than the Eurasian beaver (Danilov and Kan'shiev, 1982). For example, in the Russian Northwest 66.3% of North American beaver settlements had dams, while the value for Eurasian beavers was 45.2%. Corresponding figures for settlements with lodges were 75% and 33.9%, and for settlements with bank burrows, 25% and 64.1% (Danilov, 1995). These figures suggest that in this part of its geographic range, the Eurasian beaver tends to live in burrows and is less likely to construct dams than the North American beaver. However, for the Eurasian beaver within this area, building activity declines in a northerly direction. Almost 50% of the beavers live in lodges in the southern part of the Russian north west (Pskov and Novgorod regions), while only 10% of the population in the north (Lapland reserve) use lodges (Danilov, 1995).

Although comparative studies have found the Eurasian beaver to be a poorer builder than the North American beaver, the effects of their dams on the environment will not be much different (Nolet, 1996).

In relation to diet, the North American and Eurasian beavers have similar feeding habits (Lahti and Helminen, 1974; Danilov and Kan'shiev, 1983). However, although utilisation of tree species is similar for both species of beaver, Danilov (1995) recorded that the North American beaver made greater use of grey alder (*Alnus incana*). Also, Danilov (1992) noted that in northern parts of the beavers' range the North American beaver "more willingly" feed on substitutes like birch. In late spring, wood species are gradually replaced by herbaceous species in the diet of both Eurasian and North American beavers (Danilov, 1995).

Two important differences between the species are that the North American beaver matures earlier and has larger litters than the Eurasian beaver (Lahti and Helminen, 1974; Danilov and Kan'shiev, 1983). However, Hartman (1997) found that age of dispersal, and eventual reproduction, were influenced by population densities. His results suggest that at low densities the differences between the species would be less important, i.e., both species could exhibit yearling dispersal and early attainment of sexual maturity. Limited information suggests that when the species are sympatric, the North American beaver can displace the Eurasian beaver. This may, in part, be due to the higher reproductive rate of the North American beaver (Danilov and Kan'shiev, 1983). This view was supported by Lahti and Helminen (1974) who found that the differences observed in the population growth rates of the two species in Finland could not be linked to differences in habitat or food.

However, the North American beaver does not always dominate the Eurasian beaver and examples of the Eurasian beaver displacing the North American beaver are mentioned by Danilov (1995). Overall, Danilov (1995) concludes that the North American beaver is more competitive in the severe conditions of the North whereas, in more favourable habitats the competitive abilities of the two species are more evenly matched.

Macdonald et al. (1995) made the point that studies of North American beavers can provide important clues about the potential effects of Eurasian beavers. This is important because nearly all the information on the beaver's impact on the environment originates from studies of the North American beaver (Macdonald et al., 1995; Nolet, 1996). Where Eurasian beavers construct dams and fell trees, they are likely to have similar effects to the North American beaver (Macdonald et al., 1995).

General ecology and behaviour of beavers

Beavers are highly social and territorial animals which normally live as a family unit (colony), consisting of two parental adults, the yearlings born the previous year, and the young of the year (Wilsson, 1971). Rosell and Parker (1995) calculated an overall mean value for colony size of 3.8 for the Eurasian beaver and 5.2 for the North America beaver. Colony size is lower in newly established populations, in poor habitat, and in harvested populations.

The young are born in May-June and generally, the two year olds, and occasionally one year olds, leave the parental colony and move to new areas just before this time. If these dispersing sub-adults fail to establish territories they may return to the parental colony (Wilsson, 1971; Hartman, 1994a).

Colony density is influenced largely by habitat quality. When beavers were sequentially released into a previously unoccupied area in the Netherlands, they successively settled in good habitat and then poor habitat, and then became floaters (Nolet and Rosell, 1994). This pattern was regarded as evidence that territorial behaviour limited density. In Russia, Semyonoff, (1951) suggested that 1.5, 0.5 and 0.1 colonies/km of river bank might be expected in good, quite good and mediocre habitat respectively. Differences were related to gradients, physical characteristics of stream bank, and aquatic and riparian vegetation.

In areas with large beaver populations, they commonly occur in a wide range of lotic environments, from small seepages with a flow only just adequate for damming, through to large rivers. They also utilise lentic environments such as large lakes, which do not experience dramatic changes in water levels. Zurowski and Kasperczyk (1986), while studying the beaver population of the Suwalki Lakeland in Poland, noted that both river and lake sites were important. They found that when lower population densities provided better opportunities for the beavers to select preferred habitats, they were most abundant on rivers.

Beavers often do not construct dams and lodges but simply burrow into the river bank and create a bank den (Frisch, 1975; Danilov and Kan'shiev, 1982). Beavers may also excavate canals to extend their area of foraging and allow them to float branches back to safe feeding locations (Richard, 1967; Wilsson, 1971). Canals are usually constructed in low gradient areas, they are generally 30–60 cm wide and 20–35 cm deep, and canal networks can stretch for several hundred metres (Stocker, 1985).

The excavation of burrows and canals will have localised effects on site characteristics, but it is through their dam building activities that beavers exert their greatest influence on freshwater ecosystems. The size of dams differ widely in relation to topography and the availability of building materials (Curry-Lindahl, 1967). However, some exceptionally large North American beaver dams have been recorded. These include a 700 m long dam in Montana (Ives, 1942) and a dam which exceeded a height of 5 m in Wyoming (Grasse and Putnam, 1955). There are also numerous references to the dam building skills of the Eurasian beaver (Curry-Lindahl, 1967; Myrberget, 1967; Zharkov and Sokolov, 1967; Wilsson, 1971; Richard, 1983). Their dams may range in length from less than a metre to hundreds of metres and the height can vary from just a few centimetres to a couple of metres (Curry-Lindahl, 1967; Stocker, 1985; Balodis, 1994) to over 3 m high (F. Rosell *pers. comm.*). The width of the dam will, in part, be related to the height of the structure but measurements up to 2 m have been recorded (Richard, 1955; Medwecka-Korna's and Hawro, 1993). Both North American and Eurasian beaver colonies can build and keep in repair a series of dams which may remain active for many years.

In North America, dams are rarely built in streams greater than 4th order. Main river constructions on higher order streams are often destroyed during periods of high flow (Naiman et al., 1986). The same restriction appears to apply to the Eurasian beaver (Hartman, 1994a). Hartman (*pers. comm.*) suggests that dam building behaviour is suppressed if the water is deeper than one metre, and found that 80–90% of the dams were built in places where the depth was less than 0.6 m. He found several lodges without dams in narrow (1–4 m) but relatively deep streams (0.7–1.5 m).

Although beavers appear to prefer the relatively flat terrain of fertile valleys, they can occupy streams with steeper gradients (Wing, 1951; Schulte and Schneider, 1989; Zurowski, 1989; Müller-Schwarze, 1992). However, densities at sites with steep gradients generally do not reach the same levels as at preferred sites (Zurowski, 1992). Zurowski, (1989) found that dam building activity was more intensive in mountain tributaries than in lowland sites. Nevertheless, Stack and Beschta (1989) compared two Oregon coastal streams: a stream with a relatively steep gradient (5.3%) that had 12 small beaver dams, and a stream with a gentler channel slope (2.1%) that had 5 relatively large beaver dams. Both had approximately the same percentage of total pool volume behind the beaver dams (90%). They also found that beaver-influenced streams did not alter the frequency of occurrence of pool – formation processes or elements, but pool volumes were larger. They therefore suggested that utilizing beavers to increase pool habitat or rehabilitate degraded channels may provide an effective management technique for some stream systems.

