Quantitative Measures of Rearing And Spawning Habitat Characteristics For Stream-Dwelling Salmonids: Guidelines For Habitat Restoration

by

E.R. Keeley and P.A. Slaney

Watershed Restoration Project Report No. 4
1996

BRITISH
COLUMBIA

Funded by:

FOREST
RENEWAL BC

Watershed Restoration Program

Ministry of Environment, Lands and Parks
and Ministry of Forests

Quantitative Measures of Rearing and Spawning Habitat Characteristics For Stream-Dwelling Salmonids: Guidelines For Habitat Restoration

by

E.R. Keeley[1] and P.A. Slaney[2]

[1] Department of Zoology, The University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia, CANADA, V6T 1Z4.

[2] Watershed Restoration Program, Ministry of Environment, Lands and Parks, 2204 Main Mall, The University of British Columbia, Vancouver, British Columbia, CANADA, V6T 1Z4.

Watershed Restoration Project Report No. 4

1996

ABSTRACT

Keeley, E.R. and P.A. Slaney. 1996. Quantitative measures of rearing and spawning habitat characteristics for stream-dwelling salmonids: guidelines for habitat restoration. Province of British Columbia, Ministry of Environment, Lands and Parks, and Ministry of Forests. Watershed Restoration Project Report 4: 31 p.

To assist in habitat restoration, we conducted a literature survey to compile quantitative measures of rearing and spawning habitat characteristics for salmonid fishes in streams. From our search we found 70 studies that provided quantitative measures of habitat characteristics. Of these studies, 37 reported microhabitats selected for rearing, over a wide range of stream conditions, resulting in measures for 9 species. The 33 remaining studies reported microhabitats selected for spawning, resulting in measures for 13 species. The most common variables measured in these studies were water depth and velocity. Substrate composition was relatively well described for spawning site selection, and for rearing areas. Space requirements or territory size for juvenile salmonids is reasonable well reported in the literature, but with few measures for salmonids of the Pacific Northwest. Measures of territory size for spawning adults is almost non-existent. As a surrogate measure of spawning space requirements, redd area may be a reasonable estimate which is well described for many salmonid species. Our analyses of these data sets revealed a great deal of overlap in the range of habitats selected by salmonids, despite the number of different species examined. The best empirical correlate of habitat selection appears to be body size. The largest species or age-class tends to occupy the deepest and fastest water and demands the greatest amount of space for rearing or spawning. In our synthesis, we also found a second group of studies that have identified important habitat features such as large woody debris, off-channel and over-wintering habitat. These data are summarized briefly.

ACKNOWLEDGMENTS

This work was supported by the Province of B.C. Ministry of Environment, Lands and Parks; the British Columbia Conservation Foundation, and the B.C. Watershed Restoration Program. We thank Daiva Zaldokas for technical support and Wendell Koning, Don McPhail, and James Baxter for helpful discussions on the ecology of salmonid fishes. Matt Foy and Brent Lister kindly provided data from off-channel studies.

INTRODUCTION

Studies on the behaviour and ecology of stream fishes have often revealed that many factors influence their distribution and abundance (Bjornn and Reiser 1991). The British Columbia Watershed Restoration Program was established by the government and private sector to restore and mitigate past logging impacts to stream and river systems and re-establish lost or depressed fish populations (Keeley and Walters 1994). In British Columbia, the dominant group of fishes that inhabit streams are the salmonids (McPhail and Lindsey 1970). Salmonids provide an extremely important and valuable sport and commercial fishery and are also an integral component of the province's heritage. Unfortunately, habitat degradation continues to threaten many salmonid stocks with extinction (Nehlsen et al. 1991; Slaney et al. 1996). If this group of fishes is to remain a large part of B.C.'s wilderness landscape, then steps must be taken to halt or reverse declining trends in fish numbers. The Watershed Restoration Program is an attempt to help restore lost or declining fish stocks.

There is significant evidence that logging practices of the past have degraded the rearing and spawning habitat of salmonids in coastal and interior B.C. streams (Slaney et al. 1977a, b Scrivener and Brown 1993; Slaney and Martin 1997). These unsound practices have caused major sources of stream sedimentation and debris flows as well as hillside and gully failures. The result has been the scouring or infilling of prime salmonid habitat (Cederholm et al. 1980; Hogan 1986; Tripp 1994). In addition to the physical alteration, the logging of riparian areas has caused a long-term deficit of large woody debris, which appears to be critical in providing habitat features that salmonids require for survival (Koski 1992; Scrivener and Brown 1993). Unfortunately without mitigative intervention, habitat loss will require from decades to centuries to recover naturally (Koski 1992; Slaney 1994).

Despite major efforts to supplement salmonid populations through hatcheries, the benefit of artificial rearing has been low relative to the cost (Meffe 1992) and may threaten the genetic variability of wild salmonid populations (Gauldie 1991). Even when hatcheries are successful at raising and releasing fish into the wild, the environments they are released into are often unsuitable or marginal for salmonid survival (Meffe 1992). Therefore, not only is it important to understand habitat requirements for wild salmonids, but it may also improve the success of hatchery released fish, when extirpated stocks are re-introduced.

Fundamental to the implementation of fish habitat restoration is an understanding of the ecological factors that influence the abundance of stream-fishes (Hartman et al. 1996). The availability of suitable stream habitat for salmonids is crucial to maintaining healthy populations. Despite a wide variety of life-history patterns, salmonids fishes almost always use streams for spawning or rearing at some point in their life-span (McPhail and Lindsey 1970; Scott and Crossman 1973; Behnke 1992). Hence, it is not surprising that the loss of key salmonid spawning and rearing habitat is believed to be a major cause of declining salmonid populations in the Pacific Northwest (Koski 1992; Slaney et al. 1996). In several habitat restoration studies, however, biologists have found that these losses can often be reversed (Hunt 1976; Ward and Slaney 1993; Binns 1994) and fish populations can sometimes even exceed unimpacted historical levels (Binns and Remmick 1994). In order to restore damaged areas, it is essential for biologists to consider the habitat requirements for salmonids and re-establish the range of habitat features that salmonids prosper under. To maximize the benefits received from restoration efforts, quantitative measures of habitat features preferred by salmonids will be required to increase the likelihood of a restoration program being successful and cost-effective. In the past twenty-five years, studies on the behaviour and ecology of stream salmonids has increased substantially (Northcote 1988). This pool of studies should therefore provide quantitative information on habitat requirements for many salmonid species.

In this report, it is our objective to review the available literature on spawning and rearing habitat for stream-dwelling salmonids and to synthesize this information into a quantitative description of the habitat requirements. It was not our intention to provide a review of the life-history patterns of salmonid fishes; see McPhail and Lindsey 1970; Scott and Crossman 1973; Groot and Margolis 1991 for a review. We also used our survey to look for studies that have identified macrohabitat features that appear to be important in determining salmonid fish abundance. From these data, we hope to provide a synthesis of as much of the existing information to aid restoration biologists in determining the suitable range of habitat requirements for many salmonid species.

METHODS AND MATERIALS

We surveyed the literature for any study that reported habitat use for salmonids in streams. We defined habitat as being of two types: for purposes of feeding and growth which we call rearing habitat, and secondly for purposes of reproduction which we call spawning habitat. We began our literature search with the last 27 volumes of two primary fisheries journals, The Canadian Journal of Fisheries and Aquatic Sciences (volumes 26-52), and Transactions of the American Fisheries Society (volumes 98-124). We also used the 15 available volumes of the North American Journal of Fisheries Management (for the years 1980 to 1995). We supplemented our primary reference sources by using the cited references within each paper that appeared relevant from its discussion in the paper. These citations provided us with studies from other primary journals, technical reports, edited volumes, theses, and manuscripts. Although we were primarily interested in salmonids native to B.C., we also included non-native species for comparative purposes and to extend the range of the data base. From each article, we recorded physical habitat features most commonly studied over a range of species for either rearing or spawning. We only included habitat features that were reported quantitatively in a sufficient number of studies to provide estimates of habitat requirements for several salmonid species.

Whenever possible we recorded the mean and range of reported habitat features in each article. If a range of values was provided, but not a mean, we assumed a normal distribution and used the mid-point of the range as a central measure. We only included studies where microhabitat features were directly measured for fish occupying a given location in a stream. When studies recorded habitat features for different areas in a stream, we calculated a datum for each reach studied. For statistical analyses we also recorded body size of the fish directly from each study. Although most studies reported body sizes of the individuals they observed, a few did not. In these cases we used a secondary reference source that gave a general body size for the population or species (Shapovalov and Taft 1954; Scott and Crossman 1973; Sublette et al. 1990). All data sets were examined for normality, and when required were $\log_{10}$ transformed. All regression equations used an ordinary least squares technique to calculate minimum sum-of-squares (Neter et al. 1990).

RESULTS AND DISCUSSION

We found quantitative measures of habitat variables for 9 salmonid species for rearing (Table 1) and 13 species for spawning (Table 2). Studies that examined salmonid rearing conditions most commonly reported values for depth and current velocities selected by individuals, over a range of body sizes. We also found data for stream substrate associated with salmonid rearing microhabitats. In most cases, researchers categorized substrate size using an interval method such as a modified Wentworth scale (*cf:* Bovee 1982). For studies that used a different scale (e.g., Bain et al. 1985) or reported mean particle size, we converted their data into the Wentworth scale for our analyses.

Table 1. Species of salmonid fishes with quantitative measures of habitat characteristics for rearing (X), as reported in the scientific literature.

Rearing Habitat Characteristics

Species[a]	Water velocity	Water depth	Substrate type	Space requirements	Sources[b]
chinook salmon	X	X	X		7, 18 , 22, 33
coho salmon	X	X	X	X	3, 4, 8, 9, 22
cutthroat trout	X	X	X		17, 23, 27, 28, 30
rainbow / steelhead trout	X	X	X	X	1, 2, 4, 5, 7, 11, 14, 19, 21, 23, 32, 35
Atlantic salmon	X	X	X	X	6, 10, 13, 15, 25, 26, 31
brown trout	X	X	X		6, 16, 20, 23, 24, 29, 36
brook trout	X	X	X	X	12, 21, 23, 28, 37
bull trout	X	X	X		27, 34
Dolly Varden	X	X	X		3, 4

[a] Scientific names for species listed in Table 1 can be found in Robins et al. 1991.

