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Effects of beaver on stream channel form and coho salmon habitat were determind by classifying a portion of Sixmile Creek (Kenai Peninsula, Alaska) according to a hierarchical stream classification system. The study area was classified into stream segments and reaches based on geomorphic and landtype characters. Reaches were classified into ten habitat types (seven pool types, riffle, glide, and cascade). Chronosequence aerial photos and field methods were used to identify type and age of beaver structures. A cyclic pattern of beaver habitation was described, which explained stream channel changes and differences in habitat composition with dam site age. Particular patterns of habitat transformation occurred with degradation of dam sites over time. Mainstem dams produced the most channel complexity. Sideslope dams unified tributary networks, creating fish habitat at dam outfall junctions with the mainstem. Fry were most abundant in backwater and lateral scour pools in all reaches (both mainstem and side channels). The greatest amount of side channel area and pool habitat in side channels occurred in dam sites abandoned 0-5 yr (Early Post-Abandonment Stage). Fry were most abundant in mainstem pools at all developmental stages, but densities were greater in side channels at the early post abandonmént stage. Active beaver ponds were used by fry for overwintering. Neither spawning area nor access to spawning areas was affected by beaver dams. The cyclic successional pattern (10^{0} yr) created a variety of developmental stages of fish habitat at one time, while the long term effect (10^{2}-10^{3} yr)--the beaver meadow complex--appeared to perpetuate the process of habitat development along the stream segment. Short and long term implications of beaver activity to salmon fishery management are discussed.

EFFECTS OF BEAVER ON STREAM CHANNELS AND COHO SALMON HABITAT

KENAI PENINSULA, ALASKA

by

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

EFFECTS OF BEAVER ON STREAM CHANNELS AND COHO SALMON HABITAT KENAI PENINSULA, ALASKA

INTRODUCTION

Possibly no other mammal except man modifies its environment for its own benefit so much as the beaver (*Castor canadensis*) (Grasse 1951). Its dam-building behavior alters streams physically, chemically, and biologically. The beaver has been termed a "keystone species" by Sedell and Dahm (Johnson 1984) and Naiman et al. (1986). By definition, a keystone species affects ecosystem structure beyond its immediate need for food and space. Life history and certain aspects of beaver ecology have been studied, but its role as an integral link between terrestrial and stream ecosystems has not been fully explored. The goal of my research was to further understanding of the beaver as a keystone species in altering stream channels and salmon habitat.

Historical View

The beaver coevolved with forested stream ecosystems. Fossil remains dating back 23 million years place beaver in stream and lake habitats (Kurtén and Andersen 1980). At one time beavers ranged throughout Europe and North America (Canada to Mexico). The species persisted through five major ice ages and numerous climatic shifts during the Pleistocene (Zeuner 1959; Péwé 1975); beaver outlasted the Pleistocene megafauna (Nilson 1983), only to be nearly extirpated by man in the last three hundred years by trapping (Lee Rue III 1964).

So pervasive was the beaver throughout North America that the population at the beginning of the 17th century was estimated to be as high as 100 million. Even after 200 ears of exploitation, Lewis and Clark while in Montana in 1804 observed that "the streams stretched away in a succession of beaver ponds as far as the eye could see" (Mills 1913).

On the brink of extinction in the United States, the beaver was protected in the late 1800's. Immediate population rebound and reoccupation of former ranges ocurred across the U.S. with transplanting programs and bans on trapping. By the late 1920's, there were many complaints of "nuisance" beaver among foresters, farmers, and anglers (Bump 1941). Research on beaver impacts on streams ensued, both positive and negative impacts being found. Managers involved in reintroduction programs praised the soil and water conservation effects of beaver (Finley 1937; Scheffer 1938). However, some resource managers saw beaver as despoilers of sportfish waters and timber (Reid 1951; Yeager and Hill 1954), while others concluded that beavers were beneficial to trout and wildlife (Huey and Wolfrum 1956; Neff 1957). Management programs encouraged or discouraged beaver habitation according to interpretation of study results (Salyer 1935a; Platts 1962).

Research in Perspective

Until recently, most beaver ecology research centered on discrete interactions of beaver with: water supply (Bates 1963); beaver food supply (Aldous 1938; Jenkins (1975, 1979, 1980); sedimentation (Allred

1980); riparian vegetation (Hodkinson 1975); aquatic insects (Harris and Carlson 1976); timber resources (Chabreck 1958); trout (Salmo sp.) (Rasmussen 1940; Wright 1944); char (Salvelinus sp.); and wildlife habitat (Arner 1964).

Perhaps more than any other interactions, the effects of beaver on sportfish habitat have been widely documented (Yeager and Hill 1954; Avery 1983). Conclusions as to the positive or negative impacts of beaver on salmonid habitat are as varied and controversial as their other effects on streams. For example, Bailey and Stephens (1951) observed increased brook trout (Salvelinus namaycush) yields in West Virginia beaver ponds, followed by a decline in yield over time. Call (1966) reported improved brook trout and brown trout (Salmo trutta) production in Wyoming. Salyer (1935) recorded a decrease in catchable-size brook and brown trout in Michigan. Later, Gard (1961) concluded that beaver may be detrimental in areas where brook and brown trout range is already marginal such as the East and Midwest, but he found that these two species and rainbow trout (Salmo gairdneri) were benefitted by beaver in the Rocky Mountians. Cook (1940) concluded that benefit or detriment depended on region, while Bradt (1947) and Grasse (1951) noted that positive or negative effects were dependent on stream characteristics (e.g., ponds on low gradient, sediment rich streams provided less fish habitat than ponds on clear, higher gradient streams).

The progressive reoccupation of former ranges by beaver increased resource managers' concern about the impacts of beaver upon the rearing of salmon species as well as resident trout and char.

However, I have found no published studies of beaver influence on salmon habitat. Furthermore, no research has considered the beaver-fish habitat relationships with respect to different scales of time and space. Observations from other studies do indicate that coho salmon fry (Oncorhynchus kisutch) use beaver ponds (Everest and Sedell 1983; Everest et al. 1985). Coho rearing habitat is strongly correlated with the presence of instream woody debris (Bisson and Nielsen 1983; Sedell et al. 1984), a habitat condition similar to that created by beaver (Naiman et al. 1986). Nevertheless, the stigma of negative impacts of beaver on trout and char originating in some regions of the U.S. has translated into negative attitudes about the effects of beaver on salmon. Such attitudes have resulted in management programs to remove beaver dams on salmon streams, without direct evidence to support these practices.

Today, as beaver populations continue to expand into formerly occupied ranges, effects upon streams have become once again visible, stimulating an awareness of the beaver's role in influencing stream ecosystems. I attribute the renewed interest in studying beaver ecology to three recent approaches in stream research. Listed below, these are pertinent to further understanding of beaver-salmonid relationships:

1. The use of the historical record in understanding present stream behavior.
2. The view that streams develop in an encompassing watershed.
3. A habitat-centered view to describe the distribution and functional interrelationships of stream organisms.

Sedell and Luchesa (1981) examined the history of stream wood removal to explain diminished salmonid habitat availability in Oregon. Hynes (1970) and Warren (1979) suggested that streams are a product of their surrounding watershed systems and should be understood in that context. Vannote et al. (1980) expressed environmental factors in terms of habitats for stream organisms, as a means to describe the roles of stream invertebrates in processing organic matter. Bisson et al. (1982) as well as Reeves and Hankin (unpubl. ms) determined salmonid distribution in streams by classifying channel elements into habitat types. Frissell et al. (1986) integrated these three approaches to describe spatio-temporal organization of streams in a watershed; while Wevers (1982) used this integrated approach to describe the organization of stream communities.

This integrated watershed perspective study provides a useful approach to understanding the beaver's role in other watershed processes. Swanson and Lienkaemper (1978, 1981) viewed the role of woody debris in stream structure and dynamics. Cummins (1974) considered the function of aquatic insects in processing organic matter in streams.

Consideration of the role of woody debris in stream systems has practical merit in land use management as well as in ecological research. For example, understanding the importance of woody debris to stream structure enabled managers to develop criteria for removal of instream logging debris (Bryant 1983). Analogously, understanding the role of the beaver could permit managers to use beaver as a "tool" to attain ecosystem management objectives. Reintroduction of beaver has already been used to rehabilitate wildlife habitat as well as to conserve soil and water (Brenn 1958; Apple et al. 1986). A more thorough knowledge would clarify the beaver's ecological function, especially with respect to fish habitat.

Although a few studies have applied aspects of historical, watershed, or habitat perspectives to beaver ecology research, no studies to date have taken an integrated approach. Gard (1961) and Call (1966) examined complex but short term relations between beaver and fish habitat. Ives (1942), Ruedemann and Schoonmaker (1938), Lawrence (1952), and Neff (1957) considered the historical role of beaver in shaping floodplains. Retzer et al. (1956), Finn and Howard (1980), and Howard and Larson (1985) correlated geomorphic and plant community characteristics to site habitability for beaver. A watershed perspective was applied by Naiman et al. (1986) to consider the role of beaver in terrestrial and aquatic systems with regard to stream carbon budgets. Still, function of beaver in the context of a watershed system in shaping fish habitat is only partially understood.

PURPOSE OF STUDY

The goal of my research was to describe the influence of beaver on stream channels and coho salmon habitat, in an integrated watershed perspective. The objectives of the study were:

1. To determine the beaver's role in stream channel development.
2. To determine the spatio-temporal relationship of beaver to coho salmon habitat.
3. To discuss the implications of beaver to salmon management.

THEORETICAL FRAMEWORK

Warren and Liss (1983) described watershed structure as follows:

> Watersheds are composed of biotic and abiotic elements, such as climate, geology, soils, vegetation, and water. The interaction of these elements determines the kinds of stream habitats that occur. Within this system, certain events happen, e.g., forest fires, landslides, and floods, which exert influence on stream habitats over various scales of time and space.

I view beaver as one such "event" in a watershed -- the beaver event being influenced by some processes, yet affecting others, depending upon the time and stream area considered. Occupation of a stream by beaver may be an event on one time and space scale, but might be considered a stream process over a greater scale (Schumm and Lichty en sensu 1964). For example, presence of beaver on a stream might alter stream channel structure along with water and sediment transport over a period of years (Grasses 1951; Neff 1959); but dam-building itself is an event that has effects on stream habitat on a smaller spatio-temporal scale around the dam site (Gard 1961). Table 1 suggests some time-space scales for beaver related events in the context of other watershed processes.

Within a watershed, certain combinations of geology, stream order, channel gradient, soils, and vegetation determine a stream's suitability for beaver (Retzer et al. 1956; Slough and Sadleir 1977; Howard and Larson 1985). These are wide valley floors, with poorly-drained soils, and streams of low channel gradient (1-3%);

sufficient forage must also be present. These conditions of "potential" beaver habitat must exist for beaver to successfully colonize a stream. Once colonized, the largest-scale, longest-persisting feature of beaver occupation is the "beaver meadow complex". It was first described by Ives (1942), but recognized earlier by Ruedemann and Schoonmaker (1938) and Agassiz, who estimated the age of one beaver meadow at 1000 yr (Warren 1927).

The watershed characteristics that provide potential beaver habitat are also the conditions perpetuated by beaver in producing a beaver meadow. The floodplain is aggraded by sediment deposited in ponds above dams and sediment is distributed across the floodplain with flood flows. Such sediment accumulation also widens the floodplain. Beaver successively abandon and reoccupy sites up and down the stream course, as they exhaust food supplies and forage regrowth occurs (Neff 1959). Warren (1932), Lawrence (1952), and Neff (1959) attributed beaver meadow formation to this pattern of cyclic succession.

Beaver in a Hierarchical Watershed Model

In the Warren and Liss (1983) hierarchical watershed model, processes at higher levels of organization constrain and enable processes at the lower levels they encompass. Long term, broad scale watershed events, such as geology and climate, constrain and enable processes such as channel downcutting and floodplain development (Hynes 1975).

Frissell et al. (1986) adopted Warren's model to develop a stream classification system. This scheme is hierarchical in both time and space. That is, long-term, broad-scale events encompass more short-term, small-scale processes. For example, certain evolutionary events at the stream system level (e.g. geomorphology) determine processes at the stream segment level. Within a stream segment, processes such as sedimentation, riparian vegetation succession, and bank erosion define, constrain, and enable processes at the stream reach level. Within a stream reach, bedload sorting, large wood, and debris jams affect habitat units, such as pools, riffles, glides, and backwaters. These are identifiable units whose structure and persistence have consequences for salmon inhabiting the stream. Figure 1 diagrams the hierarchical stream classification model from the watershed level down to the habitat level.

Characteristics of the beaver meadow complex, the result of long-term successional habitation by beaver (10^3 yr), correspond to the same criteria used in the Frissell classification model to define a stream segment. (Segment classification criteria are presented under METHODS). According to this model, long-term beaver effects occurring at the segment level would necessarily have consequences for short-term processes at the reach and salmon habitat levels.

Applying this spatio-temporal perspective to beaver activity, I developed a view of how beaver function in a stream system. A sort of "Big Picture" model, it begins with the broadest-scale effects of beaver and proceeds down to the small-scale, short-term effects, corresponding to stream classification levels.

The following statements summarize from the literature first, how beaver come to occupy a watershed and secondly, their cyclic successional effects on streams (statements 1-9). Statements 10-13 are my hypotheses of the effects of beaver on coho salmon habitat.

Establishment

1. Beavers coevolved with forested ecosystems in the northern hemisphere and moved with the forest as it advanced or retreated with glacial ice movements and climatic fluctuations (Kurtén and Andersen 1980).

2. Within a geographic region, beavers disperse from their home colony up or downstream and across watershed boundaries when forage is no longer accessible in terms of energy efficiency (Townsend 1953; Libby 1957; Hall 1960; Jenkins 1980).

3. In a watershed, beavers select stream segments characterized by wide valleys with low gradients and with sufficient supply of forage to establish successful colony sites (Reudemann and Schoonmaker 1938; Retzer et al. 1956; Howard and Larson 1985).

Occupation

4. Once established, as long as they occupy a stream system, beaver exert certain short-term effects (10^0-10^2 yrs) upon a stream: altering the composition of the riparian vegetation community; slowing water flow; buffering flood events; impounding transported sediments; slowing the rate of channel downcutting; converting stream habitats to pond habitats; depositing organic matter in the channel; and creating

new side-channel habitats (Finley 1937; Rasmussen 1970; Wilde et al. 1951; Naiman et al. 1986).