The population densities and movements of beaver along a river are influenced by the availability of deciduous trees and bushes (Semyonoff, 1951). Herbaceous plants, especially aquatic macrophytes, and twigs of woody plants, with leaves and bark, are particularly important during the period of vegetative growth (Simonsen, 1973). During the winter, beaver can be dependent on woody plants, especially the bark (Nolet et al., 1994). The availability of woody plants is one of the most important factors in determining beaver range and distribution. Beavers may store cut tree stems in a discrete winter food cache in the water and the subsequent use of this food supply will be influenced by the severity of the winter climate (Semyonoff, 1953; Aleksiuk, 1970; Wilsson, 1971; Rosell and Parker, 1995).

Where available, aspen (*Populus tremula* and *P. tremuloides*) feature prominently as the preferred species (Semyonoff, 1951; Hall, 1960; Brenner, 1962; Johnston and Naiman, 1990). However, in the absence of aspen, beaver will show varying preferences, depending on the availability of species at study sites (Jenkins, 1979). Willows (*Salix* spp.) can be important, and in areas where these species are abundant Semyonoff (1951) noted that beaver may use less birch (*Betula* spp.) and poplar (*Populus* spp.). He also found that where there were few willows the beavers turned to birch. Danilov (1995) also reported that in areas where birch dominated the woodland, it made up the bulk of their diet. Alder (*Alnus* spp.) is often used in dams and lodges as a structural material rather than as food (Wilsson, 1971; Slough, 1978; Barnes and Mallik, 1996).

Conifers may also be used and Simonsen (1973) noted that in Norway, common juniper (*Juniperus communis*) and Scots pine (*Pinus sylvestris*) were occasionally eaten, though spruce (*Picea* spp.) appears to be avoided. However, beavers can subsist seasonally and may sometimes colonise in areas where the tree cover is almost entirely coniferous. In these areas herbaceous plants are the primary food source (Hatler, 1981; Svendsen, 1980).

Studies of beaver foraging have demonstrated that the size of trees cut varies according to what is available and the distance of the tree from the water (Jenkins, 1980; Pinkowski, 1983; Belovsky, 1984; McGinley and Whitham, 1985; Basey et al., 1988; Fryxell and Doucet, 1991; Woodard, 1994). Trees of 3–8 cm diameter are most often used (Hall, 1960; Simonsen, 1973; Woodard, 1994) however, there are exceptional records of substantial trees exceeding 1 m diameter being felled (Wilsson, 1971; Butler, 1991). Aldous (1938) estimated that trees averaging 2.7 in, 4.5 in, and 5.2 in in diameter contain approximately 103, 400, and 580 oz of outer bark and upper branches. Beaver required between 22 and 23 oz of bark and twigs daily. By coming on to land to fell trees, which are then transported back to their ponds for eating, beavers act as central place foragers (Jenkins, 1980). They rarely move more than 100 m from the water to feed but, if adequate preferred foods are available, smaller feeding areas are used (Simonsen, 1973; Barnes and Dibble, 1988).

Beavers do not use their preferred food species, poplar, in a sustained-yield manner (Hall, 1960; Northcott, 1971; Gill, 1972; Beier and Barrett, 1987). Rather, they tend to over-exploit some food resources and waste others by inundation. In short, beaver pond systems generally are not permanent. Call (1966) suggests management of beavers by trapping to sustain their food supply.

Beaver ponds generally are of two types: “stream channel”, which are long, narrow and less than 0.4 ha; and “flood plain”, which are larger impoundments and may cover several hectares of land (Pullen, 1971). Stream channel ponds are typically short lived, but flood plain ponds may persist for many years. The age of the pond affects the flora and fauna, with a greater diversity of invertebrates as the pond ages. Welch (1935) listed six successional stages, young, adolescent, mature, senescent, marsh, and dry. At the same time the pond changes from oligotrophic, to eutrophic, and in the senescent stage to dystrophic (Keiper, 1966). For the initial 3 years, ponds will contain living trees (young stage). For the next 4 to 10 years there will be many standing but dead trees, and there is an abundance of emergent aquatic vegetation. Water depths are greater than 0.3 m over most of the pond, and open water will cover about 40–50% of the surface (adolescent to mature). Senescent ponds typically contain open water only near the dam. Emergent aquatic vegetation is very extensive, and a water depth of less than 0.3 m will cover most of the area. Very few standing dead trees will be seen. Ultimately beavers abandon the pond, and a “beaver meadow” may result, with grasses and sedges, and finally the forest re-establishes (Pullen, 1971).

Beaver populations have expanded to the point of being a nuisance in some areas and there is a growing literature on methods to keep beaver under control (Hicks, 1977; Brooks et al., 1980; Hammerson, 1994). Extreme declines of beaver populations as a result of epizootics, especially tularemia, have been documented (Lawrence et al., 1956; Shelton, 1979). Local destruction by other natural events such as flash floods (Rutherford, 1955) are known. Bank erosion during spring floods may be particularly destructive to bank-dwelling beavers (Boyce, 1974), and winter ice jams occasionally tear out food caches and even lodges. Changes in water levels may be detrimental. Lodges may be extended or rebuilt in new reservoirs (Courcelles and Nault, 1983) and during drought the lodge is modified so that the entrance remains underwater (Novak, 1987). However, in reservoirs with high seasonal fluctuating regimes beavers would probably be eliminated (Novak, 1987; Gibson et al., 1999).

Predators

The list of predators reported to prey on North American beavers includes wolf (*Canis lupus*) (Forbes and Theberge, 1996), coyote (*Canis latrans*) (Packard, 1960), black bear (*Ursus americanus*) (Hakala, 1952), lynx (*Felix lynx*) (Saunders, 1963), wolverine (*Gulo luscus*) (Rausch and Pearson, 1972), otter (*Lutra canadensis*) (Seton, 1929), red fox (*Vulpes vulpes*), mink (*Mustela vison*), alligator (*Alligator mississippiensis*), puma (*Felis concolor*), and fisher (*Martes pennanti*) (Rosell et al., 1996). A similar list of predators has been reported for the Eurasian beaver and includes wolf, brown bear (*Ursus arctos*), lynx, wolverine (*Gulo gulo*) and otter (*Lutra lutra*) (Semyonoff, 1951; Tyurnin, 1984). Various large raptors may also prey on beaver. Of all these predators, the wolf appears to be the only species that regularly preys on beaver (Rosell et al., 1996).

In parts of America the wolf may be able to regulate local populations of North American beavers (Shelton and Peterson, 1983). However, this is unlikely to happen in Europe as the wolf and other potential predators are rare (Rosell et al., 1996). Hartman (1994b) suggested that the population development of beaver in Sweden might have been less irruptive in the presence of wolves.

Influence of beaver on the physicochemical characteristics of streams

Beaver can alter large areas of the landscape by damming rivers. Within a 250 km^2 area of the Kabetogame Peninsular, Minnesota, the total area impounded (flooded by dams) increased from 1 to 13% of the landscape as the beaver population increased from near extinction to a density of 1 colony per km^2 (Johnston and Naiman, 1990). By contrast, in a predominantly coniferous forested area (3,500 hectares) in southern Norway, which had a well established beaver population, only 0.2% of the total area was flooded (Rosell and Parker, 1995). In areas of Quebec where the beaver population is largely unexploited, they can influence as much as 30–50% of the total length of 2nd to 4th order streams (Naiman and Melillo, 1984).

Beaver ponds in upland V-shaped valleys are generally small whereas in flood plain areas a low dam can flood a relatively large surface area (Johnston and Naiman, 1987). Beaver impoundments also increase the area of riparian habitat and recharge ground water by elevating the water table (Bergstrom, 1985; Johnston and Naiman, 1987). Dams decrease peak discharge during a runoff event and thereby reduce the possibility of flooding (Bergstrom, 1985; Parker et al., 1985). Due to large initial differences in velocity, beaver dams which flood uplands reduce the kinetic energy of the stream more than those which flood wetlands (Johnston and Naiman, 1987).