[b] Sources for data used in analyses of rearing habitat are listed as follows: 1= Bugert (1985), 2= Smith and Li (1983), 3=Bugert et al. (1991), 4= Dollof and Reeves (1990) 5=Hill and Grossman (1993), 6=Heggenes and Saltveit (1990), 7=Everest and Chapman (1972), 8=Nielsen (1992), 9=Puckett and Dill (1985), 10=Keeley and Grant (1995), 11= E.R. Keeley (unpublished data), 12=Grant and Noakes (1988), 13=Morantz et al. (1987), 14= Riehle and Griffith (1993), 15=de Graff and Bain (1986), 16=Shirvell and Dungey (1983), 17=Moore and Gregory (1988), 18=Hillman et al. (1987), 19=Baltz et al. (1991), 20=Rincon and Lobon-Cervia (1993), 21=Lohr and West (1992), 22=Shirvell (1994), 23=Horton and Cochnauer (1980), 24=Fausch and White (1981), 25=Wankowski and Thorpe (1979), 26=Stradmeyer and Thorpe (1987), 27=Shepard et al. (1984), 28=Griffith (1972), 29=Hayes and Jowett (1994), 30= Bozek and Rahel (1992), 31=Rimmer et al. (1984), 32= Cunjak and Green (1983), 33=Nechako River Project (1987). 34= Boag 1991 (cited from Baxter and McPhail 1996), 35=Slaney and Northcote (1974); 36=Elliott (1990), 37=Grant et al. (1989).

For spawning salmonids, depth and current velocities were also often reported as well as the types and sizes of spawning substrates. We synthesized each of these studies to provide a range of depth and current velocities selected by each species and also the types of spawning substrates selected. In contrast to rearing substrate, most researchers reported geometric mean particle size as an average in spawning sites used by salmonids. Hence, we used geometric mean or median substrate size as a measure for describing spawning substrate. We also found a number of studies that reported the importance of habitat features on a larger scale. These features included large woody debris, over-wintering and off-channel habitat.

Table 2. Species of salmonid fishes with quantitative measures of habitat characteristics for spawning (X), as reported in the scientific literature.

	Spawning Habitat Characteristics				
Species[a]	Water velocity	Water depth	Substrate type	Space requirements[b]	Source(s)[c]
chinook salmon	X	X	X	X	1, 3, 5, 24, 25, 26, 27, 32
coho salmon	X	X	X	X	3, 7, 12, 24, 25, 26, 32
chum salmon	X	X	X	X	3, 24, 32
pink salmon	X	X	X	X	10, 32
sockeye salmon	X	X	X	X	3, 11, 24, 32
cutthroat trout	X	X	X	X	4
gila trout	X	X	X	X	23
golden trout	X	X		X	30
rainbow / steelhead trout	X	X	X	X	8, 16 , 24, 26, 32
Atlantic Salmon	X	X	X	X	31, 32
brown trout	X	X	X	X	2, 6, 14, 31, 32
brook trout	X	X	X	X	9, 13, 32
bull trout	X	X		X	17, 18, 19, 20, 21, 22

[a] Scientific names for species listed in Table 2 can be found in Robins et al. 1991.

[b] Space requirements based on redd area.

[c] Sources for data used in analyses of spawning habitat are listed as follows: 1=Neilson and Banford (1983), 2=Grost et al. (1990; 1991), 3= Burner (1951), 4=Thurrow and King (1994), 5=Chapman et al. (1986), 6=Ottaway et al. (1981), 7=Crone and Bond (1976), 8=Orcutt et al. (1968), 9=Young et al. (1989), 10=McNeil (1967), 11=Lorenz and Eiler (1989), 12=van den Berghe and Gross (1984), 13=Witzel and MacCrimmon (1983), 14=Shirvell and Dungey (1983), 15=Parsons and Hubert (1988), 16=Hartman and Galbraith (1970), 17=Kitano et al. (1994), 18=Baxter and McPhail (1996), 19=Shepard et al. (1984), 20=McPhail and Murray 1979, 21=Oliver (1979), 22=Leggett (1969), 23=Rinne (1980), 24=Smith (1973), 25=Sams and Pearson (1963; cited from Smith 1973), 26=Briggs (1953), 27=Hobbs (1937), 28=Chambers et al. (1955). 29=Stefferud (1993), 30=James and Sexauer (in press), 31=Heggberget (1991); 32=Kondolf and Wolfman (1993).

Rearing Habitat

The increase in observational and experimental studies of salmonid biology, as noted by Northcote (1988), was reflected in our literature search that provided 37 studies measuring microhabitats selected for feeding or rearing purposes (Table 1). We also encountered many other studies that examined salmonid fish abundance, but we did not include these studies in our data set because they often measured habitat on a larger scale, which probably included areas of unused habitat.

Depth and Velocity Characteristics

For the 9 species that we found habitat measures from the literature, there was a large range in overlap of depth and velocities selected (Fig. 1a and b). Although species that appear to prefer complex riffle habitats, like steelhead (Hartman 1965) or Atlantic salmon (Morantz et al. 1987), also tended to occupy faster areas (Fig. 1b), there was considerable overlap with depths and velocities selected by other species. This was probably due to our pooling of data that included fish sizes from several different age classes. As observed by other researchers, larger fish tend to select deeper, faster areas of the stream (Everest and Chapman 1972; Smith and Li 1983; see also Bjornn and Reiser 1991 for species specific relationships). Our data set also revealed this same trend (Fig. 2a and b). Fish size was positively related to both water depth ($r = 0.45$, $n = 72$, $P = 0.02$) and water velocity ($r = 0.51$, $n = 109$, $P = 0.015$), despite pooling data from a wide range of studies and species. The functional relationship between fish body size and water depth or current velocity was not linear; both tended to level off as fish size reached the upper end of the size distributions we had information on (Fig. 2a and b). The equations describing the relationships in Fig. 2a and b are as follows:

$\log_{10}$ water depth (cm) = 1.86 $\log_{10}$ fish length (cm) - 0.60 $\log_{10}$ fish length^2 (cm) + 0.44
($r^2 = 0.46$, $P < 0.001$),

$\log_{10}$ water velocity ($\text{cm} \bullet \text{s}^{-1}$) = 1.95 $\log_{10}$ fish length (cm) - 0.66 $\log_{10}$ fish length^2 (cm) - 0.013
($r^2 = 0.31$, $P < 0.001$).

The mean velocity selected over all studies was 17.5 $\text{cm} \bullet \text{s}^{-1}$ (range: 48.8 - 3.0 $\text{cm} \bullet \text{s}^{-1}$). The mean depth selected over all studies was 44.4 cm (range: 80.0 - 8.0 cm).

As visual predators, salmonids require an abundant food supply in the waters they inhabit to allow for growth and subsequent reproduction. Several authors have proposed that salmonids select foraging sites in areas of stream based on the trade-off between obtaining a sufficient supply of invertebrate drift, which typically increases with current velocity, and the costs of maintaining position in the current (Fausch 1984; Hughes 1992). Because energy requirements increase for fishes with increasing body weight, by the power 0.75, larger fish expend less energy swimming in fast current than smaller fish (Beamish 1978). Hence, this may be an explanation as to the tendency for large fish to occupy deeper and faster areas of the stream. It may also explain the growing number of habitat preference curves (*sensu* Bovee 1982) that find significant changes in the types of habitats characteristics preferred by different age-classes of salmonids. Given that microhabitat velocity and depth for rearing salmonids is a function of fish size, this factor should be taken into account when considering the potential for re-establishing a particular species in degraded streams.

Rearing Substrate

Substrate associated with rearing areas is believed to be important to salmonids in providing a number of habitat requirements, including cover, velocity refugia, and rearing surfaces for invertebrate prey (Bjornn and Reiser 1991). From the data we collected from the literature, most species appeared to be associated primarily with substrates that **exclude** fine particles in rearing areas (Fig. 1c). As was the case with depth and current velocity in rearing microhabitats, substrate size increased with the size of fish occupying specific areas of the stream (Fig. 2c);

substrate category = 3.11 $\log_{10}$ fish length (cm) + 3.46 ($r^2 = 0.25$, $n = 47$, $P < 0.001$).

Although, fish have been observed over a wide range of substrate sizes, most seem to be associated with substrate categories of 5 (see Bovee 1982) or greater; corresponding to gravel and larger sized substrates, such as boulders. We know of no experimental studies that have determined the exact mechanism for substrate association for stream-dwelling salmonids. We believe it is not a simple one, but is probably related to a number of factors that optimize energy intake and minimize risk of predation. In some species, such as steelhead trout, the addition of large boulders clusters has been observed to increase densities of fish (Ward and Slaney 1979). This increase may provide access to swifter, profitable areas of a stream, by providing a velocity refuge to fish. In addition, areas of stream without high proportions of imbedded fine particles, may also be excellent rearing surfaces for aquatic insects, the primary food source for stream-dwelling salmonids (Allan 1995). Regardless of the exact reason or combination of reasons, rearing streams seem to be associated with stream bottoms relatively free of high proportions of fine particles.

Space Requirements for Rearing

Behavioural observations of salmonid feeding territoriality have been of interest to fisheries biologists for some time because territory size is thought to limit the density and therefore production of stream-dwelling salmonids (Chapman 1966; Allen 1969; Grant and Kramer 1990). Territory size may be dependent on environmental factors such as food abundance because higher levels of food abundance means that fish require a relatively small area to meet energetic demands in comparison to areas of low food productivity (Slaney and Northcote 1974; Dill et al. 1981; Keeley and Grant 1995). At the population level, this may mean that streams with more food production will have higher standing crops of fish because individuals will have smaller space requirements. The benefit of higher invertebrate production has been demonstrated by adding low-level nutrient fertilizer to nutrient deficient streams. For instance when fertilizer was added to the Keogh River, on Vancouver Island, B.C., a significant decrease in age to smoltification was observed as well as a significant increase in numbers of steelhead trout smolts produced from the river (Ward and Slaney 1993).

A second and important component of territory size and limits to population density, is the relationship between territory size and fish body size, also known as the allometry of territory size (Fig. 3.). Because salmonids in streams defend territories from small post-emergent juveniles until they either become smolts or become sexually mature, they must increase the area they defend to meet increasing energetic requirements. This results in a decreasing population density as average body size within a cohort increases (Grant and Kramer 1990). Allometric territory size lines may therefore be good predictors of space requirements and hence maximum densities of salmonids in streams. Several studies have provided allometric territory size lines, including a general interspecific regression model (Grant and Kramer 1990), and intraspecific lines for brook trout (Grant et al. 1989), brown trout (Elliott 1990) and Atlantic salmon (Keeley and Grant 1995). Unfortunately, no allometric territory size regressions exist for endemic salmonids of B.C.