5. Longevity (period of continuous occupation of a site) depends upon accessible food supply; the period of abandonment, depends on the rate and process of vegetation succession (Gese and Shadle 1943).

6. There is a cyclic relationship between beaver and their food supply, resulting in a pattern of abandonment and reoccupation of dam sites on a stream segment (Warren 1932; Lawrence 1952; Neff 1959).

7. During periods of occupation beavers expand their influence over the stream channel by continued dam-building, thus increasing pond area, and establishing access to food supplies. Continual dam, canal, and tunnel construction re-routes stream flows (Warren 1927).

8. Successive occupations by beaver contribute to the aggradation of the floodplain, resulting in the beaver meadow complex, which persists on the order of 10^3 yrs (Mills 1913; Ives 1942).

Abandonment

9. During periods of abandonment, dams deteriorate, ponds drain, and shores become revegetated. The main channel resumes downcutting, redistributing pond sediments downstream in a transition back to original development patterns. The channel bed may not be eroded below its pre-beaver elevation before the site is reoccupied by beavers (Neff 1957).

Effects upon Salmon Habitat

10. Short-term effects of beaver habitation (e.g., conversion of stream to pond habitat) may cause fluctuations in habitat utilization

by salmon (10^1 yr). But successive, long-term occupation of segments provides more potential salmon habitat over a period of 10^2-10^3 yrs than would be available in those segments without beaver.

11. The scale and degree of beaver effects on a stream segment and across a floodplain depend on site longevity and period of abandonment.

12. The persistence of salmon habitat units depends on the site longevity and the rate of deterioration of beaver structures at abandoned sites.

13. The beaver meadow complex sustains development of salmon habitat over the long-term, such that salmon abundance in these streams is related to the habitat provided by beavers over thousands of years.

DESCRIPTION OF SIXMILE CREEK WATERSHED AND STUDY AREA

The Sixmile Creek drainage is located on the northern Kenai Peninsula, about 60 miles south of Anchorage (Fig. 2) within the boundaries of the Chugach National Forest (CNF). Sixmile Creek is a fourth order stream (after Strahler 1957) with a trellis-shaped drainage pattern and a total area of 600 km^2. Its tributaries originate as snowmelt or glacial meltwater on steep slopes at elevations up to 1700 m. Mainstem headwaters begin at a valley floor elevation of 290 m in Turnagain Pass, and flow 37 km to the mouth at Turnagain Arm (sea level). The channel gradient of the mainstem is gently sloping (0.5-4%) for the upper 18 km, but drops through two bedrock canyons for the remaining distance to the mouth. Average discharge of lower Sixmile Creek is about 56.6 m/s, with average bankfull discharge being about 198 m/s. Further description of the physiography, climate, and vegetation is given in Appendix I.

The study area was a section of the Sixmile Creek mainstem headwaters in Turnagain Pass (Fig. 3). The stream, called Granite Creek at this stage, is a clear, second order stream orginating from snowmelt and groundwater springs. It is a pristine system, although gold mining occurs on some tributaries.

The Granite Creek sub-drainage area is 46 km^2, or about 8% of the total Sixmile Creek basin. Length of the study section of Granite Creek was 7.1 km, about one-fifth the total length of the Sixmile Creek mainstem. The largest tributary to Granite Creek in the study site, Tincan-Lyon Creek, is a second order stream. This tributary orginates from glacial and snow melt-water, and is a turbid, sediment-rich system which drastically alters the character of Granite Creek below the confluence.

Turnagain Pass is a wide, glacial-scoured valley with subsoils composed of reworked glacial gravels. Vegetation consists of moist alpine tundra (mixed forbs and mosses) with willow (*Salix sp.*) and alder (*Alnus sp.*) as the dominant woody plant species.

Beaver occur throughout the Sixmile Creek watershed, but the study site is the only area where coho salmon and beaver are sympatric. Upper Granite Creek is the primary spawning and rearing area for coho in the Sixmile watershed. Details of the salmonid fishery resources are given in Appendix I.

METHODS

Field work for this study was conducted from May, 1986 to January, 1987, but observations from my previous seven years' experience on Sixmile Creek have been incorporated into the analysis. Study techniques are described as they relate to each working objective.

Objective 1: Determining beaver effects on stream channel development.

Task: Habitat Classification

Understanding beaver influences on Upper Granite Creek in the context of a hierarchical watershed model was facilitated by classifying stream habitat. The Frissell et al. (1986) stream classification system was applied. Their classification criteria were followed for segments, reaches, and fish habitat types, except were noted.

Segment boundaries were determined from United States Geological Survey (1976) topographic map features (scale 1;63,360) and low level color infrared (LLCI) photographs taken in 1980 (approximate scale 1:5000). At the segment level, chronosequence comparisons of beaver pond sites were made using three sets of aerial photos taken in 1961, 1974, and 1980. Overlays between photos were made using a zoom transfer scope to determine present and past dam/pond locations for field verification.

To classify reaches within segments, aerial photo, landtype map comparisons, and field observations were made. Channel gradients were determined from 1979-1980 U.S. Department of Agriculture, Forest Service (USDA-FS) stream survey data. Geomorphic characters were identified from LLCI photos. Landtype associations were taken from Davis et al. (1980).

To better understand the consequences of beaver structures for channel development, I spent several days observing beaver in their construction activities on Granite Creek, elsewhere in the Sixmile drainage, and in adjacent watersheds. I snorkeled in and around beaver ponds in the study area to examine effects of their activity.

Beaver structures were aged by comparing the "benchmark" date of their associated dam sites (obtained from chronosequence aerial photos) with field dating of sprouted willow cuttings (according to Call 1966) near the structures. Sites more recent than the latest aerial photos were dated from field observations recorded from 1980 to 1985.

Objective 2: Determining beaver effects on coho habitat

Task 1: Coho habitat availability

Within each reach, fish habitat units were classified according to Frissell et al. (1986) and Bisson et al. (1982), and were modified for the Sixmile system using USDA-FS (1981).

Task 2: Coho habitat utilization

Coho Rearing

Once all main and side channel habitats were classified in the sample reaches, a "systematic random sample" of habitat types was selected for minnow-trapping according to Reeves and Hankin (unpubl. ms). All habitat types -- if present -- were sampled at some level in each reach, regardless of the expected use by fry.

Habitat units were sampled using a baited minnow trap for 10 minutes at each site. Fish were identified, counted, weighed, and measured. Hatchery marks were noted. Trapping was accomplished at least 10 weeks after hatchery fish were stocked in the upper portion of R-1 and in the Tincan-Lyon Creek ponds. (See Figure 4 for stocking locations.)

Coho fry capture data were evaluated according to habitat type for side channel and main channel categories in each reach.

Coho Spawning

Two escapement counts were made in the study area in September and October. Spawning locations were noted relative to previous years' surveys (USDA-FS stream surveys 1979-1985) and relative to beaver dam locations.

RESULTS AND INTERPRETATION

Habitat Classification

Classifying stream habitat and beaver activity was integral to determining the time and space scales of beaver effects. I categorized the study area into stream segments, reaches and habitat units. Each level is discussed in the following section.

Segment Level

Two stream segments were identified. Table 2 shows the classification criteria and segment characteristics. Segment 1 (5.2 km long) included Granite Creek from its headwaters down to its confluence with Tincan-Lyon Creek. Segment 2 (1.9 km long) continued down Granite Creek from that point to the lower study area boundary, a channel constriction between ancient floodplain terraces (Fig. 3). Table 3 compares the study area sub-dainage to the Sixmile Creek basin.

Reach Level

Four criteria were used to delineate reaches:

1. Differences in channel bed gradient;
2. Slope breaks caused by bedrock or other geologic discontinuity (e.g., cascade or older floodplain terrace);
3. Landtype association (soils and vegetation communities);
4. Type and age of beaver structures.

Figure 4 shows the relationship of channel gradient and geomorphic features to reach boundaries and beaver dam locations. Figure 5 illustrates the landtypes used in delineating reach boundaries.

Beaver activity was classified by type of dam. Dams were classified as either mainstem or side slope. Mainstem dams completely blocked the main stream channel; sideslope dams impounded terrace tributaries (defined below). Mainstem dams consisted of the primary dam blocking the channel and the secondary dam, which extended across the floodplain to retain ponded water. Secondary dams were lower and less elegantly interwoven than primary dams. This was significant because, being less fortified, secondary dams deteriorated within months of abandonment, with resultant outflows developing into side channels. As will be shown under "Beaver Effects", side channels had important consequences for coho rearing habitat and for adult upstream passage.

Several beaver-made structures were associated with each pond system. Twelve types were identified: dam, pond, lodge, canal, tunnel, burrow, food cache, dam outfall, depression, bank den, skid trail, and scent mound. These are defined in Appendix II. Dam/pond sites and associated structures of the same age were considered a pond complex in a reach. A total of 34 dams and other structures were dated. All sites had typical beaver structures described by other authors (Warren 1927; Morgan 1986).

Based on the four criteria, six contiguous reaches were classified: five reaches (R-1 to R-5) within Segment 1 and one (R-6) in Segment 2. Reach characteristics are compared in Table 4. Figure 3 shows segment and reach boundaries.

Reaches were further subdivided into mainstem and side channel categories. Side channels were defined as subsidiary channels of the mainstem, located within the active floodplain. Tributaries to reaches were classified as either valley sidewall or terrace tributaries. Valley sidewall tributaries were first order streams originating on steep valley slopes but decreasing in gradient before joining the mainstem. These were often excavated and used by beaver as access routes to willow stands. Terrace tributaries were low gradient spring networks that drained the elevated, ancient floodplain terraces (after Sedell et al. 1984). Terrace tributaries served as water sources for side slope beaver dams. The location and type of tributaries in the study area are given in Table 4.

Habitat Level

In Segment 1, 100% of the habitat in Reaches R-1, R-2, R-3, and R-5 was classified into habitat types. Reach 6 was classified into mainstem, side channel and tributary outfall categories. The mainstem was not classified to habitat level, because previous stream surveys indicated little or no use of the mainstem by rearing coho due to the heavy glacial influence of Tincan-Lyon Creek (USDA-FS, CNF, Sixmile Creek Stream Survey Data, 1979-1981). In R-6, habitat classification was thus limited to the side channels and terrace tributary junctions.

Ten salmon habitat types were identified: seven pool types, glide, riffle, and cascade (Table 5).

Beaver Activity

Ten beaver inhabited the study area in four colonies. A colony was defined as one or more beaver inhabiting a site (Bradt 1938). Segment 1, Reach 2 had a colony of five beaver (Dams 3-6). On Segment 2, a single adult occupied Pond 5 (P-5); a pair occupid P-8.5, and another pair had constructed a bank den on the mainstem.

Dam site selection and construction were typical of that reported elsewhere (Warren 1927; Retzer et al. 1956; Call 1966; Morgan 1986). Willow was used for forage and construction. Even though alder was available, it was not used. Beaver built dams on the mainstem of Segment 1 and only on the sideslopes of Segment 2. Bank dens occurred only on the mainstem of Segment 2. I observed some differences in colony density, movements, and seasonal behavior that had not previously been reported. These are discussed in Appendix III.

Beaver Effects on Channel Form and Coho Salmon Habitat

Segment Level

Perhaps the most obvious beaver effect at the segment level was the degree of control over water and sediment routing in the mainstream channel. All fifteen major ponds on Segment 1 were formed by mainstem dams, whereas all ponds on Segment 2 were formed by sideslope dams. Hopp et al. (1972) described floodplain widening by accelerated floodplain aggradation. In this way, Ives (1948) explained beaver meadow formation. My observations support this as an explanation for the influence of beaver Segment 1, which typified the beaver meadow complex: it was a second order stream, with low channel gradient, wide valley, and narrow stream channel compared to Segment 2 (Table 2). Mean dam height was 0.7 m above the downstream channel bed. Ponds were elevated in a series of "stepped " reservoirs down the stream. Swanson and Lienkaemper (1978) and Keller and Swanson (1979) described a similar "stepped gradient" efffect formed by woody debris jams. Beaver dams and debris jams have the same impact of reducing the effective channel bed gradient, the results being increased sediment accumulation, buffered erosive effects of flood events, and delayed retransport of sediments.

The difference in channel gradient between Segments 1 and 2 can be noted in Figure 4, as can the location of beaver dams along Segment 1. In all cases, beaver dams were located at geological "nickpoints" -- points where features were more resistant to erosion than the surrounding bed material. Wolman and Miller (1960) concluded that the effectiveness of events in shaping landscape depended on both the frequency and magnitude of those events. For a channel bank to be built, overtopping must occur more frequently than effective erosional discharge. Beaver dams buffer flood events and create the conditions of floodplain construction (Grasse 1951). On Segment 1, I found that pond site longevity ranged from 6-16 yr (mean = 9.1 yr), whereas periods of abandonment ranged from 3-13 yr (mean = 8.5 yr). Peat deposits visible on partially-drained ponds (D-7 and D-8) were almost half a meter thick on top of original stream gravel and were spread out across the floodplain, beyond original channel banks. I concluded that sediment deposition on top of stream banks has probably contributed to floodplain widening.

Beaver were able to capitalize on the flow-constricting effects at nickpoints, utilizing the steep upper banks of the narrow terraces as dam abutments. Ponds formed at these locations were as much as 1 m deeper than the deepest sideslope dam. Valley sidewall tributaries associated with Segment 1 dams were flooded as far as 50 m upstream from tributary junctions. This effective reservoir formation provided flooded access to willow without need for the beaver to continually raise the dam height to flood access to new stands. This conclusion was supported by the fact that all mainstem dams on Segment 1, regardless of age, were about the same height.

In contrast, beaver were unable to impound the mainstem of Segment 2. Their effect on the stream segment was shifted to off-channel areas. The influence of Tincan-Lyon Creek has dominated the channel form of Granite Creek below the confluence. The greater power of the stream has forced beaver off the main channel and onto the floodplain terrace, where they have been able to successfully impound tributary flows.