Hydrological effects

Although a single beaver dam may have only a small effect on stream flow, a series of dams can have a significant effect (Grasse, 1951). These effects would be particularly evident during the peaks and troughs of the annual discharge patterns. During dry periods, Duncan (1984) reported that up to 30% of the water in an Oregon catchment could be held in beaver ponds. This increased storage capacity for water is important and it has been suggested that large numbers of beaver dams will lead to greater flows during late summer (Parker, 1986). They may even result in a continual flow in previously intermittent streams (Yeager and Hill, 1954; Rutherford, 1955).

During flood events, an individual dam will only be able to detain a small amount of water, but a series of dams throughout a catchment would have a much greater effect. By reducing peak discharge and stream velocity, beaver impoundments can reduce the erosion potential of a runoff event (Apple et al., 1984; Parker, 1986). Several studies have reported on the ability of beaver dams to reduce fluvial incision in areas undergoing gully erosion (Apple et al., 1984; Parker et al., 1985). Associated with the reduction in stream velocity is a reduction in the sediment carrying capacity of the stream and consequently an increase in deposition. Naiman et al. (1988) found that relatively small dams could retain as much as 2000–6500 m^3 of sediment. Parker (1986) suggested that beaver dams can protect areas from erosive perturbations, if these perturbations are not too great. While beaver dams normally reduce the severity of flooding events, they can contribute to them if dam failure occurs (Butler, 1991, 1995).

Most studies have concluded that beaver dams stabilise stream flow. However, Reid (1952) reported that increased evaporation from beaver ponds in the Adirondacks could reduce the volume of flow. Woo and Waddington (1990) also found that, in the sub arctic wetlands of Ontario, the enlargement of the open water area by beaver activities resulted in an enhancement of evaporation in the summer. However, they reported that this loss from enhanced evaporation could be offset by the reduction in water loss through runoff in areas where the dams were well maintained.

Burns and McDonnell (1998), in studies of headwater catchments in the west-central Adirondack Mountains of New York, found that a beaver pond could significantly affect downstream delivery of event water through evaporation and mixing. While the pond could effectively contain all the event water for a moderate storm (51 mm) under dry antecedent conditions, it provided only minimal retention during large runoff events such as snowmelt. Summer evaporation from the beaver pond increased the concentration of solutes. In addition, in the same study area, liming of wetlands and beaver ponds was found to be more effective than whole catchment liming in neutralizing acidic surface waters during most of the year, but would have little neutralization effect during snowmelt (Newton et al., 1996).

The movements of water within bed sediments can result in the downstream movement of dissolved and particulate substances. In a typical convective pattern, stream water penetrates the bed, travels through the sediment along the longitudinal gradient and then upwells back into the river (White, 1990). As porewater moves beneath a beaver dam it is no longer affected by the pressure of the impounded water. The pressure decrease immediately downstream from the dam therefore causes a sharp upwelling of underflowing stream water and upwelling of cooler porewater from deeper in the substrate. The convective flow patterns beneath beaver dams may therefore function to store stream water components temporarily and to bring pore-water/stream water to the surface, thereby affecting distributions of surface dwelling organisms (White, 1990).

Water temperature

The effects of impoundment include changing the temperature regime, which becomes more stabilised (Gard, 1961). The increased area of shallow slow water may increase temperatures, both upstream and downstream of the dam. In a New Brunswick stream, beaver impoundments caused outflow temperatures to be greater than inflow temperatures, with the effect extending a few hundred metres downstream before return to temperature of the inflows (Alexander, 1998). In marginal habitat for cold water species the changes may eliminate some species such as salmonids from the impoundment. However, in some circumstances an increase in temperature could increase fish production (Call, 1966).

The effect of beaver activity on water temperature, particularly the creation of impoundments and the harvesting of shade producing riparian vegetation, can vary greatly depending on the region and site characteristics. Areas of Canada and Western States, such as Colorado and Wyoming, where waters are well below the critical temperatures for trout, and which have different associations of fish species from those prevailing in Eastern States, have few problems with beaver-induced temperature changes (Bailey and Stephens, 1951). Increases in water temperatures in beaver ponds were recorded in Utah (Rasmussen, 1941) and New Mexico (Huey and Wolfrum, 1956) and were considered to be beneficial to trout. Likewise, in Wyoming where trout streams are often too cold for optimum trout development, the warming effect of beaver ponds during the growing season was reported to be advantageous (Grasse and Putnam, 1955).

Alteration of water temperature regimes by beavers is often referred to as being detrimental for salmonids in Eastern States. In New York State, Cook (1940) found that a single pond on a stream may have little warming effect but the cumulative effect of a series of ponds could be damaging to trout. Summer warming of beaver ponds was recorded in Maine (Rupp, 1955) but the development of adverse conditions for trout in these sites was probably prevented by inputs of cooler water from numerous springs. Hale (1966) also recorded an increase in summer temperatures in ponds in Minnesota which may have reached temperatures above the limits tolerated by trout. While beaver ponds helped to maintain trout populations during an unusually dry season in an area of Michigan, excessive temperatures in the ponds also created problems for the trout (Adams, 1949).

Beaver impoundments served as heat collecting units in summer and cold storage units in winter, which markedly affected the survival of resident trout in Wisconsin (Avery, 1983). In the same State, Patterson (1951) found that beaver dams were detrimental in increasing the water temperature of feeder streams which consequently deprived the main river of a supply of cold water. The removal of dams in a low gradient Wisconsin river system generally resulted in an overall decrease in water temperature (Avery, 1992).

Water temperatures were often not the main interest of these previous studies, and McRae and Edwards (1994) considered that no clear relationship had been established between different sizes or numbers of impoundments and the degree of stream warming. They found that in Wisconsin headwater streams, local differences in vegetative and topographic shading, ground water inflow contribution and stream volume meant that the thermal effects of beaver impoundments were highly site dependent. There was no consistent relationship between size and number of impoundments and the degree of downstream warming. Their data indicated that large ponds act as thermal buffers, raising downstream water temperatures slightly in some instances, but they also dampened diel fluctuation.

Water chemistry

The effects of beaver-induced changes on water chemistry to fish will vary depending upon the original (pre-beaver) water chemistry. For example, if nutrients were limiting, then an increase in nitrates and phosphates from beaver activity would have a positive effect on salmonid production, while in a rich eutrophic site effects might be negligible or negative. Likewise, in an acid stream any beaver-induced increase in pH and acid-neutralising capacity (ANC) would be positive for salmonids, but would have little effect in an alkaline stream. The water quality requirements of freshwater fish have been reviewed by Alabaster and Lloyd (1980).

While it is difficult to generalise on the implications of beaver-induced water quality changes, the following examples describe the chemical processes which occur in beaver ponds.

Studies in a 2nd order Adirondack Mountain stream indicated that water physico-chemical parameters and sediment chemistry are modified as a result of beaver activity (Smith et al., 1991). They generally found that pH, ANC, dissolved organic carbon (DOC), iron (Fe^{2+}) and manganese (Mn^{2+}) values were elevated and sulphate (SO_4^{2-}), ionic forms of aluminium (Al^{n+}) and dissolved oxygen concentrations (DO) were decreased following passage of water through the beaver impoundment. The reduced oxygen concentration of the water was increased immediately during outflow from the dam and complete reoxygenation was achieved within the next 0.25 km of stream.