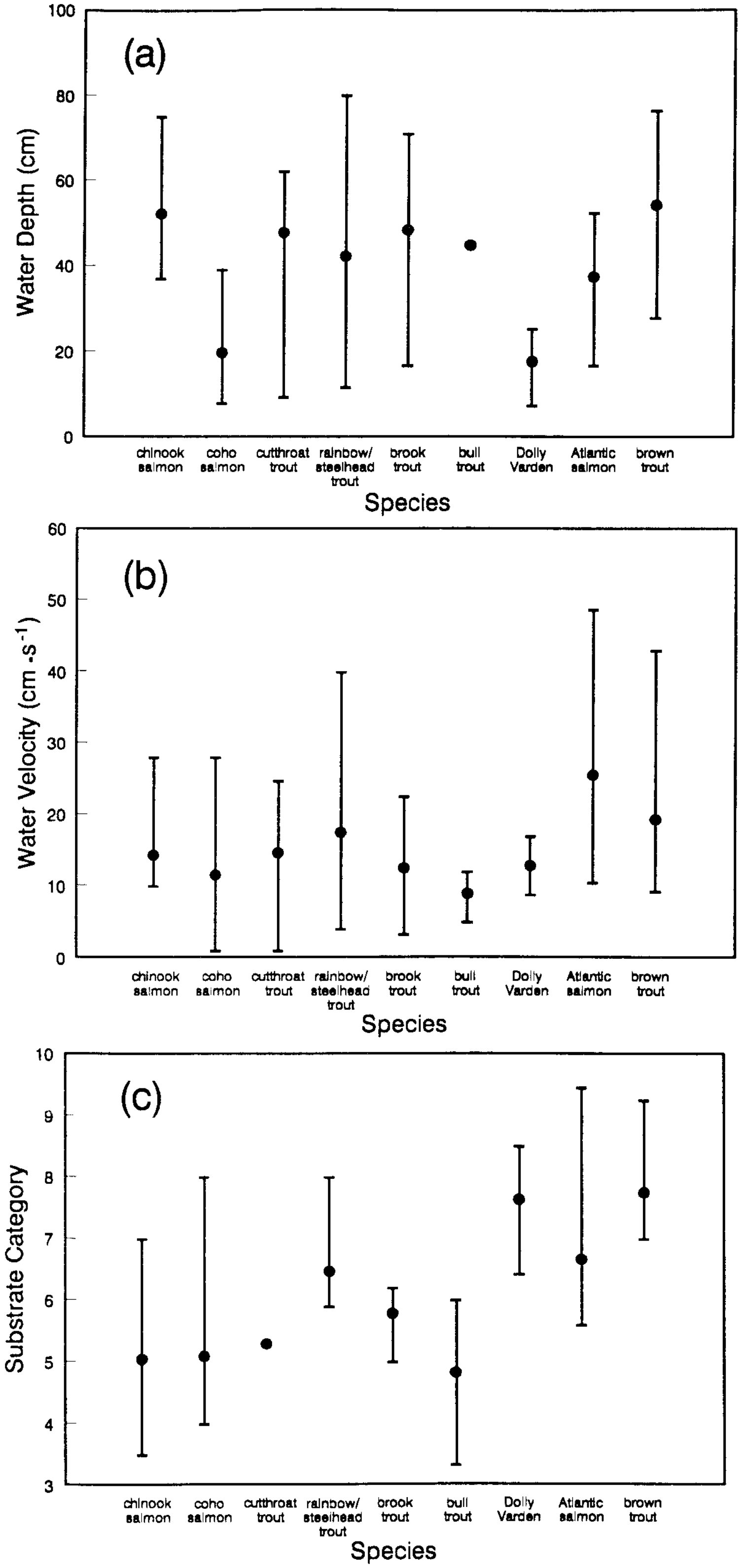

Figure 1. Rearing microhabitats selected by 9 stream-dwelling salmonid species for (a) depth of stream (mean ± range), (b) water velocity (mean ± range), and (c) substrate type (mean ± range). Data are compiled from the literature, see Table 1 for a list of sources.

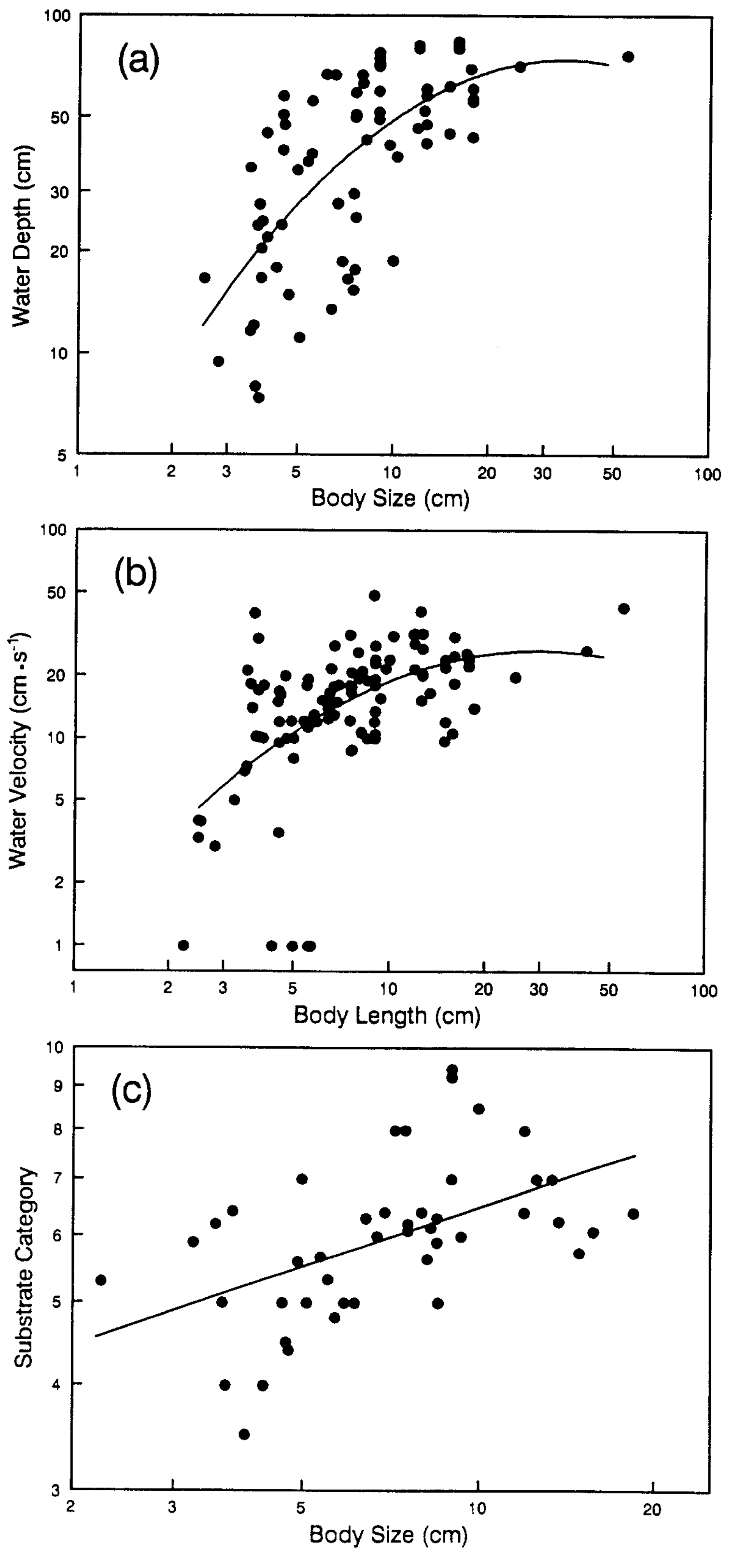

Figure 2. Rearing microhabitats selected by stream-dwelling salmonids in relation to body size for (a) depth of stream, (b) water velocity, and (c) substrate type. Data are compiled from the literature, see Table 1 for a list of sources.

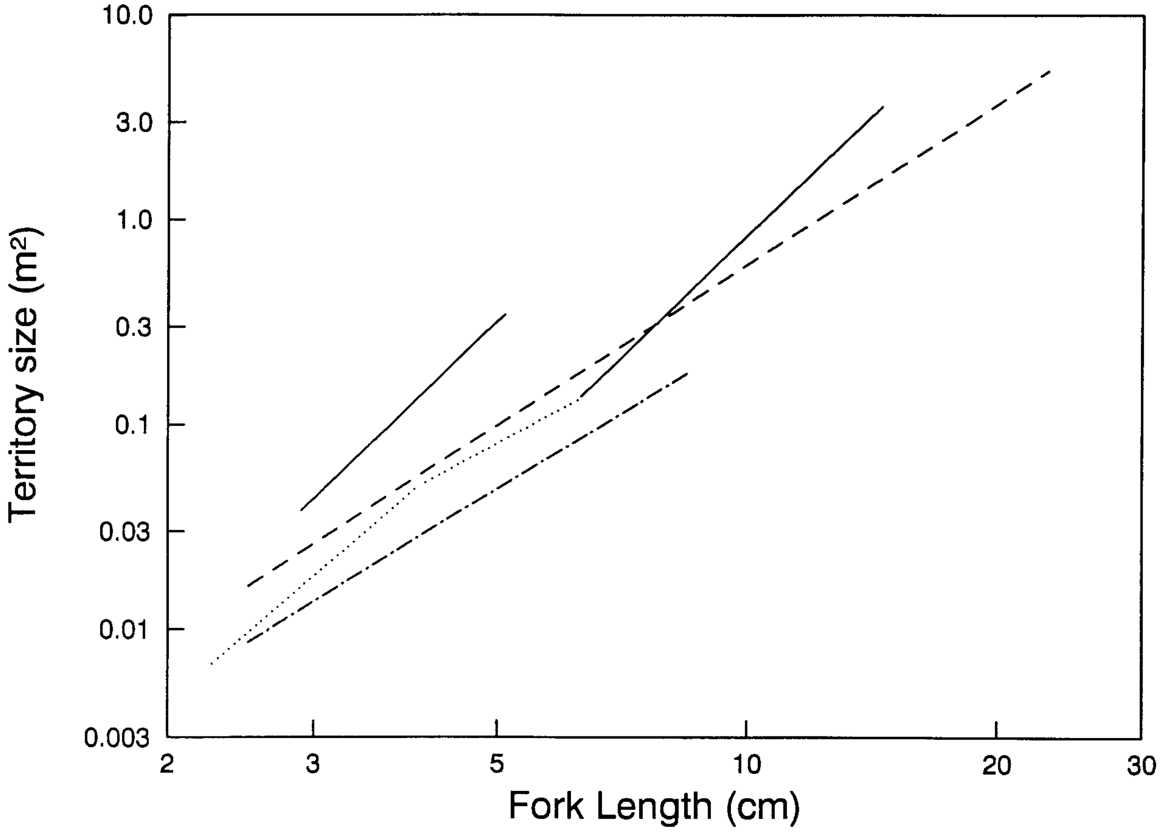

Figure 3. Regression lines of territory size versus body size (after Keeley and Grant 1995). Regression lines are depicted as follows: solid lines, Atlantic salmon; dashed line, interspecific; dotted line, brown trout; dot-dashed line, brook trout.