In addition to the difference in main channel impoundment, the two segments differed in the amount of floodplain area with ponded water. Table 6 shows ponded floodplain area in 1986. Total floodplain area of Segment 1 was 15.47 HA, 0.74 HA of which was beaver pond. This comprised 4.8% of the total segment floodplain area. On Segment 2, however, beaver ponds covered 1.79 HA of the total area (16.67 HA), comprising 10.7% of the segment floodplain. On Segment 2, not only was the proportion of floodplain covered by beaver ponds greater, but the actual ponded area was greater than it was on Segment 1. Table 6 also gives the hectares of ponded area as a function of thalweg length. With a floodplain width almost half that of Segment 1 (Table 2), Segment 2 had 0.95 HA of pond per kilometer of stream channel, compared to 0.14 HA pond/km on Segment 1.

To put this in a historical perspective, Table 7 compares the ponded areas of Segments 1 and 2 in 1961, 1974 and 1986. Although the amount of floodplain retained as ponded water was similar on Segment 2 for all three years compared (10.4%, 10.0% and 10.7% in 1961, 1974, and 1986, respectively), there was a notable difference between years on Segment 1. Maximum ponded area on Segment 1 occurred in 1961 (8.4% of floodplain area), but declined to 1.8% in 1974. Ponded area increased between 1974 and 1986 to 4.8% on that segment.

The decline and subsequent increase in beaver pond area on Segment 1 was attributed to the history of dam construction since 1961. Since 1961, two major pond complexes were abandoned: Dams 9-10 on R-4 and Dams 11-12 on R-5 (Table 8). The slight decline in ponded area on Segment 2 is explained by the abandonment of Ponds 6, 7, and 8 after 1961. By 1986, proportion of ponded area on Segment 2 had increased slightly over the 1974 level. This was attributed to the construction of P-8.5 in 1986.

The cyclic pattern of beaver habitation in the study area provides that some fraction of flows are retained as ponded water in the floodplain. The accumulation of organic and inorganic sediments and bank overtopping which accompany impoundment contributed to the development of the beaver meadow, as well as to development of stream habitats.

Reach Level

While the long-term, cumulative effects of the stepped gradient with impoundment of water on the floodplain contributes to beaver meadow formation, each pond complex had consequences for the stream at the reach and habitat levels.

For the fifteen major pond complexes on Segment 1, I correlated site longevity (years of continuous occupation) and abandonment with the relation state of dam repair, pond level, and condition of associated structures. A pattern of stream habitat development emerged from which a cycle of dam site evolution was defined. I recognized these as four developmental stages in a cycle of occupation-abandonment-reoccupation, based on the following criteria:

1. percent of reach area as side channel;
2. period since abandonment;
3. relative pond level; and
4. relative repair of primary dam.

Using these criteria, the following developmental stages (discussed below) were established:

a. Occupation (O);
b. Early-Post Abandonment (EPA);
c. Late Post-Abandonment (LPA);
d. Reoccupation (R).

Each reach contained ponds at the same developmental stage, except for R-1. Dam 1 was at the LPA stage and Dam 2 at the EPA stages. For purposes of better understanding habitat relationships, I separated R-1 into upper and lower parts, by dating willow cuttings and beaver structures. Table 8 gives developmental stages for all pond sites in the study area. No side channels occurred in sideslope dams, but developmental stage characteristics applied in all other respects.

Fraction of floodplain at each developmental stage is given for all reaches in Table 6. This includes beaver ponds, dams, and surrounding radii of beaver activity. Figure 7 indicates the location of dam/pond sites at each developmental stage. The involvement of floodplain area in beaver activity was greater for reaches on Segment 1 than for R-6 on Segment 2. The exception was R-1, where the area affected by beaver was quite small (0.69%) compared to the floodplain area (7.24 HA). Hectares of ponded water per kilometer of stream channel, however, were smaller in all Segment 1 reaches than on Segment 2, because of the greater floodplain width and smaller channel width to floodplain width ratio (Table 2).

Developmental stages are discussed in terms of representatives sites from the study area in the next sections. Mainstem and sideslope dams are discussed separately where the two differ in development.

Occupation

Mainstem Dams

Dams 5 and 6 in R-2 were representative of the Occupation Stage (Fig. 3). These sites had been occupied since 1981. The mean site longevity of all mainstem dam sites was 9.1 yr; the longest occupied sites was Dam 11, which had been occupied 16 yr (Table 8).

The D-5 and D-6 sites consisted of two primary dams and their well-developed secondary dams. Total pond area was 0.13 HA, the upstream boundary of which was contiguous with D-4. Other structures included a lodge, several old and new food caches, numerous bank burrows, and skid trails. Continued travel along skid trails had begun to remove vegetation and some drainages were developing as a result. Small seeps up the steep bank were so heavily travelled by beaver that the drainages were enlarging and backwaters were developing at their junctions with the pond edge. Fine peat deposits layered the pond bottom, and beaver had extensively excavated depressions and canals throughout the pond.

No well-developed side channels existed at this site, as the pond had flooded all the active stream channels above its banks, but outfalls of secondary dams on D-6 were beginning to erode through the moss and sedge vegetation, exposing the subsoils. Where these outfalls rejoined the main channel below the dam, small plunge pools were created.

Sideslope Dams

Site P-9 on Segment 2 was the oldest, continuously occupied site in the study area. Over 25 yr old, in 1986 it covered an area of 0.15 HA (Table 8), but had been nearly half again that size according to 1961 aerial photos. The upstream part of the pond was overgrown with marshy sedge. All willows in a several meter radius had been harvested or were killed by flooding. The beaver maintained an elegant canal system radiating out from the pond perimeter and had channelized all the outfalls. The extensive use of trails and canals has formed new drainages with pools at junctions with the main channel of Granite Creek. A few burrows were noted, as well as a lodge, several old food caches, and skid trails. The sole inhabitant was harvesting most willow downstream of the dam, activity that had created several connected backwater pools.

The mean longevity of sideslope ponds was 17 yr --considerably older than mainstem dams. This is probably due to the lower, stabler flows of the terrace tributaries. Beaver have been able to successfully maintain pond levels with low dams made of sedge and mud, requiring less willow for dam construction or repair. Willow in the vicinity has been available for forage, along with alternative types of forage present in the variety of wet marsh plants found at pond margins.

Early Post-Abandonment (EPA)

Dams 2, 7, 8, and P-5 represented the EPA stage. The period lasted from 0 to 5 yr after beaver left the site (mean = 3.8 yr). During that time, beaver structures had deteriorated with successive flood events, altering downstream habitat. For example, bank burrows collapsed, becoming backwaters; canals and depressions became backwaters or side channels. Appendix II describes the tranformations observed in the deterioration of the various beaver structures.

At the EPA stage, primary and secondary dams had breached and the pond had partially drained. Breaches were narrow, less than 10% of the dam length, so the pond form was retained. Some of the pond sediments had been transported downstream, while the original stream channel form and substrate had reappeared in some places. Dam and food cache debris had formed small jams along the pond and downstream areas. Willow had begun to resprout on Dams 7 and 8 and within the harvest radius. by the second year after breaching, the exposed bars of lose peat sediments were being revegetated with mosses and herbaceous plants.

Maximum side channel development occurred at the EPA stage. The greatest pool area in side channels also occurred at this stage, compared to other developmental stages (Table 9). Outfalls of secondary dam had become incised side channels; those that had been channelized by beaver were the deepest and u-shaped in cross section. The exception was D-1. Though it was classed at the LPA stage, side channel pool area exceeded that of D-7 and D-8, probably because all side channels and valley wall tributaries had been excavated by beaver, foraging canals with pools up to 0.3 m deep. In the other dams at the EPA stage, fewer side channels had been excavated by beaver, and being shallower, these did not persist as pool habitats once the pond had drained.

Changes in P-5 (sideslope dam) at the EPA stage were similar to those of mainstem dams. The pond level, however, was not greatly altered from when it had been occupied. Pools at the outfall at the mainstem junction were at the bankfull stage, having lost little volume even though the dam had been breached above.

Late Post-Abandonment (LPA)

Mainstem Dams

The LPA stage was represented by Dams 1, 11, 11.5, and 12. This stage occurred 6 to 12 yr (mean = 10 yr) after abandonment and continued up to the time of reoccupation.

The distinctive features of this stage included enlargement of the dam breaches and revegetation of the remaining structure. The pond shores were also overgrown with resprouted willow and sedge. Fine sediments had been redistributed downstream, and large gravel and cobble substrate were visible in the main channel. Bars, vegetated with forbs and willow, were composed of gravel. Channel banks were also overgrown. New channel undercutting accompanied by formation of lateral scour pools had occurred.

Side channel habitat area at the LPA stage was less than in the EPA stage (Table 8), though some backwaters persisted where excavation by beaver had occurred.

Sideslope Dams

On R-6, sideslope sites P-6, P-7, and P-8 were classed as the LPA stage. The mean period of abandonment was 11.5 yr. Although dam structures remained in place, pond area had been reduced by encroachment of wet marsh. Dams were heavily overgrown with grass and willow, stabilizing the remaining structure with the overgrowth. Pond outflows had been reduced, thus decreasing the area of backwaters at the mainstem junctions.

Reoccupation (R)

The reoccupation stage completed the cycle of beaver-influenced stream habitat development. The pond complex D-3, 3.5, 3.6, 3.7, and 4 was constructed at a site that had been an active pond from 1961 to 1973. The site had been abandoned for 13 yr, and was 25 years of age when reoccupied.

Dams constructed in 1986 were built in almost precisely the same locations as the 1961 dam. In five weeks, the four dams were completed; a few weeks after, all side channels and depressions (probably remnants of the earlier complex) were also flooded.

Observations of beaver during construction revealed how rapidly they altered stream habitats. Beaver excavated the main channel bottom 0.6 m below the original bed level, using the material in construction of the dam. All former side channels were excavated and new canals were constructed at the outflows of the newly-built secondary dams. Small drainages developed along skid trails were soils had been eroded from stream banks. Fine sediments and plant litter had began to settle in the pond and by October deposits were several centimeters thick.

Habitat Level

Recognition of the stages and timing of cyclic habitation at the reach level was a key to understanding the long-term segment level effects as well as short-term changes at the habitat level. Table 10 gives proportions of the ten habitat types by number of units and by area (m^2) for each reach. Data are separated into main and side channel categories for all reaches in Segment 1 and side channel and outfall categories for Segment 2.

The most notable differences in habitat were the amount of side channel area and dammed pool area. Data indicated that maximum side channel area occurred at the EPA stage (Table 8). Side channel habitat units attributed to beaver activity were determined by examining the proximity of side channel units to recognizable beaver structures. Side channels of Segment 1 were formed by dam outfalls. Table 11 shows that 64% of the side channel habitat units on Upper R-1, 69% on R-6, and 100% of side channel habitat units on Lower R-1 and R-3 were attributable to beaver. Only 33% of the side channel habitats on R-5 were attributable to beaver, possibly because the degree of revegetation and deposition that had occurred in the 11-12 yr since abandonment had obscured identifiable beaver structures.

Erosion of beaver structures in the main channel precluded reliable correlation of mainstem habitat units to beaver activity. For example, backwaters and lateral scour pools at the LPA stage could not be related to collapsed burrows or skid trails because most evidence of beaver activity had been eroded or overgrown.

The persistence of dammed pools was important to the development of side channel habitat units because ponds drained into downstream side channels via breaches in secondary dams. At the LPA stage, when the primary dam breach had widened sufficiently to completely drain the pond, the main channel once again resumed downcutting and dominated the routing of flows. Water flow through side channels diminished, more deposition occurred, and revegetation resulted in less habitat available for fish. This was exemplified in the proportion of side channel habitat in R-3, at the EPA stage, compared to R-5, at the LPA stage. The dammed pool area (beaver pond) in R-3 was 5232 m^2, compared to no pond area in R-5 (Table 10). This corresponds to the proportion of side channels in pool habitats, 58% and 2%, for R-3 and R-5, respectively (Table 9).

Further relationships of habitat to utilization are discussed in the following section.

Coho Habitat Availability Versus Utilization

Coho Rearing Habitat

Numerous authors report the importance of side channels, backwaters, and other pool types as rearing habitat for coho salmon because these habitats provide a beneficial regime of space, cover and forage (Lister and Genoe 1970; Bisson et al. 1982; Sedell et al. 1984; Bryant 1983). The results of this study were consistent with those findings in that more coho juveniles were captured in pools than other habitat types (Table 12). To evaluate the influence of beaver on coho habitat, I compared area of pools to the developmental stage of beaver activity at the segment, reach, and habitat levels.

Segment Level

Within the entire Sixmile drainage, coho salmon spawn and are reared almost exclusively in the study area. Of this, only Segment 1 and outfalls or side channels of Segment 2 provided pool rearing areas. The main channel area of Segment 2 provided little or no coho rearing habitat, as most of the channel consisted of riffles and rapids. Main channel area of Segment 1 was less than one third that of Segment 2, even though Segment 1 was 2.7 times longer (Table 9). however, 75% of the main channel area in Segment 1 was pool habitat.

Segment 1 had 0.13 HA side channel area compared to 0.10 HA in Segment 2. In Segment 1, 56% of this was in pool habitat, whereas in Segment 2, 100% of the side channel and outfall area was pool habitat. The main and side channels of Segment 1 along with side channels and outfalls of Segment 2 provided most of the available coho salmon rearing area in the Sixmile drainage, with beaver influencing most of that area through cyclic habitation. One could conclude, then, that most of the available rearing area in the drainage was affected by beaver.

Reach Level

Hatchery coho presmolts were stocked at three locations in the study area on June 30, 1986 (Fig. 3). Sampling began in September, which allowed time for hatchery fish to disperse downstream. Marked hatchery fish were captured in all reaches sampled, indicating that fish had distributed downstream. The number and proportion of habitat units sampled compared to the total number of units are given in Table 13.

Figure 8 shows the relationship of fish capture to downstream distance. Highest capture was closest to stocking sites. Coho fry capture was greatest in R-1, diminishing downstream to R-3. On R-5, below the confluence of T.P. Creek (one of the stocking sites), abundance increased slightly. No increase in capture was detected below the outlet of Lyon Creek rearing ponds on R-6, however.

In comparing fry abundance between mainstem and side channel habitats, more fry were captured in the mainstem of R-1 and R-5 than in the side channels of those reaches. Capture was also higher in R-2, compared to other reach side channels. On R-3, at the EPA stage, 99% (n = 93) of the fry were captured in side channels (Table 12) even though this comprised only 5% of the total reach area. All of the side channel habitat in R-3 was attributable to beaver activity (Table 11), 58% of which was in pools. On Lower R-1 (also at the EPA stage), 10% of the total area was in side channels, 74% of which was pool habitat (99 m^2). Side channels accounted for 39% (n = 47) of the fry captured in lower R-1, but main channel pool area accounted for 61% (n = 75) of the fry captured in that reach section. Although the absolute number of fry captured in main channel habitat was greater, the density (fry/m^2) was slightly higher for side channels of Lower R-1 (0.47 fry/m^2 versus 0.33 fry/m^2).