Further studies at this Adirondack site revealed that in addition to Al^{n+} and SO_4^{2-} the beaver pond was also a net annual sink for inlet nitrate (NO_3^-) and silica (H_4SiO_4) (Cirmo and Driscoll, 1993). Also, along with the previously reported DOC and Fe^{2+}, the ponds were a net annual source of ammonium ions (NH_4^+). They reported that the losses of ANC, which were associated with Al and basic cation retention, and organic anion release, were more than compensated for by SO_4^{2-} and NO_3^- retention and Fe^{2+} and NH_4^+ release and this produced a net production of ANC (Cirmo and Driscoll, 1993). The impounded areas provide sites where substantial alterations in water chemistry are possible, due to the ability of beaver pond sediments to store large amounts of organic matter, together with the development of anoxic zones which act as sites for ANC generation. However, Smith et al. (1991) found that differences in ANC among sites were evident only in the low flow summer period. During major run off events, the wetland areas can be short-circuited and therefore have less influence on water quality (Cirmo and Driscoll, 1993).

The role of beaver dams in modifying nitrogen (N) dynamics was studied in a 2nd order stream in Quebec (Naiman and Melillo, 1984). They found that sediment in beaver ponds stored approximately 1,000 times more N/m of stream channel, than riffle areas and this was solely a function of the amount of sediment accumulated in the different habitats. In the riffle areas of this stream most of the N input was from allochthonous (terrestrial) sources, mainly deciduous leaves, while most of the annual input was accounted for by N fixation associated with sediment microbes in the beaver pond. The amount of N contributed by N fixation is therefore proportional to the quantity of sediment available for microbial colonisation. However, Songster-Alpin and Klotz (1995), using electron transport system activity as a measure of microbial biomass and respiration, demonstrated that beaver ponds greatly increased microbial activity along streams. Francis et al. (1985) estimated that total N accumulation in sediment, per unit area, is enhanced by between 9 and 44 fold by beaver damming a section of stream.

Beaver ponds were identified as one of the likely sources of the high total organic nitrogen (TON) and total phosphorus (TP) export in forested stream catchments in Ontario (Dillon et al., 1991). Francis et al. (1985) also noted that beaver ponds could act as source or sink for phosphorus (P) and N. They found that N fixation may be enhanced downstream of beaver-influenced areas and this was possibly linked to an increase in P levels.

Gross export and absolute retention of P and N in a beaver pond in Ontario were primarily controlled by seasonal variations in runoff (Devito and Dillon, 1993). Positive monthly retention coincided with low run off and high biotic assimilation during the growing season. Large flow-through of waterborne inputs and flushing of regenerated P and N occurred during peak snowmelt resulting in low annual retention.

It has been calculated that the feeding activities of a colony of six beavers could contribute as much as 10.3 g $N/m^2/yr$ to a beaver pond in Quebec (Naiman and Melillo, 1984). Fallen wood from trees killed by inundation and wood used for the construction of dams and lodges would add to this total. This input of organic matter by beaver, augmented by the initial accumulation of flooded forest material, is probably very important to P and N dynamics and represents a long-term source of nutrients to the pond water and outflow (Devito and Dillon, 1993).

In addition, France (1997) concluded that beaver are a valuable resource for littoral communities in Canadian Shield lakes through their role as importers of allochthonous material across ecotonal boundaries. He suggested that endorsement of limiting beaver populations through increased trapping should be reexamined for regions containing macrophyte-impoverished lakes with a rocky shore.

Several studies have reported on the ability of a complex of beaver dams to improve water quality. Beaver ponds can increase the self-purification capacity of small streams which are polluted by communal sewage, cattle farms and other agricultural discharge (Balodis, 1994). The biological self-purification capacity was 10 times higher per river length with beaver dams, as compared with rivers without dams. In a 2nd order stream in Wyoming, which was prone to erosion and had a large mineral sediment load, differences in water quality following passage through a series of beaver ponds were recorded in the spring and summer (Maret et al., 1987). During periods of high flow, associated with spring runoff, concentrations of suspended solids (SS), TP, sodium hydroxide – extractable P (NaOH-P, an index of biologically available P) and total Kjeldahl nitrogen (TKN) were reduced in water flowing through the beaver ponds. Generally, the amount of SS could explain the variation in TP, TKN and NaOH-P. During low summer flows the beaver ponds did not reduce nutrient levels when mineral particulate load and deposition was reduced. Thus the retentive function of beaver ponds may be greater in high gradient systems with large mineral sediment loads where dams result in deposition of that sediment.

Under certain circumstances, for example in sites with enhanced decomposition processes, dissolved oxygen concentration (DO) can be reduced in water flowing through beaver impoundments (Naiman et al., 1986). Beaver dams in a number of Wisconsin streams reduced DO levels to as low as 0.1 mg/l in some ponds in the winter during periods of ice cover, and in the summer some of the ponds became anoxic with depth (Avery, 1992). While oxygen requirements of fish are influenced by water temperature, 5–6 mg/l is normally quoted as the minimum necessary for salmonids, though the requirements of non-salmonids can be less (Davis, 1975).

By contrast, Komadina-Douthwright (1994) found that in New Brunswick beaver ponds subjected to prolonged periods of snow and ice cover, the lowest oxygen saturation values recorded were still far in excess of the minimum values considered to be required by salmonids at low water temperatures. It appears likely that, depending on site conditions, complete reoxygenation would generally be achieved within a short distance downstream of the dam. Prolonged deprivation of oxygen, due to the activities of beaver, would not be expected in unpolluted, low order woodland streams (Smith et al., 1991).

The anaerobic zones in the sediment interstitial waters of beaver ponds may be enriched in dissolved nutrients. Increased concentrations of these nutrients result in their movement, through turbulent diffusion, into the sediment/water interface (Dahm and Sedell, 1986). The resulting enrichment in this zone stimulates increased primary production. Coleman and Dahm (1990) compared algal production in two streams in New Mexico. One was poorly retentive and the other was highly retentive due to several decades of beaver activity. They suggested that the higher algal production in the stream with beavers was linked to greater nutrient availability at the sediment/water interface due to enhanced retention and processing of organic matter in the hyporheic zone.

Anaerobic zones created within the sediments of beaver ponds may result in the cycling of nutrients into soluble forms which enhance the productivity of the stream (Dahm et al., 1987). Anaerobic conditions in the winter can cause a release of P from beaver ponds in Canada (Devito and Dillon, 1993). In a study of five beaver ponds in New York, Klotz (1998) showed that the ponds differed in how they influenced stream water P concentration. The shape of one pond led to anaerobic conditions during the ice-cover period, which coincided with high levels of soluble reactive P (SRP). Processes in three of the ponds increased SRP of the stream water during warmer months. Two ponds were consistent in reducing SRP in stream water at all times of year. Elevated levels of P occurred for only short distances downstream of ponds before equilibrium processes reduced the concentration. Along with the nutrient changes, beaver ponds dramatically increase the unshaded water surface area, allowing sunlight to reach aquatic primary producers. In ponds where SRP increases, the combination of sufficient light and higher P should lead to greater primary production.

Beaver activity affects biogeochemical cycles and the accumulation and distribution of chemical elements over time and space by altering the hydrological regime (Naiman et al., 1994). Only a portion of the chemical elements, derived from retained organic matter and sediment, are exported downstream (except for calcium and magnesium) or returned to the atmosphere (Carbon and N), and substantial standing stocks are accumulated in the pond sediment (Naiman et al., 1994).