Spawning Habitat

Salmon, trout and char are well known for their characteristic oval shaped nests or "redds" they excavate for spawning. Historically, these obvious areas seem to have had an early impact on researchers. Some of the first quantitative ecological studies on salmonid habitat requirements, recorded spawning habitat features for several species (Hobbs 1937; Burner 1951; Briggs 1953; Chambers et al. 1955). In the adjoining time since those early studies, many other researchers have recorded a great deal of information (Table 2). However, most studies are empirical records of spawning areas, and few have provided experimental evidence for explaining the distribution of spawning sites. Qualitative observations suggest that salmonids often prefer to spawn in areas of accelerating current, such as in transitional pool to riffle zones (Hobbs 1937; Briggs 1953; Tautz and Groot 1975). In these areas, downwelling currents are likely to provide well oxygenated water to developing embryos over the incubation period. A few experimental studies have demonstrated that some species also ensure sufficient oxygenation of embryos by selecting areas of groundwater seepage (Scott and Crossman 1973).

Depth and Velocity Preferences

Despite a wide range of studies, there appears to be a great deal of overlap in spawning site characteristics for many of the salmonid species studied (Fig. 4a and b). The basic criteria for suitable spawning habitat seems to be water flows greater than 10 cm • s^{-1} and 10 cm deep (mean velocity selected = 48.8 cm • s^{-1} , range = 75.0 -11.2 cm • s^{-1} ; mean depth selected = 35.2 cm, range = 95.8-10.2 cm). The most commonly cited explanation for differences in habitat characteristics is fish size (*cf:* Bjornn and Reiser 1991; Stalnaker and Arnette 1976). In fact, from the data compiled from the literature, fish tend to spawn in deeper faster water with increasing body size (Fig. 5a and b; r = 0.45, n = 26, $P = 0.021$ for depth; r = 0.51, n = 22, $P = 0.015$ for current velocity). Presumably, the deepest, fastest areas of a stream afford the greatest likelihood of a spawning site remaining within suitable conditions for developing embryos. However, spawning fish may be constrained to spawning in certain areas because body size will determine the maximum sustained swimming speed (Beamish 1978) and only the largest species (e.g., chinook salmon) can maintain position in swift current for sufficient lengths of time to complete spawning.

Spawning Substrate

The importance of substrate composition for spawning salmonids is one of the few habitat characteristics that have been examined experimentally to determine its importance to salmonid ecology. Because salmonids bury their eggs in gravel nests, substrate composition must provide interstitial spaces to allow sufficient waterflow and oxygenation of embryos. Chapman (1988) reviewed the literature on embryo survival in relation to proportion of fine substrate sizes (particles less than 6 mm in diameter) in salmonid redds. Chapman's (1988) synthesis of published studies generally showed that embryo survival decreases significantly with high proportions of fine substrate in salmonid redds. As one might expect, permeability of water to developing embryos is reduced, resulting in lower oxygen levels, increasing mortality of embryos, and decreasing size at emergence for surviving individuals.

Kondolf and Wolfman (1993) compiled an extensive data set of salmonid spawning gravels, and found that the median and geometric mean gravel size used for spawning (25 mm and 16 mm) were several times larger than the fine gravels that have been shown to reduce embryo survival. Kondolf and Wolfman's (1993) data set also revealed that a great deal of overlap exists in the sizes of spawning gravels used by 8 different salmonid species as well as in a few additional studies for 3 other species (Rinne 1980; Stefferud 1993; Thurrow and King 1994 (Fig. 4c). This suggests that salmonids can use a wide range of gravel sizes as long as fine particles are low in abundance. Like depth and velocity selection, larger species tend to have the largest median gravel sizes present in their redds ($r = 0.42$, $n = 139$, $P < 0.001$; Fig. 5c). Whether larger salmonid species actively seek areas with the largest gravels, has never been confirmed experimentally. However, larger salmonids have larger eggs and may therefore require larger spawning gravels with wider interstitial spaces to allow sufficient water percolation (van den Berghe and Gross 1989).

Space Requirements for Spawning

Both male and female spawners defend spawning sites against conspecifics. If the amount of available habitat for spawning is limited, then space requirements (territory size) per spawning pair will dictate the number of spawners that can be accommodated within a stream. While the description of aggressive behaviour during spawning has been documented for some time (Tautz and Groot 1975), there are few quantitative measures of territory size for spawning adults. Researchers have most often measured space use for spawning salmonids by measuring the area of gravel disturbed by the female while constructing the redd. Redd area can differ greatly between salmonid species, although the data we compiled also show some degree of overlap (Fig. 6). As several authors have speculated (Bjornn and Reiser 1991; Crisp and Carling 1989; Chapman 1988) redd area increases with fish size (Fig. 7). If redd area is directly related to spawning territory size then the largest species will have the lowest maximum spawning densities. Burner (1951) recognized over 40 years ago, the importance as well as the paucity of quantitative measures of territory size. He suggested that an area four times that of the redd would be a reasonable estimate of territory size for spawning salmonids. Since 1951, the number of studies examining spawning in salmonids has increased estimates of redd area, but there are still very few measures of territory size. However, the few studies that do exist, suggest that territory size may be roughly 4 times that of the redd area (Fig. 7). Hence, the data available from the literature for redd area may serve as a reasonable estimate of space requirements for spawning adults over a wide range of species.

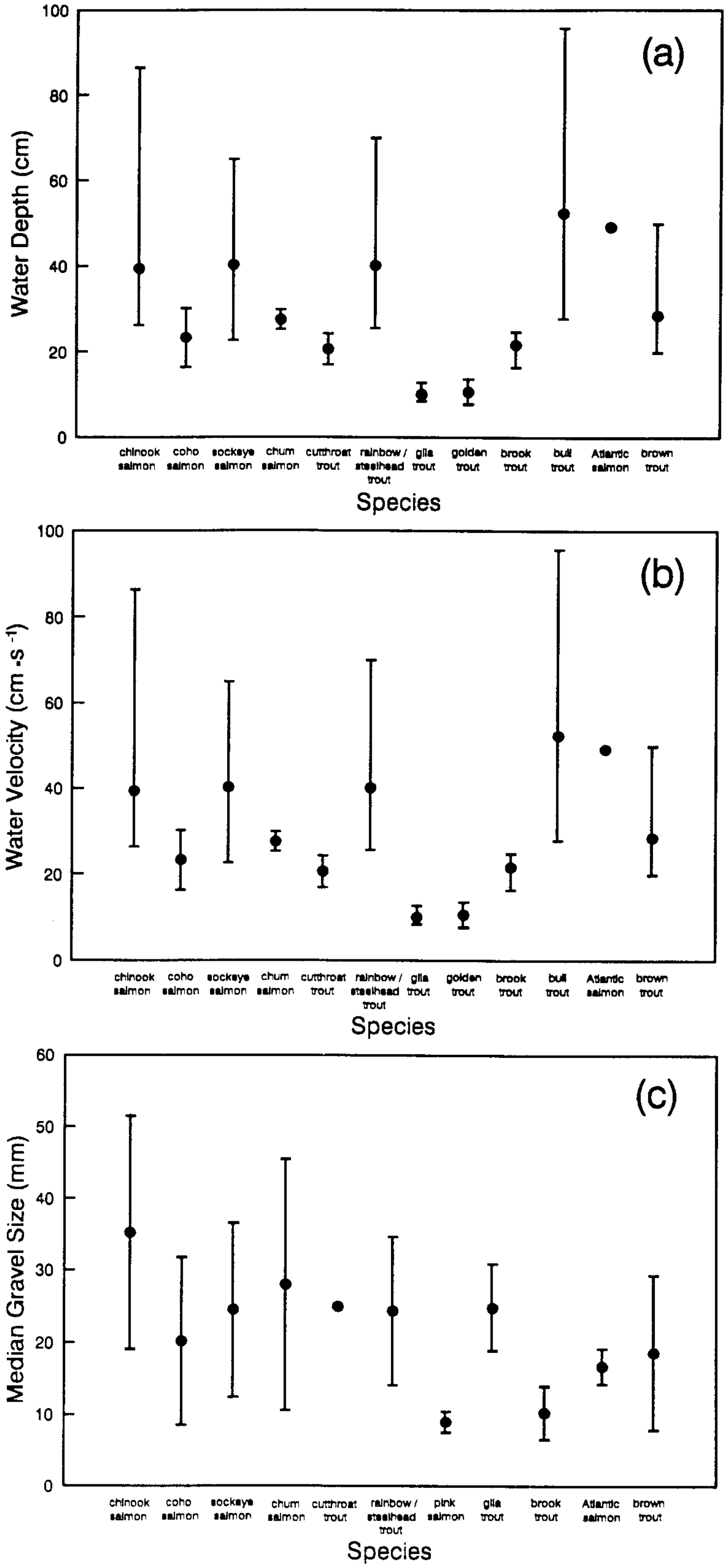

Figure 4. Spawning microhabitat selected by salmonid fishes for (a) depth (mean ± range), (b) water velocity (mean ± range), and (c) substrate sizes (mean ± range) at spawning sites. Data are compiled from the literature, see Table 2.