On R-6, more fry were captured in terrace tributary outfalls than side channels, all of which were pools attributed to beaver activity. Fry captured in side channels of R-6 were taken at junctions of beaver pond outfalls where temperatures were 2-3° C higher than adjacent mainstem waters.

Trapping data analysis was confounded by temperature dependent results in the fall. In late October, daily water temperature fluctuated between 2.2° and 5° C. Table 14 shows the differences in fry capture relative to water temperature for the autumn months.

Prior to the wide temperature fluctuations, if fish were observed, they could be trapped. However, when water temperatures began dipping below 3° C, fish were not observed and few were captured.

Snorkeling observations were made during October and November on R-1 and R-2. In October, at 2.2° C, few active fish were observed in either reach, but more were seen in R-2. Those observed, were concealed among beaver-cut sticks, beaver dams, and food caches. Individual fish were also found under boulders, but none were found among the dense, rooted material of undercut banks as had been expected from other reports (pers. comm., James Sedell, PNW Forest and Range Expt. Sta., Corvallis).

Trapping and snorkeling in November at a water temperature of 1.4° C revealed a completely different situation at the sites visited in October. No fish were seen or captured in the R-1 sites. However, 60 fish were trapped in a 10 minute period above Dam 3.6 in R-2. Snorkeling revealed abundant, active fish throughout ponds, among dam interstices as well as in open water. In January, the trapping yielded 49 fish at the same site.

Two conclusions were drawn from the late fall and winter observations: 1) Fish acclimated to lower water temperatures by late fall and winter. 2) Coho fry moved from R-1 downstream to R-2 to overwinter in beaver ponds.

Snorkeling observations complemented trapping by providing a relative abundance measure in the absence of reliable trapping data. Furthermore, snorkeling revealed that fry utilized woody debris associated with beaver activity, observations that trapping alone would not have indicated. Trapping data for statistical comparisons of fry abundance or density between reaches may have limited value, due to the temperature dependent results and stocking site concentrations. Therefore, fry capture results are presented only as indices to relative fry abundance and utilization of habitat.

Habitat Level

A total of 2172 juvenile coho were captured. Of those, 1.4% were marked hatchery fish. Twenty-five chinook presmolts were trapped, as well as 51 Dolly Varden fry and adults. The most notable finding was that fry capture did not correspond to the proportion of pool habitat types (Fig. 9). Figure 9 summarizes total fry capture relative to area of habitat types. In all reaches -- both main and side channel categories -- fry were most abundant in lateral scour pools (50% of the total capture) and backwaters (22% of the total capture), despite their fractional representation in each reach. Fry were rarely taken from riffles, while none were captured in cascades or boulder pools. Capture from eddy pools, slightly exceeded that from glides or trench pools (Table 12).

Although dammed pools (beaver ponds) comprised 72% and 46% of the main channel habitat of R-3 and R-2, respectively (Table 10), few fry were taken from those areas until after October. At that time, no coho fry were captured or observed in the pool habitats of R-1, where fry had been captured in September. Snorkeling observations indicated that fry had moved into beaver ponds by November. Observations by Andy Doloff (pers. comm. USDA-FS Forest Sciences Lab, Juneau) support the conclusion that coho juveniles move into beaver ponds in the late fall to overwinter.

In summary, the main channel area of Segment 1 comprised 93% of the available rearing area in the study site and yielded 81% of the fry captured. Most of the side channel habitat in Segment 1 was attributed to beaver activity. This accounted for 10% of the total fry capture, but represented only 5% of the total Segment area.

Of the available (off-channel) rearing area in Segment 2, beaver pond outfalls accounted for about 10% of the total fry capture but comprised about 25% of the off-channel area. Side channels on Segment 2 (comprising the remaining 75% of off-channel area) accounted for 2% of the total fry catch.

Nearly all side channel habitat in Segment 1 was attributed to beaver activity. This amounted to only 6% of the total channel area, but side channel pool habitat accounted for 10% of the total fry captured in the study. In the whole Upper Granite Creek study area, approximately 17% of the total fry capture occurred in habitat created by beaver.

Coho Spawning Habitat

Beaver activity had no apparent effects upon the availability or utilization of spawning habitat on Upper Granite Creek. Spawning and post-spawning counts were made in late September and late October, respectively. Most of the spawning occurred in Segment 1. A total of 31 spawners were counted: 5 in R-1; 3 in R-2; 8 in R-3; 8 in R-5, and 7 in R-6, just below the Tincan-Lyon Creek confluence. This count was comparable to past returns of native fish (pers. comm., Kurt Nelson, USDA-Fs, CNF). No adult hatchery-marked fish were observed, even though returns of fish stocked in 1983, 1984, and 1985 had been expected by 1986.

Adults appeared to use the same riffle areas where they had been observed in the last seven years. Recent beaver dam construction did not hamper upstream movements, as spawners were observed negotiating secondary dam outfalls without difficulty. In fact, one pair spawned in the beaver pond above Dam 3.6.

CONCLUSION

Summary of Beaver Effects

Coho salmon idigenous to Sixmile Creek spawned and were reared almost exclusively in the Upper Granite Creek area. The results of this study indicated that beaver influenced nearly all of the available spawning and rearing habitat in that section of Sixmile Creek.

The cyclic successional pattern created by the sequential occupation and abandonment of sites by beaver contributed to salmon habitat availability on Segment 1. While beaver occupied a site, the pond provided seasonal refuge for fry during the winter. Side channels developed in and below beaver ponds during the early post-abandonment phase (0-5 yr after abandonment). Reaching maximum area at this stage, most side channel area was in pool habitat. Decaying beaver structures were transformed into backwater and lateral scour pools utilized by fry. Late post-abandonment followed the EPA stage, and lasted 6-12+ yr until willow stands could again support beaver, at which time sites were reoccupied (about 25 yr after last occupation). Side channel habitat diminished at the LPA stage, with more fish habitat available in the mainstem.

The process of rearing habitat development was perpetuated with this cycle. All stages of the cycle were concurrent in the study area, with rearing habitat existing in various stages of development.

On Segment 2, sideslope dam outfalls provided additional off-channel habitat, thus improving the inhospitable habitat for coho rearing on that segment.

Beaver activity did not impede access to spawning grounds, nor did it appear to limit available spawning area, because escapement was small.

In conclusion, beaver appear to contribute to the long-term availability of salmon habitat by maintaining development of habitat over short-term cycles. Although stream processes may provide habitable conditions for coho salmon in the absence of beaver, where beaver and coho salmon have occurred sympatrically for long periods of time, the relationship is probably beneficial for coho. Coho in Upper Granite Creek in the Sixmile Creek watershed appear to have adapted to the kinds and cycles of habitat that beaver create in concert with other watershed processes.

Fishery Management Implications

Beaver and Salmon Management

Fishery biologists recognize the adaptive nature of populations of the same fish species in response to different watershed conditions. The conditions operating in a watershed produce possible "performances" - observable states - at different times. Each watershed is theoretically capable of an indefinite number of performances, the total of which could be considered the capacity of that watershed (Warren 1979). Given the contingency of processes in each watershed, it is not logical to assume that a particular management activity would be appropriate for a given species in every watershed.

With respect to managing beaver and salmon, caution should be exercised in determining management goals in light of the contingent interrelationships of the two within a watershed. Consideration should be given to watershed management goals as well as species management goals, and to the time scale over which those goals are to be achieved. For example, a program of removing beaver dams to enhance salmon production, when dams are seen as obstacles to spawning migrants, may indeed permit some adults to reach upstream riffles. However, this considers neither the immediate nor potential long-term effects on channel form and salmon habitat.

Retransport of accumulated pond sediments may clog downstream spawning beds. Dam removal can increase the effective stream bed gradient, thus increasing erosion and channel scouring. The long-term effect may be reduced habitat quality and quantity for both spawning and rearing, not to mention other impacts on riparian and stream habitats.

Wherever beaver occur in pristine watersheds, they should be considered as much a part of the integrity of that watershed as vegetation or soils. They function both as geological and biological agents in influencing stream channels (Naiman et al. 1986). Alteration of that relationship would have both long and short-term consequences for salmon inhabiting that system.

A move away from the stigma that beaver are a nuisance to be dealt with, and a move toward an appreciation of their role in stream ecosystem integrity, could prove valuable in fishery management. Beaver could be managed to rehabilitate fish habitat or maintain existing stream habitat, perhaps on a greater scale than they are today.

Presmolt Stocking in Sixmile Creek

Historically, numbers of indigenous salmon have been low in Sixmile Creek (less than 100 of each species), a fact that has not been attributable to human effects (Sixmile Creek Fishery Enhancement Project Plan, C.J. Sanner, USDA-FS, CNF). Non-native coho and/or chinook have been stocked in Upper Granite Creek since 1983. Outmigrant data show low survival rates for all years monitored. Since stocking began, adult returns showed no increase above pre-stocking escapements of native fish (Appendix I). Nickelson et al. (1986) evaluated presmolt stocking programs in Oregon coastal streams. They found that returns to stocked streams did not differ from returns to unstocked streams. They further suggest that non-native presmolts supplanted native stocks. In Sixmile Creek, non-native coho presmolts may not perform as successfully as the indigenous fish which have evolved there in a beaver influenced system.

Table 1. Time-space scales of beaver activity in relation to other watershed processes (after Frissell et al. 1986).

System level	Linear spatial level[a]	Evolutionary events[b]	Stream development processes[c]	Time scale feature persistence
Stream	10^3M	Volcanic, tectonic Climatic shifts (P,A)[d] Glacial advance/retreat Landslides Minor glaciation/ablation	Valley slope, width changes (P,A) Forest advance/retreat Morrainal develoment Tributary Migrations (A) Channel downcutting	10^3-10^4 yr
Segment	10^2-10^3M	(P,A) Formation of beaver meadow (P,A) Snow avalanches (P,A) Forest fires (P) Extirpation by trapping	(P) Depletion of forage (P,A) Cyclic succession (P) Floodplain aggradation (A) Peat soil development	10^2-10^3 yr
Reach	10^2M	(P,A) Large flood events (P,A) Catastrophic dam breaching (A) Colony abandonment (P) Colony reoccupation (P) Forage depletion	(P,A) Dam degradation (P,A) Retransport of sediments (A) Side channel development (P) Water table elevation, tree death (P) Pond sedimentation (P) New pond outflow patterns (A) Bedload resorting, development (A) Forage succession	10^1-10^2 yr
Habitat (pool/riffle)	10^1-10^0M	(P) New dam construction (P) Auxiliary structure (canal, burrow, etc.) (P) Tree felling, caching (P,A) Moderate flood events	(P) Enlargement or shaping of ponds (A) Shift in pool/riffle ratio (P) Organic matter accumulation (P,A) Sediment retransport (A,P) Lateral scouring (A) Revegetation of bars	10^0-10^1 yr
Microhabitat	10^0-10^{-1}M	(P,A) Annual flood flows (P) Seasonal dam maintenance (P) Seasonal foraging	(P) Seasonal pond level changes (P) Seasonal velocity changes (P) Seasonal changes in aquatic plants (A) Organic matter and fines transported from backwaters and eddies	10^{-1}-10^0 yr

[a] = Space-time scales for a glacial outwash stream

[b] = Evolutionary events are beaver-releated or extrinsic forces affecting beaver at that stream level

[c] = Intrinsic, progressive changes following and evolutionary event

[d] = P = beaver present; A = beaver absent at that stage

Table 2. Stream segment characteristics and classification criteria, Upper Granite Creek study area, 1986.

Classification Criterion	Segment 1 Upper Granite Creek	Segment 2 Below Tincan-Lyon Confluence
1. Landtype association number (see Figure 6)	34, 35, 71, 82, 102	71, 82
2. Beaver activity		
No. number mainstem dams	16	0
No. number sideslope dams	0	6
No. number bank dens	0	1
3. Stream order	2	3
4. Geomorphic boundaries		
upper	Upper Tributary Junction	Tincan-Lyon Confluence
lower	Tincan-Lyon Confluence	Ancient Terrace Constriction
5. Channel gradient (%)	0.5-2.0	3.0-4.0
6. Thalweg length (km)	5.2	1.9
7. Number of reaches	5	1
8. Valley side slopes		
west side	moderate to steep, no floodplain	steep, no floodplain
east side	flat, wide floodplain	moderate, narrow floodplain
9. Mean valley width (m)	461	293
10. Ratio $\frac{\text{channel width}}{\text{valley width}}$	0.01	0.04

Table 3. Comparison of Upper Granite Creek study area sub-basin with Sixmile Creek Basin.

Characteristic	Sixmile Basin	Segment 1	Segment 2
Basin area (km^2)	600	12.1	34.2
Glacier area (km^2)	8.8 (1%)	0	3.5 (10%)
Main channel length (km)	38.4	5.2	1.9
Elevation range (m)	228-Sea Level	305-274	274-259
$\overline{x}$ Valley width (m)	241	167	286
Stream order	4	2	3
Tributaries above 1st order (number)	8	0	1
Hydrograph			
peak flow season	Jul, Oct	Jun, Oct	Jul, Oct
low flow season	Feb	Feb, Jul	Feb
discharge (m^3/sec)			
mean	56.6	0.23	5.6
bankful	198	1.1	20

Table 4. Physical characteristics of reaches in Upper Granite Creek study area, 1986.

Characteristic	Reach R-1	R-2	R-3	R-4	R-5	R-6
Segment	1	1	1	1	1	2
Channel length (m)	1625	1159	690	1175	636	1897
Geomorphic boundaries						
upper	Trib. Jct.	Terrace	Terrace	Terrace	Cascade	Trib. Jct.
lower	Terrace[a]	Terrace	Terrace	Terrace	Trib. Jct.	Terrace
Mean channel slope (%)	0.5	1.0	1.0	1.5	2.0	3.5
Associated landtypes[b]	82,102	82,102	82	34,35,71	82,101	71,82
Beaver activity major dam sites[c]	D-1 D-2	D-3 D-3 D-3 D-4 D-5 D-6	D-7 D-8	D-9 D-10	D-11 D-11 D-12	P-5 P-6 P-7 P-8 P-8.5 P-9 B-1
No. 1st order tributaries[d]	5 VW 1 TT	2 VW 0 TT	3 VW 0 TT	3 VW 0 TT	1 VW 2 TT	0 VW 9 TT

[a] Constriction of ancient floodplain terrace
[b] See Figure 6 for description
[c] D = mainsteam done; P = side slope dams
[d] VW = valley wall tributaries, TT = terrace tributaries

Table 5. Salmon habitat types.