Influence of beaver on aquatic invertebrates

Beavers alter channel geomorphology by dam construction, and riparian canopy cover by flooding and harvesting. These activities normally lead to an increased input and storage of organic material and sediment in the impounded areas (Francis et al., 1985), with effects on the invertebrate community. Sprules (1941) studied the effects of a beaver dam across a stream in Ontario, Canada. The dam raised the water level about 40 cm and caused the deposition of sandy silt. This reduced the total number of insects emerging, especially of obligate lotic species amongst the Ephemeroptera (mayflies), Plecoptera (stoneflies) and Trichoptera (caddis-flies), and it increased the proportion of Chironomidae (midges). Although the biomass of invertebrates per unit area was reduced, the amount of fish food was more than doubled due to increase in areas inundated by the dam. Hale (1966) similarly found that the production of Ephemeroptera, Trichoptera and Plecoptera, was higher in the streams while oligochaetes (segmented worms), chironomids, pelecypods (mussels), Odonata (dragon flies) nymphs, and Hirudinea (leeches) dominated the beaver pond fauna.

Beaver-induced changes in streams could have effects on fish populations due to changes in abundance of aquatic invertebrates the principal prey of many fish species. However, the extent of these changes will depend on the original (pre-beaver) conditions and the species of fish present. Where fish production is limited by invertebrate production, any beaver-induced increase in the latter is likely to be beneficial for the fish.

Generally, low order sites, with natural riparian vegetation, receive large inputs of coarse particulate organic matter (CPOM) from terrestrial sources and the invertebrate fauna of these streams is dominated by shredders (consumers of CPOM) (Vannote et al., 1980). In beaver-impounded sections of such streams the relative importance of shredders decreases, even though large quantities of CPOM are available. McDowell and Naiman (1986) suggested this may be due to inadequate velocity and substrate types for the shredders. They also reported that collectors (consumers of fine particulate organic matter (FPOM) gathered from the substrate) and predators were most abundant in impounded sites, and that filterers (consumers of FPOM filtered from the water) remained important but the taxa changed compared to non-impounded areas.

In beaver-impounded areas of a small 2nd order stream in Quebec, the typical low order stream invertebrate community was replaced by assemblages which were functionally more similar to large order systems (McDowell and Naiman, 1986). Specifically, the running water communities of the non-impounded sites were dominated by Simuliidae (black flies), Tanytarsini chironomids, scraping Ephemeroptera and net-spinning Trichoptera. Following impoundment by beaver these species were replaced by Tanypodinae and Chironomini chironomids, predacious Odonata, Tubificidae (sludge worms), and filtering pelecypods. In contrast to some workers they found that the total density and biomass of invertebrates in impounded sites could be 2–5 times greater than riffle sites in spring and summer, while no differences were found in the autumn.

While studying a simulated beaver pond in Finland, Nummi (1992) recorded that large amounts of cladocerans (water fleas) were produced in the first year of inundation. In the second year the number of free swimming invertebrates was reduced but emerging insects and benthic invertebrates, notably *Asellus* (water-hoglouse), increased and remained high during the third year. Nummi (1989) noted differences in the invertebrate response in the flooded littoral area and the original stream bed. For example, in the stream bed there was a considerable increase in the numbers of *Pisidium* (pea mussel) in the first year of inundation. Also, some species, such as *Sialis* (Alder flies), were lost from the littoral area but remained in the stream bed.

Although the change from lotic to lentic invertebrate species following beaver impoundment is well documented, the situation on the dam structure itself can, depending on site characteristics, be different. In a low gradient, meandering 3rd order stream in Alberta, Clifford et al. (1993) found that the macroinvertebrate assemblages associated with the dam differed from those in the beaver pond and the main stream sites. They discovered that the invertebrate community of the dam was typical of a free-flowing environment. In particular the dam had a large proportion of simuliid larvae, while other sections in the stream had a fauna more characteristic of slow-flowing or lentic environments. In slow moving streams beaver dams can therefore have an important role in maintaining a lotic fauna.

Beaver can enhance overall stream production by increasing the aquatic surface area and consequently allow greater contribution of material from terrestrial sources. Where littoral zone processes are important, the total mass of aquatic insects emerging each year will be significantly increased by beaver activity (Wright, 1944; Naiman et al., 1984). The construction of beaver impoundments will also reduce the influence of hydrological extremes on benthic invertebrates (McDowell and Naiman, 1986).

Influence of beaver on fish

Changes in fish communities

The role of beaver ponds in structuring fish communities varies among regions but, in general, may be divided into effects in cold water and in warm water systems. Salmonids are generally favoured for angling in cold water streams, and centrarchids in warmer waters in N. America. With the change from lotic to lentic conditions, pool and pond dwellers may become dominant over riffle dwellers. For example, in cold water systems inhabited by Atlantic salmon (*Salmo salar*) and a co-habiting trout, juvenile salmon have highest densities in riffle type habitats, whereas generally brown trout (*Salmo trutta*), in Europe, or brook trout (charr) (*Salvelinus fontinalis*), in North America, are mainly pool dwellers (Gibson, 1993). Trout are likely to become the dominant salmonid in the impoundment. Since impoundments are frequently created on first and second order streams, trout populations may increase considerably, and create opportunities for angling where few would occur without the beaver dams (Neff, 1957; Call, 1966; Young, 1995). In a stream in Newfoundland, Canada, with predominantly shallow riffle habitat, beaver dams increased pool areas, thereby increasing the rearing area for larger juvenile Atlantic salmon and brook charr (Scruton et al., 1998).

Competitive interactions have also been shown to change between other salmonid species. Gard (1961) found in Sagehen Creek, California, that brook charr and brown trout benefited more than rainbow trout (*Oncorhynchus mykiss*), because of their ability to feed on the bottom fauna in the ponds. Rainbow trout maintained its drift feeding habit, and when floods destroyed a dam it replaced brown trout as the dominant species (Gard and Seegrist, 1972; Gard and Flittner, 1974). Similarly, the juveniles of some Pacific salmon species are preferentially pool dwellers, such as coho (*Oncorhynchus kisutch*) (Sedell et al., 1985; Heland and Beall, 1997), and sockeye (*Oncorhynchus nerka*) (Murphy et al., 1989), which can be benefited by beaver dams. Bryant (1984) found that coho salmon in southeast Alaskan streams were able to exploit the additional habitat created by beaver ponds and the importance of the ponds was linked to their role of increasing stream habitat heterogeneity. The benefit of beaver pond habitat to coho salmon in Oregon was reported during late summer flow conditions (Leidholt-Bruner et al., 1992). Murphy et al. (1989) demonstrated that, in addition to coho salmon, sockeye salmon benefited from beaver created-habitat during the summer period in south east Alaskan streams.

Beaver ponds can provide important winter habitat for many stream fishes, and in streams lacking large deep pools the importance of these impoundments increases (Cunjak, 1996). Cutthroat trout (*Oncorhynchus clarki*) and bull trout (*Salvelinus confluentus*) were reported to overwinter in large mixed aggregations in beaver ponds in a Montana headwater stream (Jakober et al., 1998). Similarly, Cunjak (1996) observed brook charr aggregating in a beaver pond in a shallow stream in New Brunswick. He suggested that such ponds may provide one of the few available wintering sites in streams where ice cover is often in contact with the stream bed. The importance of beaver-created winter habitat has also been recorded for coho salmon in Oregon (Nickelson et al., 1992a,b) and brook charr in Wyoming (Chisholm et al., 1987). Cunjak (1996) considers that the value of beaver ponds as wintering habitats for fishes is underappreciated.

In general it appears that beaver are more beneficial to salmonids in cold streams of mountainous or semi arid areas than they are in warmer streams of lower altitudes. For example, various studies have reported them to be generally beneficial in areas of California (Gard, 1961), Colorado (Neff, 1957), New Mexico (Huey and Wolfrum, 1956), Utah (Rasmussen, 1941), Wisconsin (Patterson, 1951) and Wyoming (Grasse and Putnam, 1955), whereas in areas of Maine (Hodgdon and Hunt, 1953), Michigan (Bradt, 1947) and New York (Bump, 1941) they have been considered harmful. In many cases it is difficult to identify a single outcome and it is a question of weighing up the balance of their effects. For example, many eastern North American authorities have discussed the beneficial early effects of beaver ponds and their later detrimental influences. Similarly, while many western authorities have generally agreed on the overall benefits of beavers, some have mentioned problems such as adverse effects on fish movements.