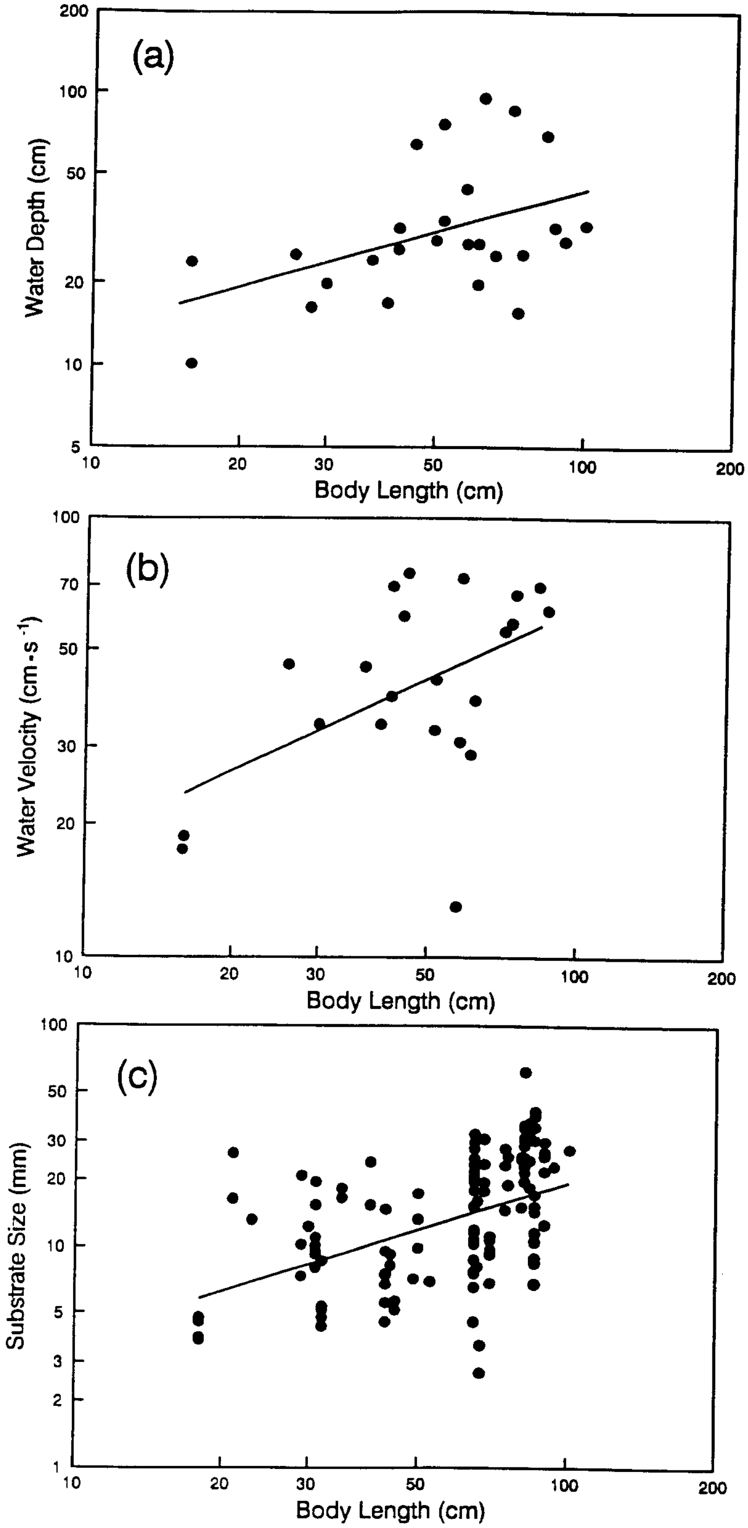

Figure 5. Spawning microhabitats selected by salmonid fishes in relation to body size for (a) depth of stream ($\log_{10}$ depth (cm) = 0.51 fish length (cm) + 0.62, n = 26, $r^2 = 0.20$, $P = 0.021$), (b) water velocity ($\log_{10}$ velocity (cm • s^{-1}) = 0.53 fish length (cm) + 0.73, n = 22, $r^2 = 0.26$, $P = 0.015$), and (c) substrate sizes at the spawning sites (median substrate size = 0.28 fish length (cm) + 8.43, n = 139, $r^2 = 0.18$, $P < 0.001$). Data are compiled from the literature, see Table 2.

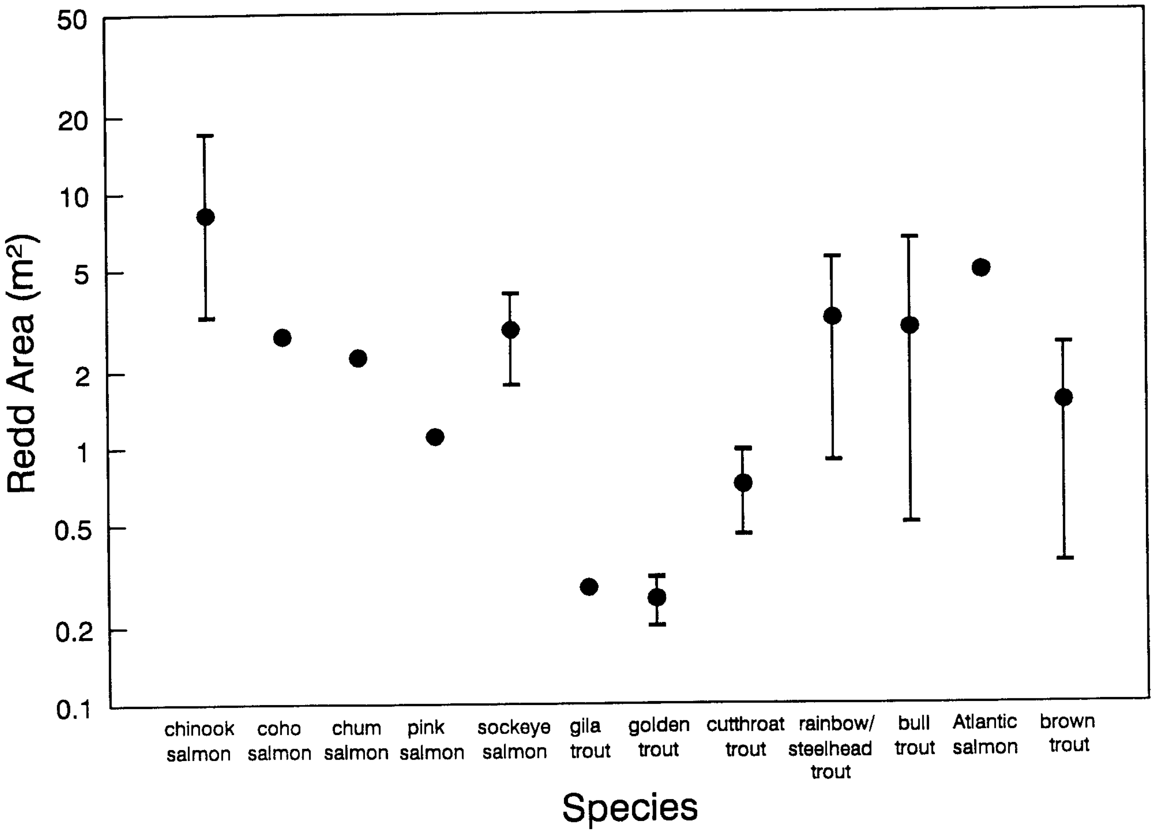

Figure 6. Size of redds constructed by salmonid fishes (mean ± range). Data are compiled from the literature, see Table 2 for sources.

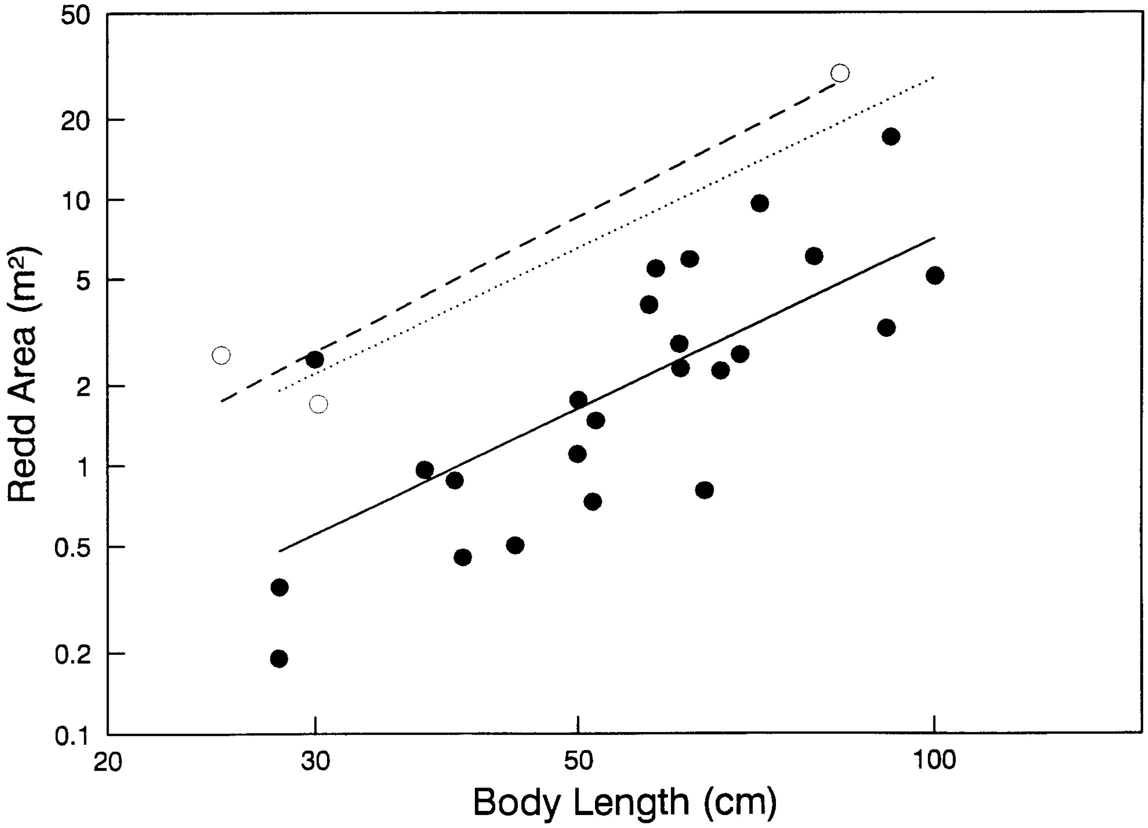

Figure 7. The relationship between body size of spawning adults and the size of the area excavated for redd construction (solid line and circles): Log_{10} redd area (m^2) = 2.12 $\log_{10}$ fish length (cm) - 3.39, n = 25, $r^2 = 0.62$, $P < 0.001$). Data are compiled from the literature, see Table 2 for sources. Dashed line represents the area recommended by Burner (1951) for space requirements of spawning adult salmonids based on qualitative observations. Dotted line and open circles represents spawning territory size measurements from 3 studies: Fabricius and Gustafson 1954; Fabricius and Gustafson 1955; Hartman 1969).

Macrohabitat Correlates of Fish Abundance

Large Woody Debris

In the past few decades, fisheries biologists have come to realize that the input of fallen trees from the riparian area surrounding a stream is an important process in maintaining a healthy and productive salmonid stream (Lisle 1986; Andrus et al. 1988; Fausch and Northcote 1992). Studies have found that an increasing presence of large woody debris tends to be correlated with fish abundance (Elliott 1986; Lisle 1986; Fausch and Northcote 1992). The exact mechanism by which large woody debris may improve fish habitat has never been confirmed experimentally. However, the benefit of its presence appears to serve several functions within a stream system. Researchers have found that large woody debris is an important structural component to a stream, maintaining regular stream sinuosity, channel depth, and creating pools and riffles (Elliott 1986; Hogan 1986; Tripp 1986; Andrus et al. 1988; Crispin et al. 1993). In addition, large woody debris is also thought to provide instream cover from predators (Bugert et al. 1991) as well as improve substrate habitat for the rearing of aquatic invertebrates, an important source of food for salmonid fishes (Angermeier and Karr 1984).