Unit type	Description
A. POOLS	
1. Backwater	along channel margins or connected to main channel; little or no water velocity
2. Lateral scour	along channel bank, elongated shape associated with undercut banks; lateral flow towards bank
3. Trench	mid-channel, elongated, u-shaped in cross-section; not associated with bank
4. Plunge	below a dam or other obstruction; flow a turbulent drop
5. Eddy	specialized lateral scour pool, associated with undercut banks, sharp bend or steep lower banks; flow and sediments recirculate in pool
6. Boulder	formed below or around a boulder cluster
7. Dammed	obstruction at lower end retains flows
B. RIFFLES	aggraded zone between pools or glides; water surface rippled with standing waves; gradient steeper than in pools
C. GLIDES	intermediate between pools and riffles; uniform surface flow, stable banks with uniform substrate size.
D. CASCADE	high gradient riffle; large cobble, boulder or bedrock, flow tumbles in steps

Table 6. Amount of floodplain area ponded and fraction of floodplain at developmental stage, Upper Granite Creek, 1986.

Site	Total flood-plain area (HA)	Develop-mental stage	% flood-plain at develop-mental stage	Beaver pond area (HA)	% flood-plain ponds by beaver	HA ponded water/km channel
Segment 1	15.47	-	-	0.74	4.78	0.14
Reach						
R-1	7.24	LPA	1.9	0	0	0
		EPA	5.8	0.05	0.69	0.03
R-2	0.50	R	73.7	0.03	6.0	0.02
	1.40	0	22.1	0.13	9.2	0.11
R-3	R2.04	EPA	68.6	0.53	25.9	0.76
R-4	0.47	LPA	24.5	0	0	0
R-5	1.76	LPA	66.3	0	0	0
Segment 2	16.67	-	-	1.79	10.7	0.94
Reach						
R-6	16.67	0	10.1	1.79	10.7	0.94
		EPA	2.3	-	-	-
		LPA	24.4	-	-	-

Table 7. Proportion of ponded area to floodplain area of stream segments in Upper Granite Creek 1961, 1974, and 1986.

	Segment 1	% flood-plain area	Segment 2	% flood-plain area
Total floodplain area (HA)	15.47	-	16.67	-
Ponded Area (HA)				
1961	1.30	8.4	1.74	10.4
1974	0.29	1.8	1.67	10.0
1986	0.74	4.8	1.749	10.7

Table 8. Classification criteria of Beaver Dam development stages.

Segment	Reach	Dam Site[1]	Dev. stage[2]	OC[3]	AB[4]	Pond area (HA)	% reach in side channel
1	R-1	D-1	LPA	1-2	6	0	5
		D-2	EPA	6	8	.05	25
1	R-2	D-3.5	R	0.5	13	-	0
		D-3.6	R	0.5	13	-	0
		D-3.7	R	0.5	13	-	0
		D-4	R	0.5	13	.03	0
		D-5	0	4	0	-	0
		D-6	0	4	0	.13	0
1	R-3	D-7	EPA	6	5	.02	22
		D-8	EPA	8	3	.51	-
1	R-4	D-9	LPA	5	7	0	5
		D-10	LPA	12	13	0	-
1	R-5	D-11	LPA	16	12	0	7
		D-11.5	LPA	16	12	0	-
		D-12	LPA	14	11	0	-
2	R-6	P-5	EPA	>21	4	.09	25[5]
		P-6	LPA	>13	12	.57	N/A
		P-7	LPA	14	11	.61	N/A
		P-8	LPA	>13	12	.08	N/A
		P-8.5	0	0.5	-	.29	N/A
		P-9	0	>2.5	-	.15	N/A
		B-1	0	0.5	-	0	N/A

1 D = mainstem dam; SS= sideslope dam; BD = bank den
2 LPA = late post-abandonment; EPA = early post-abandonment; 0 = occupation; R = reoccupation
3 number of years of continuous occupation
4 number of years abandoned before 1986
5 Includes side channels and outfalls

Table 9. Wetted area and percent of pool habitat, Upper Granite Creek, 1986.

Site	TL channel area (HA)	Main channel area (HA)	% TL area	% in pools	Side channel area (HA)	% TL area	% in pools
Segment 1	2.25	2.12	94	75+	0.13	6	56+
Upper R-1	0.51	0.46	91	60	0.05	9	72
Lower R-1	0.22	0.21	90	53	0.01	10	74
R-2	0.16	0.16	100	77	0.0	0	0
R-3	0.75	0.72	95	86	0.03	5	58
R-4	0.38	0.36	96	*	0.02	4	*
R-5	0.25	0.23	92	51	0.02	8	2
Segment 2	6.77	6.67	99	*	0.10	1	100
R-6	6.77	6.67	99	*		1	
outfalls					0.02		100
side channels					0.07		100
pond area (m^2)					1.79		

+ excludes R-4
* not classified at habitat level

Table 10. Habitat composition by number and area of habitat units, Upper Granite Creek, 1986.

MAIN CHANNEL

Segment 1

Habitat type	Reaches: Upper R-1		Lower R-1		R-2		R-3		R-5		Total by habitat type	
	No.	Area‡	No.	Area	No.	Area	No.	Area	No.	Area	No.	Area
BW*	30	459	1	10	3	31	16	367	14	403	64	1270
LS	63	421	7	59	11	112	33	294	20	306	134	1192
TP	39	1112	2	90	7	141	9	97	4	112	61	1552
EP	18	213	4	59	3	203	10	149	6	334	41	958
G	63	1187	7	70	8	150	26	625	14	322	108	2354
R	34	631	8	130	5	204	18	347	14	809	79	2121
DP	2	528	0	1645	2	721	1	5232	0	0	5	8126
PP	0	0	1	4	1	3	3	60	0	0	5	67
C	0	0	0	0	0	0	0	0	0	0	0	0
BP	1	10	0	0	0	0	0	0	0	0	1	10
Totals	240	4561	30	2067	40	1565	116	7171	72	2286	498	17,650

Table 10. continued

SIDE CHANNEL

Habitat type	Segment 1 Reaches: Upper R-1 No.	Upper R-1 Area	Lower R-1 No.	Lower R-1 Area	R-3 No.	R-3 Area	R-5 No.	R-5 Area	Segment 2 R-6: Side channels No.	Side channels Area	outfalls No.	outfalls Area	Total by habitat type No.	Total by habitat type Area
BW*	4	129	4	37	5	43	0	0	0	0	4	103	17	312
LS	7	30	7	27	9	32	0	0	3	711	2	30	28	830
TP	11	190	5	23	4	42	0	0	0	0	1	24	21	279
EP	1	7	1	11	3	83	1	3	2	41	1	98	9	243
G	8	46	2	16	4	97	0	0	0	0	0	0	14	159
R	12	76	7	20	7	46	5	186	0	0	0	0	31	327
DP	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PP	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C	1	6	0	0	0	0	0	0	0	0	0	0	1	6
BP	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Totals	44	478	26	134	32	343	6	189	5	752	8	255	121	†

‡ Area = m^2

* BW = backwater, LS = lateral scour pool; TP = trench pool; EP = eddy pool; G = glide; R = riffle
DP = dammed pool; PP = plunge pool; C = cascade; BP = boulder pool.

† Total area: Segment 1 = 1144 m^2; Segment 2 = 1007 m^2

Table 11. Fraction of side channel habitats attributed to beaver activity, Upper Granite Creek, 1986.

Segment	Reach	Developmental stage[1]	# side channel habitat units	% attributed to beaver activity
1	R-1			
	Upper	LPA	44	64
	Lower	EPA	26	100
1	R-2	0,R	0	0
1	R-3	EPA	32	100
1	R-5	LPA	6	33
2	R-6[2]	0,EPA,LPA	13	69

[1] 0 = occupation stage, EPA = early post-abandonment; LPA = late post-abandonment; R = reoccupation

[2] includes both side channels and outfalls

Table 12. Coho fry capture in segments and reaches, Upper Granite Creek, September-October, 1986.

Habitat Type*	Segment 1										Segment 2			
	Reaches													
	R-1 Upper		R-1 Lower		R-2		R-3		R-5		R-6		Total by type	% of total
	MC	SC	MC	SC	MC	SC	MC	SC	MC	SC	OF	SC		
BW	141	40	-	31	46	-	-	88	77	-	57	-	480	22
LS	667	13	14	13	218	-	1	5	37	-	87	39	1094	50
TP	80	3	6	3	85	-	-	-	-	-	6	-	183	8
EP	122	22	55	-	10	-	-	-	22	-	5	11	247	11
G	58	-	-	-	75	-	-	-	-	-	-	-	133	6
R	3	-	-	-	-	-	-	-	-	-	-	-	3	<1
DP	-	-	-	-	31	-	-	-	-	-	-	-	31	1
PP	-	-	-	-	-	-	-	-	-	-	-	-	1	<1
C	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BP	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total	1072	78	75	47	465	-	1	93	136	-	155	50	2172	100
% of TL segment	93	7	64	39	100	0	1	99	100	-	75	25		

* BW = backwater, LS = lateral scour pool; TP = trench pool; EP = eddy pool; G = glide; R = riffle; DP = dammed pool; PP = plunge pool; C = cascade; BP = boulder pool.

Table 13. Number of habitat units sampled compared to total.

	R-1			R-2			R-3			R-5			R-6*		
	N[a]	n[b]	%[c]	N	n	%	N	n	%	N	n	%	N	n	%
MAIN CHANNEL															
BW[d]	31	3	10	3	2	66	16	8	31	14	4	30	4	4	100
LS	70	22	31	11	8	73	33	8	24	20	9	45	2	2	100
TP	41	3	73	7	1	14	9	1	11	4	1	25	1	1	100
EP	22	6	27	3	3	100	10	5	50	6	3	50	1	1	100
G	60	9	15	8	2	25	27	2	7	14	3	20	0	-	-
R	42	5	13	5	1	20	18	2	11	14	0	0	0	-	-
DP	2	1	50	2	2	100	1	1	100	0	-	-	0	-	-
PP	1	1	100	1	1	100	3	2	66	0	-	-	0	-	-
C	0	0	0	0	-	-	0	-	-	0	-	-	0	-	-
BP	1	0	0	0	-	-	0	-	-	0	-	-	0	-	-
TOTAL	271	50		40	20		117	29		72	20		8	8	
SIDE CHANNELS															
BW	3	3	38	0			5	4	80	0	-	-	0	-	-
LS	14	7	50	0			8	3	37	0	-	-	3	3	100
TP	16	3	19	0			4	1	25	0	-	-	0	-	-
EP	6	2	33	0			3	1	33	1	1	100	2	2	100
G	10	2	20	0			3	1	33	0	-	-	0	-	-
R	19	1	5	0			7	1	14	5	5	100	0	-	-
DP	0	-	-	0			0	-	-	0	-	-	0	-	-
PP	0	-	-	0			0	-	-	0	-	-	0	-	-
C/BP	0	-	-	0			0	-	-	0	-	-	0	-	-
TOTAL	73	18		0	0		30	11		6	6		5	5	

* outfalls and side channels
[a] N = total number habitat units
[b] n = number sampled
[c] % = percent of total sampled
[d] BW = backwater pool; LS = lateral scour pool; TP = trench pool; EP = eddy pool; G = glide; R = riffle; DP = dammed pool; PP = plunge pool; C = cascade; BP = boulder pool

Table 14. Fry capture in relation to water temperature, Upper Granite Creek, Sept. 1986-Jan. 1987.

Date	Sample location	Water temperature (°C)	$\bar{x}$ number fish/trap
9/22/86	R-1	5.5	52
10/2/86	R-2	5.5	65
10/6/86	R-2	3.3	14
10/17/86	R-2	2.2	8
10/23/86	R-1	3.8	5
11/17/86	R-1	1.1	0
11/17/86	R-2	1.1	38
1/21/87	R-2	1.1	49

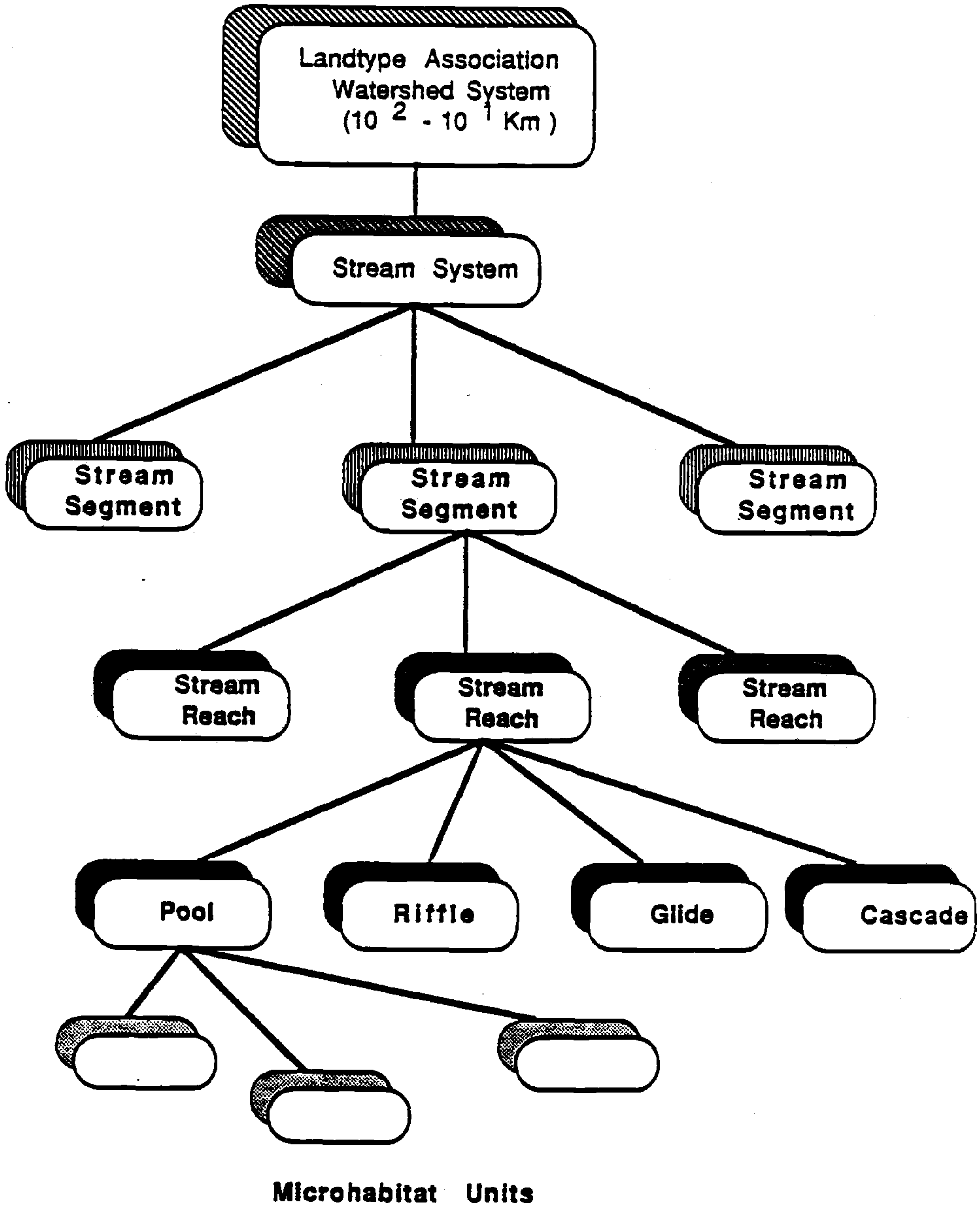


Figure 1. Diagram of a hierarchical watershed model (after Warren and Liss 1983).