New beaver ponds in Minnesota may carry a higher standing stock of brook charr than streams, although they may contain fewer young fish, while older ponds appear to be less productive than adjacent stream areas (Hale, 1966). Patterson (1951) found that fishing in Wisconsin beaver ponds was good for 2 to 4 years after primary dam construction but deteriorated subsequently. A similar pattern was described in West Virginia, where for a few years the initial dams erected on a stream could be highly productive, and although this could continue for many years in some streams, in others the trout declined dramatically (Bailey and Stephens, 1951). The management of beaver-trout issues is important in areas of south-eastern Wyoming where brook charr in the beaver ponds on small mountain streams support a substantial segment of the available sport fishing (Winkle et al., 1990). In a mountain stream in Colorado, Neff (1957) suggested that the removal of beavers and drainage of their ponds resulted in a great reduction in trout numbers and fishing potential. Similarly the natural deterioration of a beaver dam in a Michigan stream and the subsequent loss of the productive fishing in the associated pond prompted the wildlife department to manually reinstate the dam (Shetter and Whalls, 1955).

In western states, Yeager and Hill (1954) concluded that beavers benefit fish so long as the colonies are active, but following abandonment of sites the benefits may be lost. In California, brown trout production was largely dependent upon the extent and condition of beaver impoundments (Gard and Seegrist, 1972). In sections which were abandoned by beavers the population of brown trout declined substantially (Gard, 1961). Partly as a result of dams not being rebuilt, numbers of brook charr and brown trout in the stream as a whole declined significantly ($P < 0.05$) during the 10-year period, whereas rainbow trout abundance remained stable (Gard and Flittner, 1974). Where beavers were managed on a sustained yield basis in Colorado, they had a beneficial influence on fish in streams with suitable gradients and soil characteristics (Rutherford, 1955). However, the permanency of these benefits appeared to depend on careful management of the beaver population.

Beaver ponds in Utah and Colorado, which were derived from streams and had retained good spawning areas, often had stunted populations of brook charr. Ponds developed from seepage inlets, with limited spawning potential, had smaller numbers of larger fish (Rabe, 1962, 1970). Chisholm et al. (1987) suggested that irrespective of their spawning potential, beaver ponds with low current velocity were important habitat components for brook charr in high elevation Wyoming streams during the winter.

Brook charr from Colorado beaver ponds were significantly larger than those taken from adjacent streams, although their condition factor was lower (Rutherford, 1955). He suggested that relatively new impoundments provided good habitat and produced more trout than streams, but older ponds produced fish in poorer condition. Murphy et al. (1989) recorded that the mean length of both coho and sockeye salmon was larger in beaver ponds than in other habitats. They found that beaver ponds were particularly important for parr and less important for fry. Although the ponds only provided a small percentage of the total available habitat, they contained a large percentage of the coho population.

Bailey and Stephens (1951) recorded that beavers in West Virginia have probably produced far more biomass of trout than they have destroyed. However, since beavers can produce fine trout fishing in some streams and reduce it to zero in others, the evaluation of each site is necessary to determine appropriate management. Hale (1966) concluded that a small beaver population is beneficial, but a large population is detrimental to a trout stream. Overall it is apparent that the presence of beaver on a salmonid stream can be either beneficial or harmful according to the region and topography (Cook, 1940).

Cyprinids and many other warm water fish often increased in beaver ponds in Wisconsin (Knudsen, 1962). Similarly, beaver ponds provided habitat for cyprinids in New Brunswick (Alexander, 1998), and for minnow (*Phoxinus phoxinus*) fry in Sweden (Hägglund and Sjöberg, 1999). Increased numbers of small fish in beaver ponds, primarily ninespine sticklebacks (*Pungitius pungitius*), and redbelly dace (*Chrosomus eos*), were used as forage by brook charr (Rupp, 1955). In some locations pike (*Esox lucius*) were found to increase in numbers, particularly in large ponds with abundant shallow grassy areas. Beaver activity appeared to improve the carrying capacity of a Missouri stream for non-salmonid warm water fishes and provided conditions which were suitable for a large variety of fish (Hanson and Campbell, 1963). Even after abandonment by the beavers, these beneficial effects persisted for a few years. They suggested that beaver ponds could provide important fish refuges in times of low flow, and consequently serve as reservoirs for fish recolonisation.

Although beaver ponds can be important sites in streams for communities of warm water fish, these populations may be different from those found in natural lakes in a river system. Keast and Fox (1990) found that a small, shallow beaver pond in Ontario lacked the range of habitat types and associated fish species which occurred in nearby lake environments. They concluded that the size, depth and reduced recolonisation potential of beaver ponds resulted in fish communities which contained fewer species and individuals of small body size when compared with lake communities. Working in the same area, on similar beaver ponds, Fox and Keast (1990) suggested that the smaller body size of one of the species, the pumpkinseed (*Lepomis gibbosus*), was due to high annual mortality and not stunted growth. These populations changed dramatically in the beaver ponds as a result of winter kills associated with hypoxia and a decline in water level.

France (1997) showed that beaver in boreal lakes can provide an important habitat resource for littoral communities. He reported that in headwater lakes of northwestern Ontario, the richness and abundance of ten macroinvertebrate taxa, six species of small fishes, and two species of amphibians were significantly elevated near beaver lodges compared with areas of sand and rocks otherwise characteristic of the littoral areas of boreal lakes. Similarly in a Manitoban lake, perch (*Perca flavescens*) were seen to be attracted to the debris of a beaver lodge (Gibson, 1969).

In West Virginia, Bailey and Stephens (1951) noted that in streams, particularly the warmer ones, which were generally considered to be marginal for trout, other species such as cyprinids and catostomids could displace trout through competition. A similar situation was reported in Ontario where a change in dominance from brook charr to yellow perch was caused by environmental changes produced by beaver activity (Balon and Chadwick, 1979). In this case the activities of the beaver may have resulted in a major shift from lithophils to a dominance by other fish species including phyto-lithophils and phytophils.

From a study of otter faeces, the following fish species were associated with beaver ponds in Latvia: Pike, roach (*Rutilus rutilus*), belica (*Leucaspius delineatus*), chub (*Leuciscus cephalus*), gudgeon (*Gobio gobio*), bleak (*Alburnus alburnus*), carp (*Carassius* spp.; *Cyprinus carpio*), stone loach (*Barbatula barbatula*), weather loach (*Misgurnis fossilis*), eel (*Anguilla anguilla*), burbot (*Lota lota*), sticklebacks (*Gasterosteidae* spp.), perch (*Perca fluviatilis*) and bullheads (*Cottus cottus*) (Ozolin and Rantin, 1992).

This indicates that a wide range of fish species can utilise beaver-created habitat.

Schlosser (1998) found that beaver ponds, in a small stream in northern Minnesota, increased the density of underyearling creek chub (*Semotilus atromaculatus*). Older year classes were not consequentially increased, suggesting that the lotic regions adjacent to the beaver ponds acted as reproductive "sinks". A similar situation occurred with minnows in forest streams in Sweden (Hägglund and Sjöberg, 1999). Schlosser et al. (1998) found that *Phoxinus eos*, was more abundant in active beaver ponds, while *Phoxinus eos-neogaeus*, gynogens were at higher frequencies in collapsed pond and stream environments. The increased frequencies of gynogens in pelagic and benthic zones, along with their greater survival times under oxygen stress, indicate that the gynogenetic clone is more general in its use of marginally suitable habitats and is physiologically more tolerant to anoxic conditions than its sexual progenitors.