A large riparian zone is required to supply large woody debris to a stream because the input of wood is a dynamic process that results in slow net losses of woody debris from a watershed. Hence, new trees must be recruited into the stream over time. The removal of riparian trees often leads to a deficit of large woody debris within a stream, particularly in large streams where trees must be of substantive size to remain within a watershed long enough to provide complexity to fish habitat (Murphy and Koski 1989). In the absence of large trees capable of withstanding freshets, researchers have found that smaller wood mechanically anchored to the streambed, can serve as a surrogate possibly until larger trees can be recruited into a stream (House and Boehne 1985; Armantrout 1991; Ward and Slaney 1993; Slaney et al. 1994).

Off-Channel and Winter Rearing Habitat

As ectotherms (cold-blooded animals) salmonids metabolize and grow very slowly in cold water temperatures. Usually growth is non-existent or nearly so in temperatures below 8-10°C (see Elliott 1994 for a review of temperature and growth). Corresponding to seasonal changes such as in the beginning of autumn where temperatures fall below a range where growth occurs, salmonids often begin to seek over-wintering areas until water temperatures increase sufficiently to make active feeding a worthwhile endeavor (Rimmer et al. 1984; Campbell and Neuner 1985; Cunjak 1996).

Depending on the species and availability of over-wintering habitat, salmonids may make short migrations into over-wintering habitat. For instance, coho salmon often seek out slow flowing side channels and ponds as areas of congregation in winter months (Peterson 1982; Tschaplinski and Hartman 1983; Murphy et al. 1984.). These channels and ponds can often harbor large numbers of fish (Fig. 8). They are thought to provide refugia, where mortality rates are much lower than in mainstem stream channels (Bustard and Narver 1975; Tschaplinski and Hartman 1983).

Salmonid species that appear to prefer swifter riffle habitats with large substrate in summer, such as steelhead trout (Hartman 1965) and Atlantic salmon (Morantz et al. 1987) often remain in similar areas during winter but behave differently. For instance, Cunjak (1988) observed that juvenile Atlantic salmon became photonegative and hid under large substrate where water velocity was zero, but remained in channel areas with swift current. Therefore, while off-channel habitat may be important for species like coho salmon, others such steelhead trout and Atlantic salmon, may require large substrate and debris within the main channel for over-winter survival (Bustard and Narver 1975; Campbell and Neuner 1985; Cunjak 1988).

CONCLUSIONS

Anyone who has walked or snorkeled a trout stream will have noticed that the abundance of fish is often not evenly distributed throughout all areas. Presumably, this is related to differences in habitat quality between sites and to differences in habitat preferences between species of salmon, trout and char. Being able to provide stream habitat that falls within the range of suitable or preferred habitat for growth and reproduction is essential to increase and stabilize populations of salmonids threatened by habitat degradation. To accomplish this, we must first quantitatively describe or provide an index of preferred habitat features. We hope that this document will aid biologists by providing a reference point in describing habitat requirements for stream-dwelling salmonids. Unfortunately, the few simple measures we have summarized here, cannot represent the entire suite of habitat characteristics that salmonids require because they live in highly complex and dynamic ecosystems. Our hope is that the few features we have described will be well correlated enough with all habitat features, that restoring them will satisfy the minimum requirements for stable fish populations.

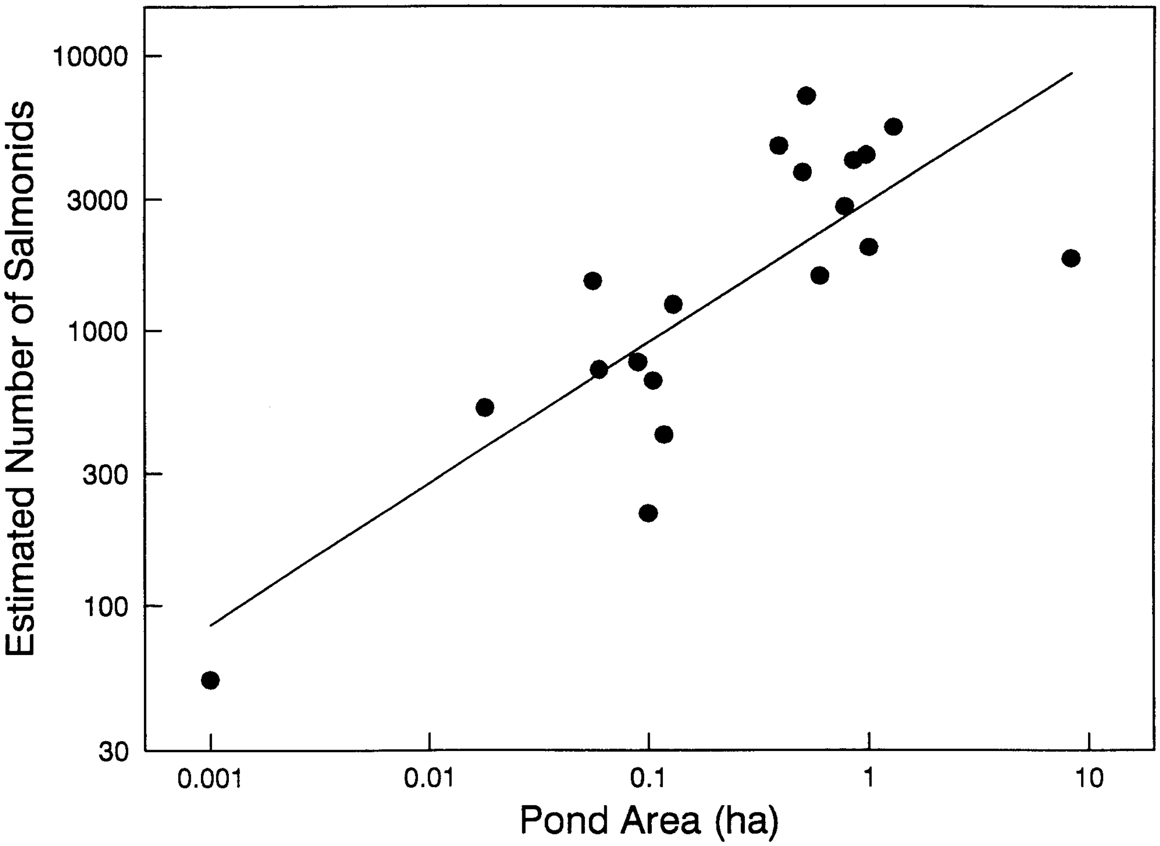

Figure 8. The relationship between surface area of off-channel ponds and estimated number of salmonid fish present. Equation of the line is: Log_{10} fish number = 0.51 $\log_{10}$ pond area (ha) + 3.47, n = 19, $r^2 = 0.64$, $P < 0.001$ (data are from Bustard and Narver 1975; Lister et al. 1980; Peterson 1982; Swales et al. 1986; Beniston et al. 1987; Swales et al. 1988; Beniston et al. 1988; Cederholm et al. 1988; Swales and Levings 1989; Lister and Dunford 1989; Cederholm and Scarlett 1991; M. Foy, Department of Fisheries and Oceans, Vancouver, B.C., unpublished data).

REFERENCES

Allan, J. D. 1995. Stream ecology. Chapman and Hall, London, UK.

Allen, K.R. 1969. Limitations on production in salmonid populations in streams. Pages 3-18 *in* T.G. Northcote [ed.] Symposium on salmon and trout in streams. University of British Columbia, Vancouver.

Andrus, C.W., B.A. Long, and H.A. Froehlich. 1988. Woody debris and its contribution to pool formation in a coastal stream 50 years after logging. Canadian Journal of Fisheries and Aquatic Sciences 45: 2080-2086.

Angermeier, P.L., and J.R. Karr. 1984. Relationships between woody debris and fish habitat in a small warmwater stream. Transactions of the American Fisheries Society 113: 716-726.

Armantrout, N. B. 1991. Restructuring streams for anadromous salmonids. American Fisheries Society Symposium 10: 136-149.

Bain, M. B., J. F. Finn, and H. E. Booke. 1985. Quantifying stream substrate for habitat analysis studies. North American Journal of Fisheries Management 5: 499-506.

Baltz, D. M., B. Vondracek, L. R. Brown, and P. B. Moyle. 1991. Seasonal changes in microhabitat selection by rainbow trout in a small stream. Transactions of the American Fisheries Society 120: 166-176.

Baxter, J.S., and J.D. McPhail. 1996. Bull trout spawning and rearing habitat requirements: summary of the literature. British Columbia Ministry of Environment Lands, and Parks. Fisheries Technical Circular 98: 27 p.

Beamish, F.W.H. 1978. Swimming capacity. Pages 101-187 *in* W.S Hoar and D.J. Randall [eds.] Fish physiology. Vol. VII. Academic Press, London, UK.

Behnke, R. 1992. Native trout of western North America. American Fisheries Society Monograph 1: 275 p.

Beniston, R.J., W.E. Dunford, and D.B. Lister. 1987. Coldwater River juvenile salmonid monitoring study-year 1 (1986-1987). D.B. Lister and Associates, Chilliwack, B.C. Report prepared for B.C. Ministry of Transportation and Highways, Victoria, B.C. 130 p. + appendices.

Beniston, R.J., W.E. Dunford, and D.B. Lister. 1988. Coldwater River juvenile salmonid monitoring study-year 2 (1987-1988). D.B. Lister and Associates, Chilliwack, B.C. Report prepared for B.C. Ministry of Transportation and Highways, Victoria, B.C. 269 p.

Binns, N.A. 1994. Long-term responses of trout and macrohabitats to habitat management in a Wyoming headwater stream. North American Journal of Fisheries Management 14: 87-98.

Binns, N. A., and R. Remmick. 1994. Response of Bonneville cutthroat trout and their habitat to drainage-wide habitat management at Huff Creek, Wyoming. North American Journal of Fisheries Management 14: 669-680.

Bjornn, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. American Fisheries Society Special Publication 19: 83-138.

Bovee, K. D. 1982. A guide to stream habitat analysis using the Instream Flow Methodology. United States Department of the Interior, Fish and Wildlife Service. FWS/OBS-82/26. Instream Flow Information Paper 12: 248 p.

Bozek, M. A., and F. J. Rahel. 1992. Generality of microhabitat suitability models for young Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) across sites and among years in Wyoming streams. Canadian Journal of Fisheries and Aquatic Sciences 49: 552-564.

Briggs, J. C. 1953. The behaviour and reproduction of salmonid fishes in a small coastal stream. State of California Department of Fish and Game, Fisheries Bulletin 94: 62 p.

Bugert, R.M. 1985. Microhabitat selection of juvenile salmonids in response to stream cover alteration and predation. M.Sc. thesis, University of Idaho, Moscow.