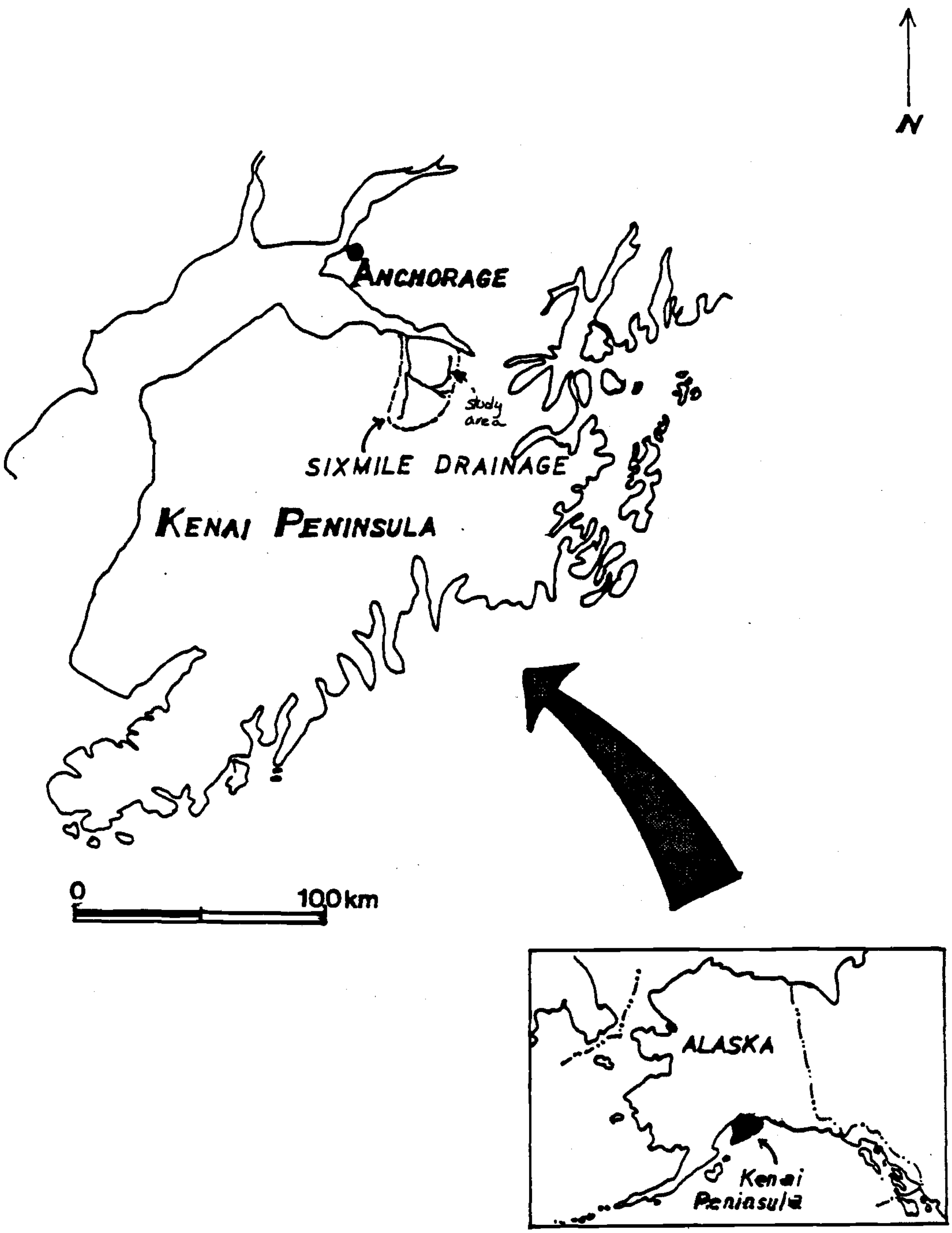


Figure 2. Location of Sixmile Creek watershed, Kenai Peninsula, Alaska.

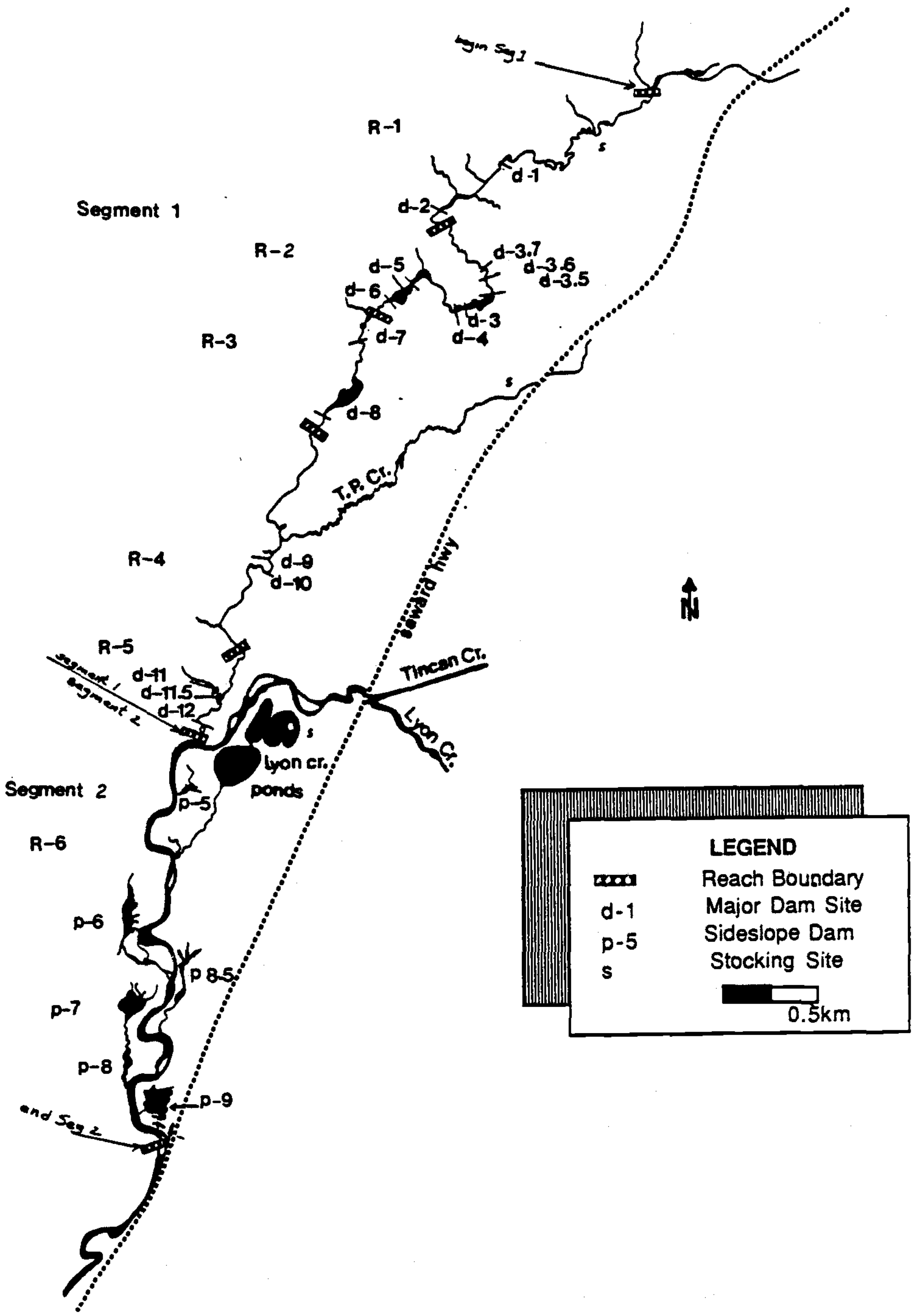


Figure 3. Upper Granite Creek study area.

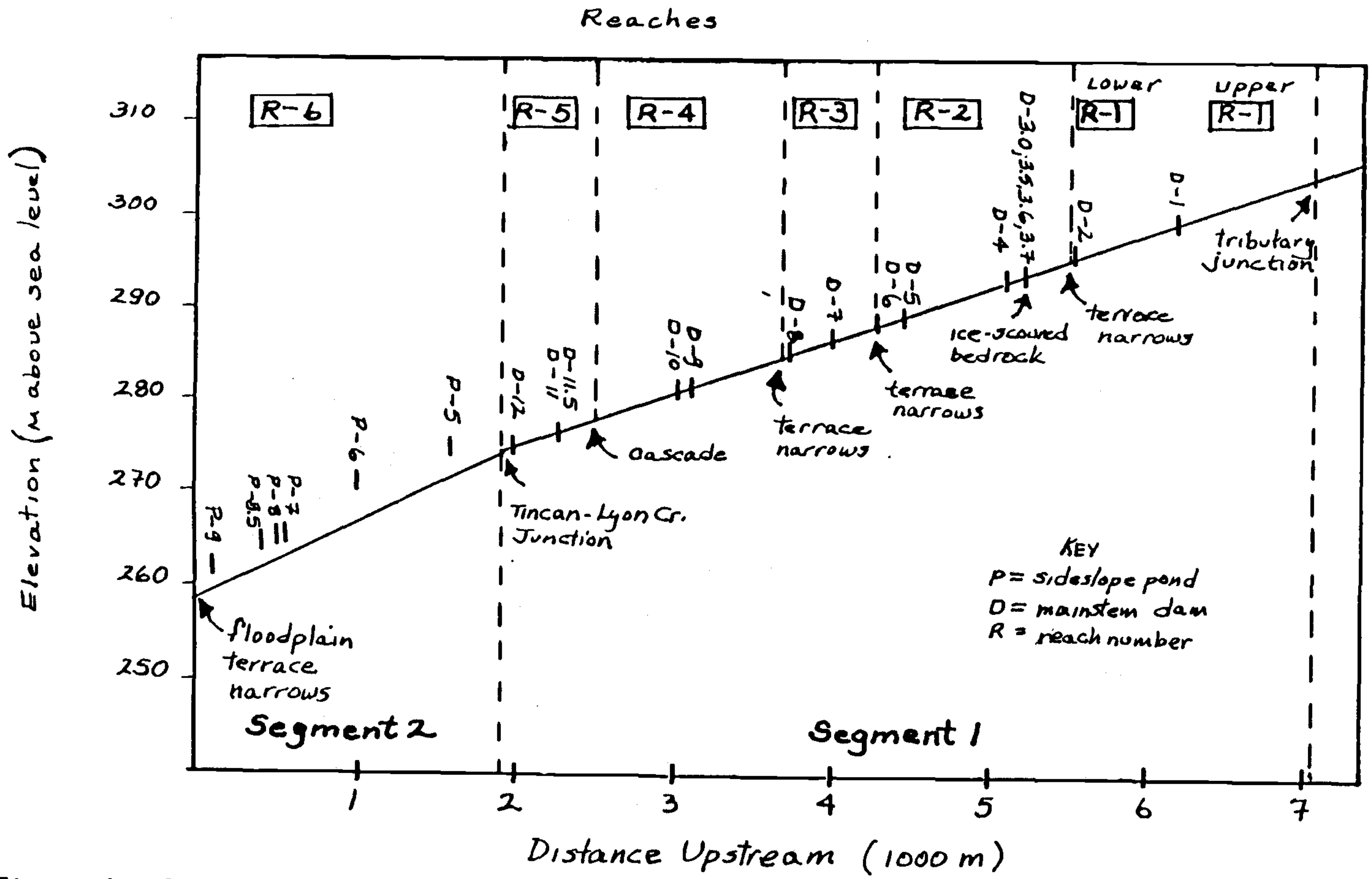
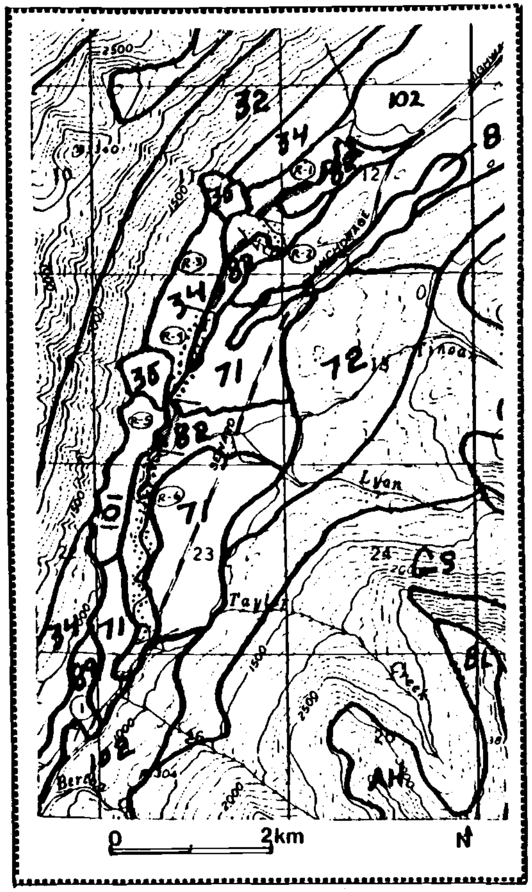


Figure 4. Segment and reach boundaries in relation to beaver dams, channel gradient, and geomorphic features, Upper Granite Creek, 1986.