Pullen (1971) recorded a shift in fish population structure, in warm water streams in Georgia and South Carolina, from one dominated by Cyprinidae in the stream situation to one dominated by the Centrarchidae in the pond situation, the latter being of more interest to anglers. Population diversity and standing crop of fish present were both increased in areas affected by beaver. Similarly, a change from a run-dwelling assemblage dominated by large numbers of cyprinids and immature centrarchids towards an assemblage containing fewer and larger centrarchids, due at least partially to temporary beaver dams, was recorded in a Mississippi stream by Shields et al. (1998). Rohde and Arndt (1991) related the decrease of the sandhills chub (*Semotilus lumbee*) and the pinewoods darter (*Etheostoma mariae*), in North Carolina and South Carolina, to habitat changes caused by beaver activities, although impoundments and eutrophication due to golf courses were partly responsible. Changes from lotic to lentic conditions, change in substrate to one of soft bottom, increase in temperatures and water depths, were detrimental to the two species, and favoured warm water species which competed and preyed on the chub and darter.

In South Carolina, stream impoundment by beavers affected species richness at the reach scale, but this effect was highly dependent on the drainage area above the pond, and the dynamics of pond creation and abandonment (Snodgrass and Meffe, 1998). In headwater streams, species richness per pond peaked in abandoned mid-aged ponds (9–17 years old) and was lowest in old active ponds (>17 years old). Further downstream, species richness was similar across all site types and pond ages. As ponds aged, small bodied cyprinids were replaced by larger predators, suggesting that predators eliminated prey species from old ponds. They suggest that the positive relationship between stream fish species richness and drainage area described for many streams may be a recent phenomenon resulting from the extirpation of beavers from much of their historical range. Beavers create habitat heterogeneity over larger scales of stream habitats by creating patches of lentic habitat within a corridor of lotic habitat. Snodgrass and Meffe (1999) suggest that removal of ponds from southeastern headwater streams would reduce species richness by over half. They found that most species could be classified as either "stream species" or "pond species", with approximately 11 species found mainly in streams and 16 species mainly in ponds. However, age 0 fishes of four species were found almost exclusively in ponds whereas adults were found in ponds and streams, suggesting movements of adults to ponds to breed. For two species a higher ratio of age 0 to adult fish were in streams compared to ponds. Assemblage structure was less stable in ponds when compared with streams, suggesting that beaver ponds are temporally dynamic resource patches that are rapidly colonized and exploited, and from which organisms rapidly disperse. The ponds possibly provided refugia for fish from high flow conditions.

Fish migration

Beaver dams may interfere with fish movements and distribution, depending on size, structure and location of the dam, and the season. Rasmussen (1941) considered beavers to be beneficial to cutthroat trout in mountain sites in the Rockies, although their dams could obstruct fish movements during periods of low stream flow. However, the cutthroat trout were spring spawners and experienced little difficulty in negotiating the dams during the increased spring run off associated with snowmelt. Grasse and Putnam (1955) found spring spawners in the Rockies (cutthroat trout and rainbow trout) could usually negotiate dams, but autumn spawners (brook charr) could be blocked because they spawn during a period when the water flow is lowest and the dams are in the best condition.

Beaver dams were reported to hinder autumn spawners (brook charr and/or brown trout) during low flow conditions in New York State (Cook, 1940), western Montana (Munther, 1983) and Maine (Rupp, 1955). Rupp (1955) concluded that as trout habitat was well distributed throughout his study site, extensive seasonal migration was probably unimportant. This would not be the case in sites where free access was essential and where delaying obstacles could present problems.

Brown trout were more inclined to cross beaver dams in a California stream, than were brook charr or rainbow trout (Gard, 1961). He concluded that some trout are able to cross dams in both directions and that the dams are not complete barriers. Movements could occur at all seasons but were influenced by river flow conditions. Beaver dams presented some obstacles to colonising fish (sockeye and coho salmon) in a southeast Alaskan stream, and colonisation of the ponds probably required high water levels such as autumn freshets (Murphy et al., 1989). Dams up to 2 m high did not prevent adult coho salmon migration in southeast Alaskan streams (Bryant, 1984).

Fish may use side channels to bypass dams, or leap over them or penetrate through interstices which may leak (Gard, 1961). Well-maintained beaver dams in Wyoming often prevented upstream migration of spawning fish so that while some ponds had populations derived from natural reproduction others provided excellent sites for artificial stocking programmes (Grasse, 1979).

At high water levels, dams can usually be negotiated by adult salmon and those which leak may allow some movement of juveniles (Bryant, 1984; Swanston, 1991). Dams in areas with sandy soils can be more 'leaky' than dams in areas with heavy soils (Knudsen, 1962).

Some beaver dams may prevent further upstream migration of Atlantic salmon (Cunjak and Therrien, 1998). However, Gibson et al. (1996) found that although a beaver dam apparently prevented migration of adult Atlantic salmon in a river in south-western Newfoundland, and no fry were found upstream of the dam, older juvenile salmon in low densities did occur above the dam, suggesting that some parr had been able to swim through interstices in the dam. In a New Brunswick stream, an active beaver dam prevented migration of juvenile and adult Atlantic salmon and brook charr, but they were able to pass freely through an abandoned beaver dam (Alexander, 1998).

Cunjak et al. (1993) also reported on the effect of dams on the downstream migration of Atlantic salmon smolts. They found that during a period of below-average spring flows, the beaver dams did not appear to affect downstream movements of the smolts.

Schlosser (1995) recorded that downstream fish movement in warm water streams in Minnesota occurred primarily during periods of high flow while upstream movements occurred over a wider range of flow conditions. However, it appeared that upstream movements were reduced during periods of low discharge.

Dams may act as barriers to pike movements, as they were sometimes seen lying below beaver dams in large numbers during spring spawning runs in a Wisconsin stream (Knudsen, 1962).

Spawning sites

Beaver dams may damage salmonid spawning areas by reducing stream flow and causing excessive siltation of the spawning gravel (Knudsen, 1962). This relationship however depends on stream gradient (Rasmussen, 1941). The viability of spawning areas could also be reduced if they are covered with deeper, slow moving water as a result of beaver activity (Swanston, 1991).

In areas with limited spawning facilities, and with high beaver densities, dam building might be a cause for concern. However, beaver dams and log jams may induce extensive deposits of gravel and smaller sediment in high gradient boulder-bed streams, providing important spawning substrate for salmonids, but these may be impermanent and subject to washout (Kondolf et al., 1991). Also, spawning areas in streams with high silt loads might benefit from a reduction in the silt-carrying capacity due to increased sedimentation rates in beaver ponds (Grasse, 1951; Macdonald et al., 1995). While beaver ponds will trap sediment, Butler and Malanson (1995) have suggested that significant amounts of sediment in some ponds could have been generated by the excavational activities of the beavers themselves.

In streams which feature a high proportion of beaver impoundments, it is possible that non-salmonid species which spawn in silt or aquatic vegetation could be the major beneficiaries (Balon and Chadwick, 1979).

Fraser (1982) described an atypical spawning area for brook charr, in a small boreal lake, which consisted of old cuttings from a beaver lodge. The brook charr successfully spawned on a thick aggregation of the waterlogged sticks, which overlay the soft ooze bottom where groundwater seeped up through the sticks.

Piscivores

Beaver ponds can provide habitat for a wide variety of species which prey on salmonids and other species. These include fish species such as Esocidae, a variety of birds, and several mammals, including otters and mink.