Bugert, R. M., T. C. Bjornn, and W. R. Meehan. 1991. Summer habitat use by young salmonids and their responses to cover and predators in a small southeast Alaska stream. Transactions of the American Fisheries Society 120: 474-485.

Burner, C.J. 1951. Characteristics of spawning nests of Columbia River salmon. United States Fishery Bulletin 61: 93-110.

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

Campbell, R. F., and J. H. Neuner. 1985. Seasonal and diurnal shifts in habitat utilized by resident rainbow trout in western Washington Cascade Mountain Streams, Pages 39-48 *in* F. W. Olson, R. G. White, and R. H. Hamre [eds.] Proceedings of the symposium on small hydropower and fisheries. Aurora, CO.

Cederholm, C. J., L. M. Reid, and E. O. Salo. 1980. Cumulative effects of logging road sediment on salmonid populations in the Clearwater River, Jefferson County, Washington. *In* Conference on spawning gravel. A renewable resource in the Pacific Northwest? Seattle, WA.

Cederholm, C.J., and W. J. Scarlett. 1991. The Beaded channel: a low cost technique for enhancing winter habitat of coho salmon. American Fisheries Society Symposium 10: 104-108.

Cederholm, C. J., Scarlett, W. J. and N. P. Peterson. 1988. Low-cost enhancement technique for winter habitat of juvenile coho salmon. North American Journal of Fisheries Management 8: 438-441.

Chambers, J.S., G.H. Allen, and R.T. Pressey. 1955. Research relating to study of spawning grounds in natural areas. State of Washington, Department of Fisheries, Annual Report. Army Engineers contract DA 35026-eng-20572, 174 p. + 3 maps.

Chapman, D. W. 1966. Food and space as regulators of salmonid populations. American Naturalist 100: 345-357.

Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society 117: 1-21.

Chapman, D.W., D.E. Weitkamp, T.L. Welsh, M.B. Dell, and T.H. Schadt. 1986. Effects of river flow on the distribution of chinook salmon redds. Transactions of the American Fisheries Society 115: 537-547.

Crisp, D.T. and P.A. Carling. 1989. Observations on siting, dimensions and structure of salmonid redds. Journal of Fish Biology 34: 119-134.

Crispin, V., R. House, and D. Roberts. 1993. Changes in instream habitat, large woody debris, and salmon habitat after restructuring of a coastal Oregon stream. North American Journal of Fisheries Management 13: 96-102.

Crone, R.A. and C.E. Bond. 1976. Life-history of coho salmon, *Oncorhynchus kisutch*, in Sashin Creek, southeastern Alaska. Fishery Bulletin 74: 897-923.

Cunjak, R.A. 1988. Behaviour and microhabitat of young Atlantic salmon (*Salmo salar*) during winter. Canadian Journal of Fisheries and Aquatic Sciences 45: 2156-2160.

Cunjak, R.A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activities. Canadian Journal of Fisheries and Aquatic Sciences 53 (supplement 1): 267-282.

Cunjak, R. A., and J. M. Green. 1983. Habitat utilization by brook char (*Salvelinus fontinalis*) and rainbow trout (*Salmo gairdneri*) in Newfoundland streams. Canadian Journal of Zoology 61: 1214-1219.

deGraaf, D. A., and L. H. Bain. 1986. Habitat use by and preferences of juvenile Atlantic salmon in two Newfoundland rivers. Transactions of the American Fisheries Society 115: 671-681.

Dill, L.M., R. C. Ydenberg, and A.H. G. Fraser. 1981. Food abundance and territory size in juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Zoology 59: 1801-1809.

Dolloff, C. A., and G. H. Reeves. 1990. Microhabitat partitioning among stream-dwelling juvenile coho salmon, *Oncorhynchus kisutch*, and Dolly Varden, *Salvelinus malma*. Canadian Journal of Fisheries and Aquatic Sciences 47: 2297-2306.

Elliott, J.M. 1990. Mechanisms responsible for population regulation in young brown trout, *Salmo trutta*. III. The role of territorial behaviour. Journal of Animal Ecology 59: 803-813.

Elliott, J.M. 1994. Quantitative ecology and the brown trout. Oxford University Press, Oxford, UK 286 p.

Elliott, S.T. 1986. Reduction of a Dolly Varden population and macrobenthos after removal of logging debris. Transactions of the American Fisheries Society 115: 392-400.

Everest, F. H., and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. Journal of Fisheries Research Board of Canada 29: 91-100.

Fabricius, E., and K.-J. Gustafson. 1954. Further aquarium observations on the spawning behaviour of the char, *Salmo alpinus* L. Institute of Freshwater Research, Drottningholm Report 35: 58-104.

Fabricius, E. and K.-J. Gustafson. 1955. Observations on the spawning behaviour of the grayling, *Thymallus thymallus*, (L.). Institute of Freshwater Research, Drottningholm Report 36: 75-103.

Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology. 62: 441-451.

Fausch, K. D., and R. J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38: 1220-1227.

Fausch, K.D. and T.G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 49: 682-693.

Gauldie, R.W. 1991. Taking stock of genetic concepts in fisheries management. Canadian Journal of Fisheries and Aquatic Sciences 48: 722-731.

Grant, J. W. A., and D. L. G. Noakes. 1988. Aggressiveness and foraging mode of young-of-the-year brook charr, *Salvelinus fontinalis* (Pisces, Salmonidae). Behavioural Ecology and Sociobiology 22: 435-445.

Grant, J. W. A., D. L. G. Noakes, and K. M. Jonas. 1989. Spatial distribution of defence and foraging in young-of-the-year brook charr, *Salvelinus fontinalis*. Journal of Animal Ecology 58: 773-784.

Grant, J.W.A., and D.L. Kramer. 1990. Territory size as a predictor of the upper limit of population density of juvenile salmonids in streams. Canadian Journal of Fisheries and Aquatic Sciences 47: 1724-1737.

Griffith, J.S. Jr. 1972. Comparative behaviour and habitat utilization of brook trout, *Salvelinus fontinalis*, and cutthroat trout, *Salmo clarki*, in small streams in northern Idaho. Journal of the Fisheries Research Board of Canada. 29: 265-273.

Groot, C., and L. Margolis. 1991. Pacific salmon life-histories. University of British Columbia Press, Vancouver, B.C. 564 p.

Grost, R.T., W.A. Hubert, and T.A. Wesche. 1990. Redd site selection by brown trout in Douglas Creek, Wyoming. Journal of Freshwater Ecology 5: 365-371.

Grost, R. T., W. A. Hubert, and T. A. Wesche. 1991. Description of brown trout redds in a mountain stream .Transactions of the American Fisheries Society 120: 582-588.

Hartman, G.F. 1965. The role of behaviour in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 22: 1035-1081.

Hartman, G.F. 1969. Reproductive biology of the gerrard stock rainbow trout. Pages 53-67 *in*: T.G. Northcote [ed.] Symposium on salmon and trout in streams. University of British Columbia, Vancouver, B.C.

Hartman, G.F., and D.M. Galbraith. 1970. The reproductive environment of the gerrard stock rainbow trout. British Columbia Fish and Game Branch Management Publication 15: 51 p.

Hartman, G. F., J.C. Scrivener, and M. J. Miles. 1996. Impacts of logging in Carnation Creek, a high-energy coastal stream in British Columbia, and their implication for restoring fish habitat. Canadian Journal of Fisheries and Aquatic Sciences 53 (supplement 1): 237-251.

Hayes, J.W., and I.G. Jowett. 1994. Microhabitat models of large drift-feeding brown trout in three New Zealand rivers. North American Journal of Fisheries Management 14: 710-725.

Heggberget, T.G. 1991. Some environmental requirements of Atlantic salmon. American Fisheries Society Symposium 10: 132-135.

Heggenes, J., and S. J. Salveit. 1990. Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., in a Norwegian river. Journal of Fish Biology 36: 707-720.

Hill, J., and G. D. Grossman. 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. Ecology 74: 685-698.

Hillman, T. W., Griffith, J. S., and W. S. Platts. 1987. Summer and winter habitat selection by juvenile chinook salmon in a highly sedimented Idaho stream. Transactions of the American Fisheries Society 116: 185-195.

Hobbs, D.F. 1937. Natural reproduction of quinnat salmon, brown and rainbow trout in certain New Zealand waters. New Zealand Marine Department Fisheries Bulletin 6: 104 p.

Hogan, D.L. 1986. Channel morphology of unlogged, logged and debris torrented streams in the Queen Charlotte Islands. British Columbia Ministry of Forests. Land Management Report 49: 94 p.

Horton, W. D., and T. Cochnauer. 1980. Instream flow methodology evaluation, biological criteria determination, and water quantity needs for selected Idaho streams. Idaho Department of Fish and Game, Contract No. 14-16-0001-77090. 101 p.

House, R. A. and P. L. Boehne. 1985. Evaluation of instream enhancement structures for salmonid spawning and rearing in a coastal Oregon stream. North American Journal of Fisheries Management 5: 283-295.

Hughes, N. F. 1992. Selection of positions by drift-feeding salmonids in dominance hierarchies: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences. 49: 1999-2008.

Hunt, R.L. 1976. A long-term evaluation of trout habitat development and its relation to improving management-related research. Transactions of the American Fisheries Society 105: 361-364.

James, P.W., and H.M. Sexauer. *in press*. Spawning behaviour, spawning habitat and alternative mating strategies in an adfluvial population of bull trout. Proceedings of the Friends of the Bull Trout Conference.

Jowett, I.G. 1992. Models of the abundance of large brown trout in New Zealand rivers. North American Journal of Fisheries Management 12: 417-432.

Keeley, E.R., and J.W.A. Grant. 1995. Allometric and environmental correlates of territory size in juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 52: 186-196.

Keeley, E.R., and C.J. Walters. 1994. The British Columbia Watershed Restoration Program: summary of the experimental design, monitoring and techniques workshop. Province of British Columbia, Ministry of Environment, Lands and Parks, and Ministry of Forests. Watershed Restoration Management Report 1: 34 p.

Kitano, S., Maekawa, K., Nakano, S., and K.D. Fausch. 1994. Spawning behavior of bull trout in the Upper Flathead drainage, Montana, with special reference to hybridization with brook trout. Transactions of the American Fisheries Society 123: 988-992.

Kondolf, G.M., and M.G. Wolfman. 1993. The sizes of salmonid spawning gravels. Water Resources Research 29: 2275-2285.

Koski, K. V. 1992. Restoring stream habitats affected by logging activities. Pages 343-403 *in* G. W. Thayer [ed.] Restoring the nation’s marine environment. Maryland Sea Grant College, College Park, Maryland.

Leggett, J.W. 1969. The reproductive biology of the dolly varden charr *Salvelinus malma* (Walbum). M.Sc. thesis, University of Victoria. Victoria, B.C.