NO.	NAME	(M) ELEV.	(%) SLOPE	CHARACTERISITCS VEGETATION	SOILS
34	Nonforested Concave Lower Sideslope	180-700	15-45	alder, willow, dense grasses, fireweed	compact glacial downslope deposits
35	Scree Fan	150-550	20-70	alder, ferns, forbs, mosses	alluvial, colluvial soil and rock
71	Low Relief Moraine	270-600	15-40	willow, alder, sedge, grasses, (similar to 82)	non-sorted glacial till
82	Low Lying Floodplain	120-700	0-5	shrub willow, fireweed, grasses sedge, mosses	alluvial with organic overlay
101	Nonforested Ice Scoured	480-760 (usually)	10-65	alpine tundra, heather, crowberry, sedge, moss, anemone	glacial till over bedrock
102	Forested Ice Scoured	90-400	10-55	mtn. hemlock, blueberry, mosses	glacial till over bedrock

Denotes Reach Boundaries
(R-1) Reach Number

Figure 5. Landtypes of Upper Granite Creek study area corresponding to reach boundaries (after Davis et al. 1980).

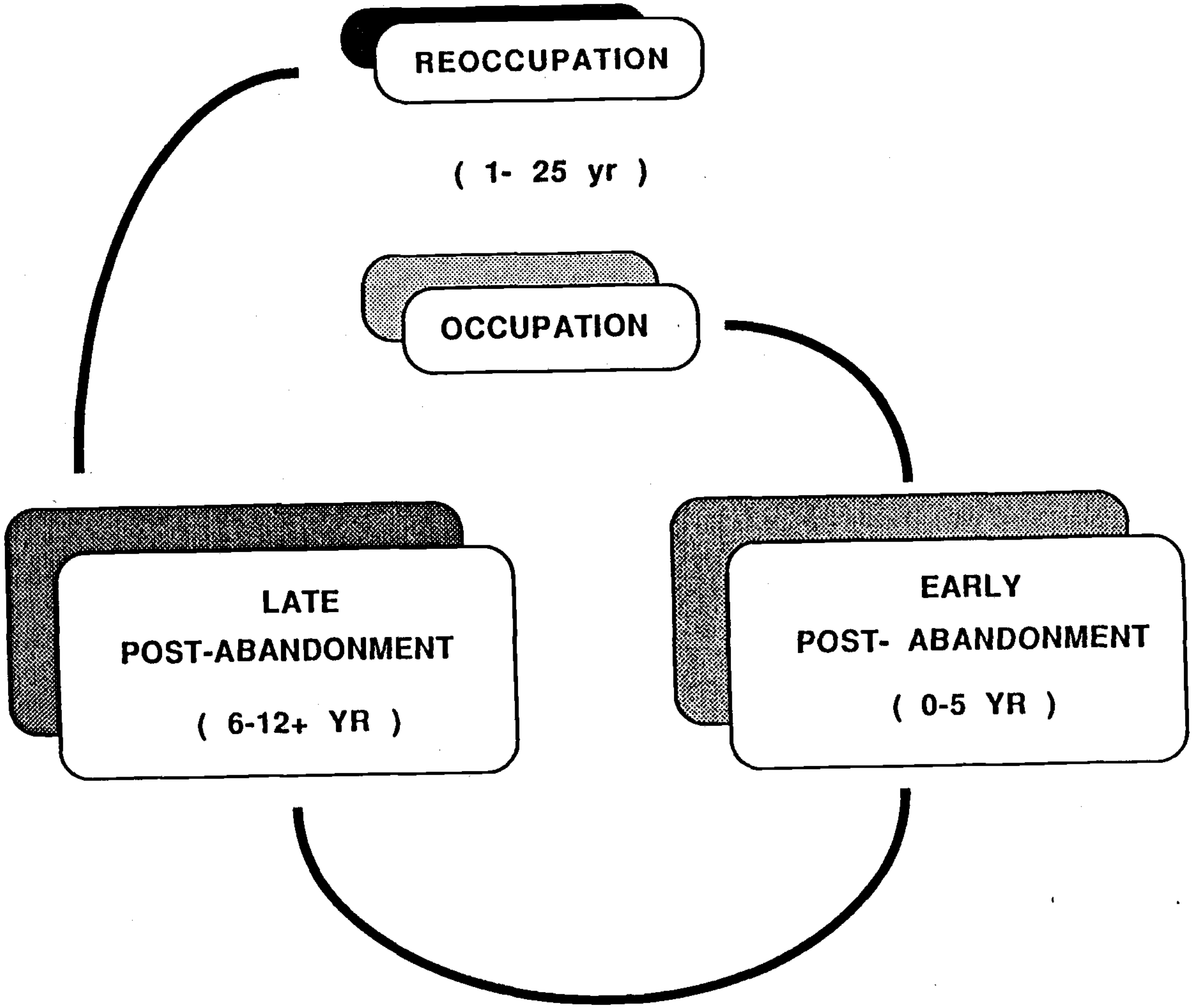


Figure 6. Cyclic successional pattern of beaver activity and observed duration of each stage on Upper Granite Creek.

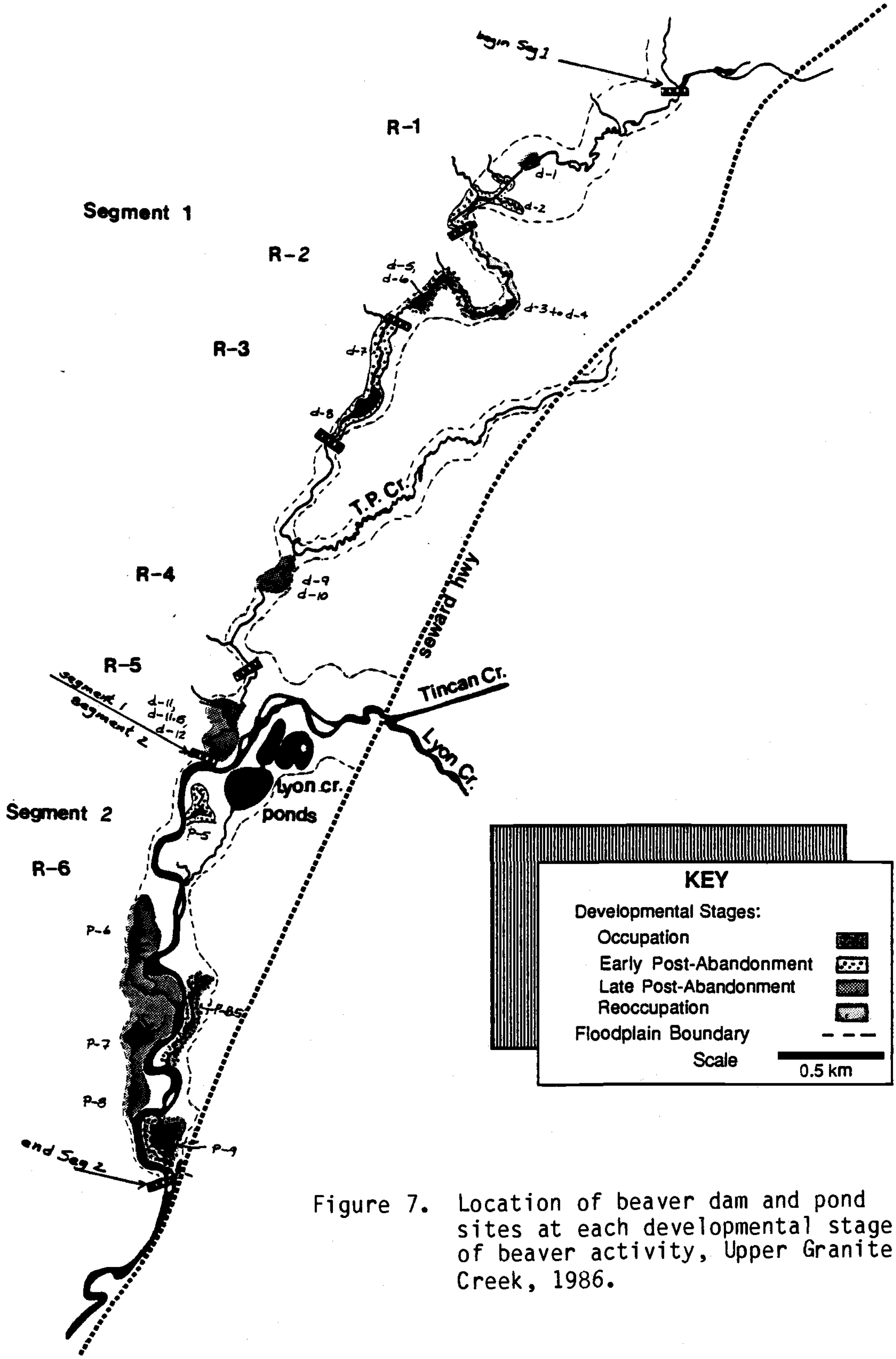
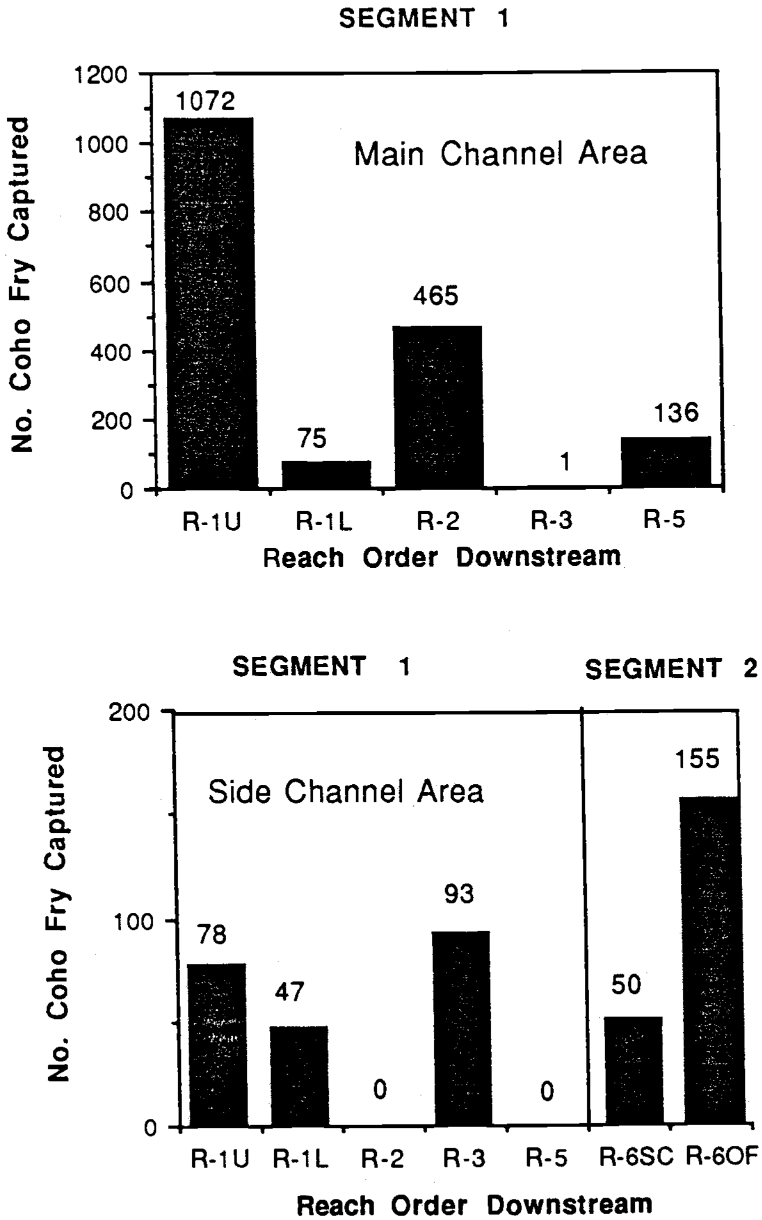


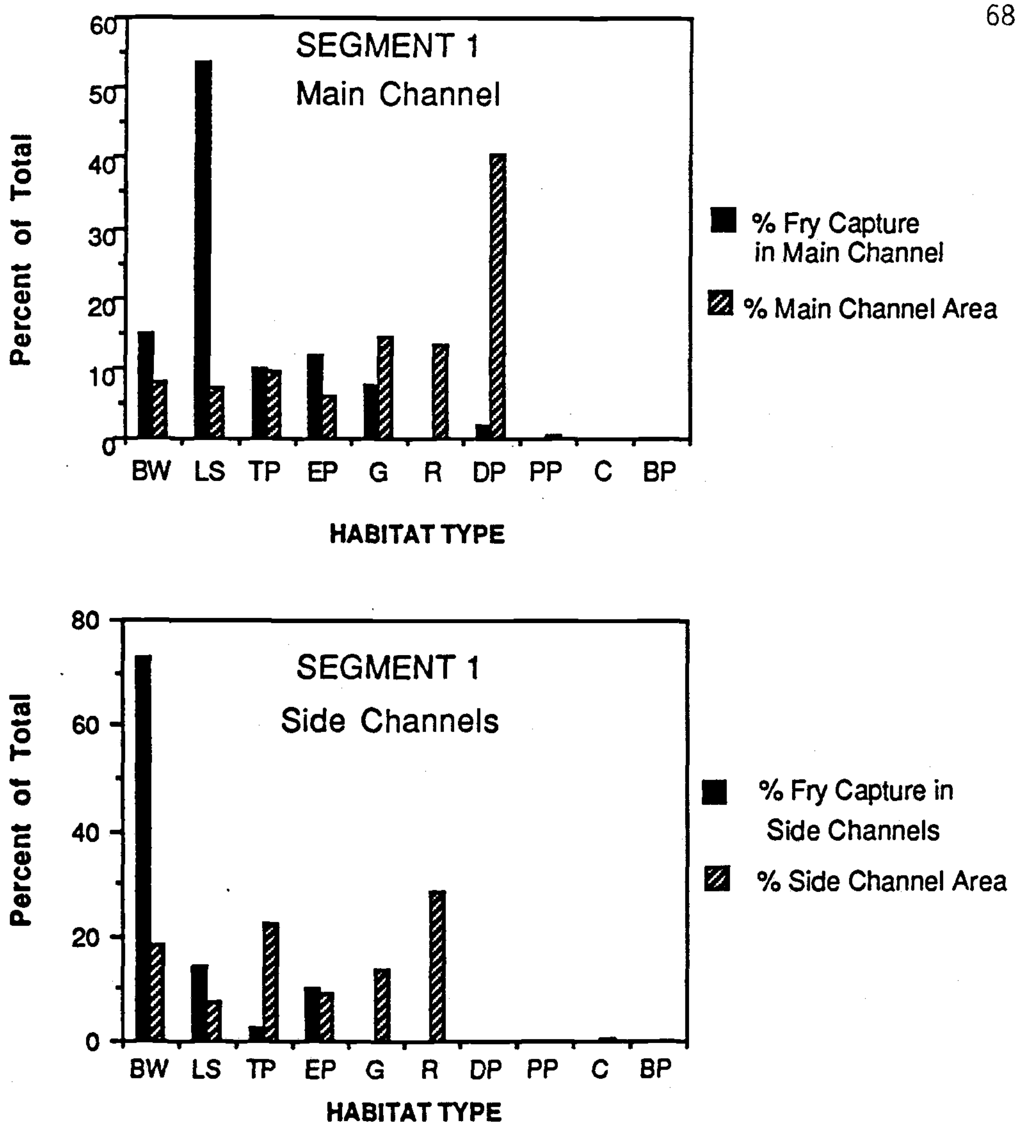
Figure 7. Location of beaver dam and pond sites at each developmental stage of beaver activity, Upper Granite Creek, 1986.