Although mink utilise beaver ponds (Beard, 1953; Rutherford, 1955; Knusden, 1962; Hammerson, 1994; Sidorovich et al., 1996) otters (*L. canadensis* and *L. lutra*) have been the subject of more detailed investigations. Tumlison et al. (1982) suggested that beaver ponds could be particularly important for otters in areas where deep water habitat was limited. In Maine, otters selected watersheds which had a high proportion of beaver-influenced streams (Dubuc et al., 1990). Zharkov and Rodikov (1975) found that otters regularly made use of beaver constructions in the middle reaches of the Pripyat river.

Beaver ponds can provide otters with a food supply, stable water levels, den sites, herbaceous/shrub cover and some protection from human disturbance (Dubuc et al., 1990). Widespread efforts in the United States to restore beaver populations have also benefited the otter (Vogt, 1981). Ozolin and Rantin (1992) found that beaver ponds in Latvia could be used by otters throughout the year. They noted however, that while beaver activity was important for creating otter habitat, one of the main threats to otters in Latvia was accidental capture in traps set for beavers.

Reid et al. (1988) discussed additional benefits provided during the winter period in areas where the water surface freezes. They reported that otters dig passages through dams thereby gaining access to the pond and allowing under-ice movements between adjacent water bodies. Similarly Sidorovich et al. (1996) reported that otters in the Białowieża Primeval Forest (Polish-Belarussian border) benefited from ice free access to water which could occur around beaver lodges and burrows.

The importance of beaver impoundments to birds, particularly waterfowl, has attracted much interest in the United States (Beard, 1953; Knudsen, 1962; Reese and Hair, 1976; Peterson and Low, 1977; and Grover and Baldassarre, 1995). As might be expected, several of the species utilising beaver ponds are important piscivores.

Grover and Baldassarre (1995) reported that hooded mergansers (*Lophodytes cucullatus*), green-backed heron (*Butorides striatus*), great blue heron (*Ardea herodias*) and belted kingfisher (*Ceryle alcyon*) occurred more frequently in wetlands where beaver were active than in sites with no beaver activity. In addition to providing foraging areas for adult birds, the beaver-created wetlands were also used by broods of both hooded and American mergansers (Beard, 1953).

Negative impacts of beavers, and methods of control

Beaver dam building activity can cause flooding of roads and domestic property. Physical removal of problem dams is often ineffective since active dams are quickly rebuilt, although inactive ones may be removed, manually, mechanically or by blasting. This should be done at low flows, and after emergence of salmonid fry, to minimise downstream effects of disturbed silt (Anon., 1980; Hammerson, 1994). Trapping may be successful until the area is recolonised. The most successful method for controlling water levels in flooded areas seems to be the installation of a pipe at the bottom of the dam, which the beavers do not locate (Roblee, 1984; Miller and Yarrow, 1994). Such pipes provide an opportunity for manipulating downstream flows and, in some situations, low summer flows can be improved for rearing salmonids by the controlled release of water from the dam (Anon., 1980).

Where migrating fish accumulate below impassable dams, their upstream passage can be aided by cutting notches in the dam. As such notches are normally repaired rapidly by the beavers, it might be necessary to reopen them on several occasions during the migration period (C. MacInnis *pers. comm.*). Fish passage can also be provided without breaching the dam using the Telkwa design (Finnigan and Marshall, 1997).

In North America, it is common for culverts to be installed in small streams instead of building bridges. In the short term culverts are the cheaper structure. Although there are installation criteria for ensuring upstream passage of fish, these are sometimes ignored and the structures become barriers or partial barriers to migration. Since beavers frequently build dams at the lower end of a pool, they may use the constriction of the stream at the upstream end of the culvert as the focal point for a dam, increasing the height of the water upstream and blocking the culvert, aggravating migration problems and causing flooding. Exclusion by fencing or screening devices can be successful (de Almeida, 1987; Miller and Yarrow, 1994; Finnigan and Marshall, 1997), although trapping of these "nuisance" beavers is the usual remedy (Hill, 1976).

In a beaver impoundment most trees die and others, such as aspen and willow, are felled for forage. Angling in beaver ponds may be difficult due to tree and bush debris. Dead trees may provide nesting sites for some species of birds, such as herons, and woodpeckers, and the felled trees may provide litter for the forest. In wilderness areas the loss of trees may not be of any consequence. However, in areas with mainly man made landscapes, where trees are not abundant or are being planted to restore riparian vegetation, such losses are likely to be unacceptable. Individual trees can be protected by enclosing the bottom metre of the tree with heavy wire mesh, hardware cloth, or galvanized metal. Other coverings that have been successful include tar paper, Clark's tree wrap, and wood preservatives. Commercial deer repellents have also been shown to be effective (de Almeida, 1987; Hammerson, 1994).

It is possible that the activities of beavers would be detrimental to some fishery-orientated woodland replanting schemes. For example in Arizona, Davis (1986) refers to a site where the objective was to reduce water temperature by increasing stream shading. Livestock grazing was reduced and riparian vegetation responded but was continuously cropped by beavers. The solution was to reduce the beaver population until the vegetation met the shading objective but was still able to support a reduced beaver population. This was an example of the need for effective management. By contrast, production of invertebrates and fish dependent on autotrophic pathways, have been shown to increase after reduction of canopy cover (Behmer and Hawkins, 1986; Noel et al., 1986; Bilby and Bisson, 1992; O'Grady, 1993; Keith et al., 1998). Although beavers were not responsible for removing riparian vegetation in these studies, they illustrate a situation where cropping by beavers might not be negative to fish production.

Trapping is a simple and effective way of controlling beavers. It has been used to manage beavers so that they do not over exploit their food supply. Hill (1976) suggests that trapping, with its recreational appeal, and income and food potential seems the better and more prudent approach to control beaver than other methods. The Conibear type of trap, No. 330, is the most effective lethal trap, although leghold traps, and live trapping with Bailey or Hancock type traps, or by snaring, are effective methods (Hill, 1976; de Almeida, 1987; Miller and Yarrow, 1994). Trapping is illegal in some areas, and in Europe it is possible that animal welfare groups would oppose lethal trapping. Other methods of control that have been used include: poisoning (Hill, 1976); sterilisation (Brooks et al., 1980) and shooting (Hammerson, 1994; Miller and Yarrow, 1994).

Summary of the possible consequences to fish of beaver activities

Positive effects

- Habitat is created for larger fish, providing angling opportunities (salmonids in cold water streams, centrarchids and some esocids in warm water streams).
- The debris cover provided by the lodge and the food cache can attract some fish species (e.g., salmonids, percids, centrarchids).
- Hydrological effects are stabilised, so that bed scouring and bank erosion are decreased. More stable stream flows are beneficial to invertebrate and fish production.
- Water temperature stabilisation and warming could increase production in cold water streams.
- In streams with high sediment loads, sediment will be trapped in the impoundment.
- Coarse, particulate and dissolved organic matter is increased in the pond, providing food for invertebrates, through fungal and microbial pathways.
- Nutrients may be generated (N, P), increasing the fertility of the pond and downstream stretches.
- Acidity may be reduced, and Al may be immobilised.
- The dam collects organic detritus, and provides a substrate for lotic type invertebrates, providing food for fish downstream.
- Refugia can be provided in the pond at certain times.

Negative effects

- Upstream migration may be impeded (larger dams; dams above culverts which were partial barriers).
- Warming of water temperatures may be detrimental in some marginal habitats for cold water fish.

- Spawning sites may be inundated and silted.
- The fish composition and interactions may change, so that less desired species for angling predominate.
- Habitat may be created for avian, mammalian or piscine predators, with negative effects on desired fish species.

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