KEY TO REACHES

R-1U = Upper Reach 1
R-1L = Lower Reach 1
R-2 = Reach 2
R-3 = Reach 3
R-5 = Reach 5
R-6OF = Reach 6 Outfalls
R-6SC = Reach 6 Side Channels

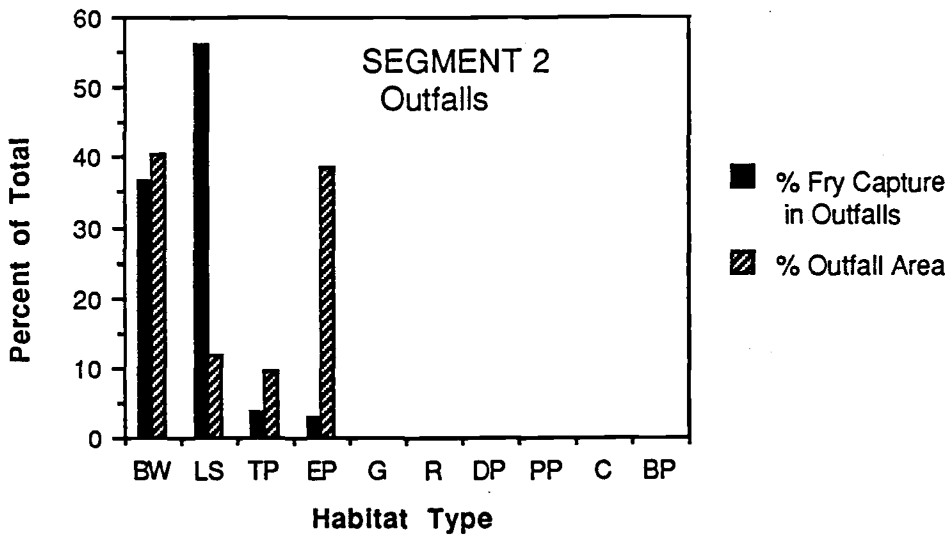
Figure 8. Relation of fry capture to downstream distance on Segments 1 and 2, Upper Granite Creek, 1986.



KEY TO HABITAT TYPES

BW = Backwater
LS = Lateral Scour Pool
TP = Trench Pool
EP = Eddy Pool
G = Glide
R = Riffle
DP = Dammed Pool
PP = Plunge Pool
C = Cascade
BP = Boulder Pool

Figure 9. Comparison of fry capture to habitat type in main and side channels of segments 1 and 2, Upper Granite Creek, 1986.



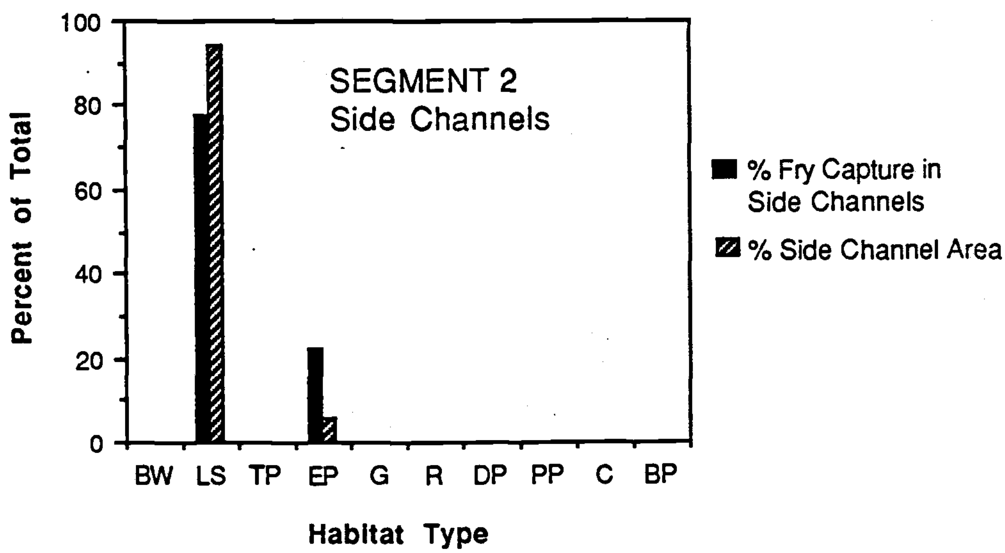


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Figure 9. Continued

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APPENDICES

APPENDIX I

DESCRIPTION OF WATERSHED AND STUDY AREA

Geology, Climate, and Vegetation

The Sixmile Creek watershed is situated in the Chugach Mountain Range, formed by uplifting of metamorphosed Cretaceous marine sediments. The area is characterized by deeply incised glacial valleys, with the most recent glaciation beginning about 100,00 yr BP and continuing until about 3000 yr BP (Davis et al. 1980). The landscape consists of peaks, ridges, and sideslopes of exposed rock with glacial till deposited in valley bottoms. Stable but active glaciers comprise about 1% of the watershed area.

Precipitation ranges between 100-150 cm, annually, mostly falling as snow between November and April. Mean annual air temperatures range from -4° to 0° C. Winter and summer extremes range from -7° to 18° C for the period of record (Blanchet 1983).

Higher mountain slopes are characterized by exposed rocky sites with dry alpine tundra vegetation. Sideslopes and valley bottoms have alluvial and fluvial soils with plant communities that include moist alpine tundra, mountain hemlock (*Tsuga sp.*), and Sitka spruce (*Picea sitchensis*) forests. Well-drained sites in valley bottoms have mixed white spruce (*Picea glauca*) and birch (*Betula papyifera*); whereas black spruce (*Picea mariana*) bogs occur on poorly drained peat soils.

Fishery Resources

Indigenous salmonids in the Sixmile basin include Dolly Varden (*Salvelinus malma*); pink salmon (*Oncorhynchus gorbuscha*); chum salmon (*O. keta*); chinook salmon (*O. tshawytscha*) and coho salmon (*O. kisutch*). Dolly Varden are resident throughout the system. Pink and chum salmon spawn intertidally within 2 km of the mouth. Chinook spawn and rear as far as 25 km upstream; coho spawn and rear from 27-37 km upstream, mostly within the Granite Creek headwaters (study area). Spawning and rearing habitat for chinook and coho overlap little, but some overlap does occur between kilometer 25 and 27 (Sixmile Creek Stream Survey Data, 1979-1986, unpubl., USDA-FS, CNF).

Native coho salmon spawn from late September to October. Fry emerge in late June, smolting at age 1 yr (the following year) at about 80-90 mm (Sixmile Creek Stream Survey Data, unpubl., USDA 1981-1982). In comparison, hatchery coho that were stocked as fry in 1983 and 1984 at a mean length of 42 mm, smolted in July, 1985. Forty-six percent were age 1 yr and 54% were age 2 yr fish. The mean length of smolts was 95 mm. Calculated fry to smolt survival of 1983 and 1984 fish was 0.06% and 0.5%, respectively. Fry to smolt survival of native fish was not known.

Chinook stocked in 1984 smolted in 1985 with a survival of about 1%. Summer growth rate of stocked chinook was slightly higher than that of coho (0.9 mm/day versus 0.6 mm/day) (Sixmile Creek Summary of 1985 Sampling Data, Kurt Nelson, USDA-FS, CNF).

Fishery Management

No salmon fishery currently exists on Sixmile Creek. The Alaska Dept. of Fish and Game along with the Chugach National Forest, have attempted to increase populations of coho and chinook through a presmolt stocking program. Since 1983, Upper Granite Creek has been stocked annually with approximately 150,000 hatchery-reared, non-native fry of each species. The intent was to use Granite Creek as a "nursery stream" to augment returns of these species for sport fishery development. Though adult returns of hatchery fish were expected in 1985 and 1986, no increased adult escapement beyond pre-stocking native population levels has been observed (pers. comm., Kurt Nelson, USDA-FS, CNF).

In 1985, three coho rearing ponds (a total of 3 HA) were excavated on the Tincan-Lyon Creek floodplain. Ponds stocked with coho fry in 1986 drain into a natural terrace tributary, which joins Granite Creek about half-way down Segment 2 (Fig. 3).

APPENDIX II

TYPES OF BEAVER STRUCTURES AND THEIR TRANSFORMATIONS INTO FISH HABITAT

Type of structure	Description	Transformation
Burrow	refuge excavated into stream bank at or near water level	bank undercutting; formation of a backwater upon collapse; on bends, may lead to lateral scour pool formation
Bank den	lodge-like residence built into or on stream bank; usually on channels where mainstem dams will not succeed; structures associated with dams also constructed	construction material washes into stream; den, burrows and skid trails erode and collapse, forming backwaters
Canal	flooded access route constructed between ponds and forage/refuge sites; U-shaped in cross-section, may be excavated in stream banks, dam outfalls or natural tributaries	persist as side channels where drainage sources continue after abandonment; connect channels to backwaters
Dam outfall	locations where flows overtop dams; used for access routes downstream; may be excavated as canals	naturally erode and become incised persisting as side channels below dams; if excavated, as a canal, side channel development is accelerated; as ponds empties and dam deteriorates, outfalls become backwaters and eventually become revegetated
Depression	excavations into original stream bottom to deepen it for food storage or as underwater routes at low water periods; excavated material used for dam, lodge construction	become side channels and backwaters and pools as pond empties
Food cache	consist of willow branches anchored and intertwined, forming a dense reef-like mass submerged in pond; built during open water seasons and exploited during winter and spring; several caches may be made by one colony	allochthonous source of wood to stream; cache and lodge material are redistributed downstream and form debris jams, trapping sediment with successive flood events
Pond	complex consisting of all other structures (except bank dens); serves as a sink for transported sediments and organic matter; increases flooded perimeter of stream and stores runoff, stabilizes flows during minor events	when dam is breached, pond drains; sediments are retransported downstream; excavated structures are exposed, deeper portions retaining water; pond becomes a complex of pools and backwaters connected by side channels
Skid trail	overland access route to forage sites; with heavy travel, vegetation is removed, soils are exposed and erosion begins	on steeper banks, drainage paths are propagated by headward piping; complete erosion may result in bank collapse and formation of a backwater
Scent mound	mud patty mixed with castor scent and vegetation; used to mark territories and advertise presence of its maker	no consequence for stream habitat, but indicates recent beaver activity, either territorial boundary or ephemeral sites
Tunnel	connects canals or other waterways with an underground passage	tunnels collapse and erode, converting to backwaters

APPENDIX III

NATURAL HISTORY OBSERVATIONS

Colony Density

In the study area, I counted 10 beavers in four active colonies. The calculated mean density was 2.5 beaver/colony. In Hay's (1958) study, colony size ranged from 2 to 10 beaver; an accepted number in several other studies in the continental US was 5.1 beaver/colony (Bradt 1938; Lee Rue III 1964; Call 1966; Warner 1976). Hay's study in Colorado and Boyce's (1974) work in Alaska reported lowest beaver densities where willow was the dominant forage. Densities were greater where aspen was available. But even their lowest mean densities (3 to 10) exceeded what was observed on Upper Granite Creek.

Seasonal Movements

Bradt (1947) and Townsend (1953) reported that transient beaver were found in the spring, when two-year-old males were drive from the colony to wander in search of new homesites. I found evidence of transiency throughout the Sixmile Creek system from May through November, until ice formed on the stream. Scent mounds, cut willows and abandoned, partially-built dens were a common sight along stream banks.

Mark Chihuly (pers. comm., Alaska Department of Fish and Game, Game Division) noted that many beaver construct food caches or bank dens in the early fall only to abandon them before winter's onset. I recorded many observations of ephemeral activity throughout the

Sixmile drainage, concluding that a transient "lifestyle" may be more common among beaver than previously believed .

Food, Forage, and Building Materials

Willow (*Salix sp.*) was the only hardwood used by beaver for food and construction in the study area. Alder (*Alnus rugosa* or *A. tenufolia*) though present near dam sites was not used. Electivity between willow and alder was also reported by Northcott (1970) and Jenkins (1979). Aleksiuk (1970) found that beaver on the MacKenzie River Delta fed mostly on the growing tips of willow in the summer and willow bark the rest of the year. I observed beaver feeding on all parts of willow throughout the year, as well as sedge and grass during spring and summer.

On Sixmile Creek, beaver constructed dams and food caches from late May until November. Most observers report these endeavors to occur only in the fall (Bailey 1926; Warren 1927; Lee Rue 1964; Aleksiuk 1970).