Lisle, T.E. 1986. Effect of woody debris on anadromous salmonid habitat, Prince of Wales Island, southeast Alaska. North American Journal of Fisheries Management 6: 538-550.

Lister, D. B., D. E. Marshall, and D. G. Hickey. 1980. Chum salmon survival and production at seven improved groundwater-fed spawning areas. Canadian Manuscript Report of Fisheries and Aquatic Sciences 1595: 58 p.

Lister, D.B., and W.E. Dunford. 1989. Post-construction monitoring of compensatory fish habitat at Cook Creek (1987-88). D.B Lister and Associates, Chilliwack, B.C. Report prepared for Canadian National Railway Engineering Services. Edmonton, AB. 53 p.

Lohr, S. C., and J. R. West. 1992. Microhabitat selection by brook and rainbow trout in a southern Appalachian stream. Transactions of the American Fisheries Society 121: 729-736.

Lorenz, J.M., and J.H. Eiler. 1989. Spawning habitat and redd characteristics of sockeye salmon in the glacial Taku River, British Columbia and Alaska. Transactions of the American Fisheries Society 118: 495-502.

McNeil, W.J. 1967. Randomness in distribution of pink salmon redds. Journal of the Fisheries Research Board of Canada 24:1629-1634.

McPhail, J.D., and C.C. Lindsey. 1970. Freshwater fishes of northwestern Canada and Alaska. Fisheries Research Board of Canada Bulletin 173: 381 p.

McPhail, J.D., and C.B. Murray. 1979. The early life-history and ecology of dolly varden (*Salvelinus malma*) in the upper Arrow Lakes. Department of Zoology and Institute of Animal Resource Ecology, University of British Columbia. Vancouver, B.C.

Meffe, G. K. 1992. Techno-arrogance and halfway technologies: salmon hatcheries on the Pacific Coast of North America. Conservation Biology 6: 350-354.

Moore, K. M. S., and S. V. Gregory. 1988. Summer habitat utilization and ecology of cutthroat trout fry (*Salmo clarki*) in Cascade Mountain streams. Canadian Journal of Fisheries and Aquatic Sciences 45: 1921-1930.

Morantz, D. L., R. K. Sweeney, C. S. Shirvell, and D. A. Longard. 1987. Selection of microhabitat in summer by juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 44: 120-129.

Murphy, M. L., J. F. Thedinga, K. V. Koski, and G. B. Grette. 1984. A stream ecosystem in an old-growth forest in southeast Alaska: Part V: seasonal changes in habitat utilization by juvenile salmonids. Pages 89-98 *in* W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley [eds.] Fish and wildlife relationships in old-growth forests: proceedings of a symposium held in Juneau, Alaska, 12-15 April 1982. American Institute of Fishery Research Biologists, Morehead City, NC.

Murphy, M.L., and K.V. Koski. 1989. Input and depletion of woody debris in Alaska streams and implications for streamside management. North American Journal of Fisheries Management 9: 427-436.

Nechako River Project. 1987. Studies of juvenile chinook salmon in the Nechako River, British Columbia 1985 and 1986. Canadian Manuscript Report of Fisheries and Aquatic Sciences 1954: 152 p.

Nehlsen, W., J.E. Williams, and J.A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16: 4-21.

Neilson, J. D., and C. E. Banford. 1983. Chinook salmon (*Oncorhynchus tshawytscha*) spawner characteristics in relation to redd physical features. Canadian Journal of Zoology 61: 1524-1531.

Neter, J., W. Wasserman, and M.H. Kutner. 1990. Applied linear statistical models. 3rd. edition. Irwin, Homewood, Ill, 1181 p.

Nielsen, J. L. 1992. Microhabitat-specific foraging behaviour, diet, and growth of juvenile coho salmon. Transactions of the American Fisheries Society 121: 617-634.

Northcote, T.G. 1988. Catching the rise: ascent of experimental approaches in trout stream research and its challenges. Polish Archives of Hydrobiology 35: 231-265.

Oliver, G. G. 1979. A final report on the present fisheries use of the Wigwam River with an emphasis on the migration, life history and spawning behaviour of Dolly Varden char (*Salvelinus malma*) (Walbaum). Province of British Columbia, Fish and Wildlife Branch, Kootenay Region, 82 p.

Orcutt, D. R., B. R. Pulliam, and A. Arp. 1968. Characteristics of steelhead trout redds in Idaho streams. Transactions of the American Fisheries Society 97: 42-45.

Ottoway, E. M., P. A. Carling, A. Clarke, and N. A. Reader. 1981. Observations on the structure of brown trout, *Salmo trutta Linnaeus*, redds. Journal of Fish Biology 19: 593-607.

Parsons, B.G.M., and W.A. Hubert. 1988. Influence of habitat availability on spawning site selection by kokanees in streams. North American Journal of Fisheries Management 8: 426-431.

Peterson, N.P. 1982. Population characteristics of juvenile coho salmon (*Oncorhynchus kisutch*) overwintering in riverine ponds. Canadian Journal of Fisheries and Aquatic Sciences 39: 1303-1307.

Puckett, K. J., and L. M. Dill. 1985. The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). Behaviour 92: 97-111.

Riehle, M. D., and J. S. Griffith. 1993. Changes in habitat use and feeding chronology of juvenile rainbow trout (*Oncorhynchus mykiss*) in fall and the onset of winter in Silver Creek, Idaho. Canadian Journal of Fisheries and Aquatic Sciences. 50: 2119-2128.

Rimmer, D. M., U. Paim, and R. S. Saunders. 1984. Changes in the selection of microhabitat by juvenile Atlantic salmon (*Salmo salar*) at the summer-autumn transition in a small river. Canadian Journal of Fisheries and Aquatic Sciences 41: 469-475.

Rincon, P. A., and J. Lobon-Cervia. 1993. Microhabitat use by stream-resident brown trout: bioenergetic consequences. Transactions of the American Fisheries Society 122: 575-587.

Rinne, J.N. 1980. Spawning habitat and behavior of gila trout, a rare salmonid of the southwestern United States. Transactions of the American Fisheries Society 109: 83-91.

Robins, C.R., R.M. Bailey, C.E. Bond, J.R. Brooker, E. A. Lachner, R.N. Lea, and W.B. Scott. 1991. A list of common and scientific names of fishes from the United States and Canada, 5th edition. American Fisheries Society, Special Publication 20: 183 p.

Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Bulletin 184:966 p.

Scrivener, J. C., and T. G. Brown. 1993. Impact and complexity from forests practices on streams and their salmonid fishes in British Columbia. Pages 41-49 *in* G. Shooner and S. Asselin [eds.] Le développement du saumon Atlantique au Québec: connaître règles du jeu pour réussir. Colloque internaltional de la Fédération québecoise pour le saumon atlantique. Québec, PQ.

Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. State of California Fisheries Bulletin 98: 375 p.

Shepard, B. B., K. L. Pratt, and P. J. Graham. 1984. Life histories of westslope cutthroat and bull trout in the Upper Flathead River basin, Montana. Environmental Protection Agency, Denver, Colorado, Contract No. R008224-01-5. 95 p.

Shirvell, C. S. 1994. Effect of changes in streamflow on the microhabitat use and movements of sympatric juvenile coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) in a natural stream. Canadian Journal of Fisheries and Aquatic Sciences 51: 1644-1652.

Shirvell, C. S., and R. G. Dungey. 1983. Microhabitats chosen by brown trout for feeding and spawning in rivers. Transactions of the American Fisheries Society 112: 355-367.

Slaney, P.A., and T.G. Northcote. 1974. Effects of prey abundance on density and territorial behaviour behavior of young rainbow trout (*Salmo gairdneri*) in a laboratory stream channel. Journal of the Fisheries Research Board of Canada 31: 1201-1209.

Slaney, P. A. 1977 a. Some effects of forest harvesting on salmonid rearing habitat in two stream in the central interior of British Columbia. British Columbia Ministry of Environment, Fish and Wildlife Branch. Fisheries Management Report 71: 26 p.

Slaney, P. A. 1977 b. Effects of forest harvesting on spawning habitat of stream salmonids in the Centennial Creek watershed, British Columbia. British Columbia Ministry of Environment, Fish and Wildlife Branch. Fisheries Management Report 73: 45 p.

Slaney, P. A. 1994. The watershed restoration program of British Columbia: an opportunity and a challenge. Pages 117-133 *in* W. T. Dushenko, H. E. Pollard, and K. Johnston [eds.] Environmental impact and remediation: towards 2000. Proceedings of the 34th annual meeting of the Canadian Society of Environmental Biologists, Royal Roads Military College, Victoria.

Slaney, P. A., B. O. Rublee, C. R. Perrin, and H. Goldberg. 1994. Debris structure placements and whole-river fertilization for salmonids in a large regulated stream in British Columbia. Bulletin of Marine Science 55: 1160-1180.

Slaney, T. L., K. D. Hyatt, T. G. Northcote, and R. G. Fielden. 1996. Status of anadromous salmon and trout in British Columbia and Yukon. Fisheries 21: 20-35.

Smith, A.K. 1973. Development and application of spawning velocity and depth criteria for Oregon salmonids. Transactions of the American Fisheries Society 102: 312-316.

Smith, J.J., and H. W. Li. 1983. Energetic factors influencing foraging tactics of juvenile steelhead, *Salmo gairdneri*. Pages 173-180 *in* D.L.G. Noakes, D.G. Lindquist, G.S. Helfman, and J.A. Ward [eds.] Predators and prey in fishes. Dr. W. Junk, The Hague, Netherlands.

Stalnaker, C.B, and J.L Arnette. 1976. Methodologies for determining instream flows for fish and other aquatic life. Pages 89-137 *in* C.B. Stalkner and J.L. Arnette [eds] Methodologies for the determination of stream resource flow requirements: an assessment. Utah State University. Logan, UT.

Stefferud, J.A. 1993. Spawning season and microhabitat use by California golden trout (*Oncorhynchus mykiss aguabonita*) in the Sierra Nevada. California Fish and Game 79: 133-144.

Stradmeyer, L., and J. E. Thorpe. 1987. Feeding behaviour of wild Atlantic salmon, *Salmo salar* L., parr in mid- to late summer in a Scottish river. Aquaculture and Fisheries Management 18: 33-49.

Sublette, J.E., M.D. Hatch, and M. Sublette. 1990. The fishes of New Mexico. University of New Mexico Press, Albuquerque. 393 p.

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

Swales, S., R.B. Lauzier, and C.D. Levings. 1986. Winter habitat preferences of juvenile salmonids in two interior rivers in British Columbia. Canadian Journal of Zoology 64: 1506-1514.

Swales, S., and C.D. Levings. 1989. Role of off-channel ponds in the life cycle of coho salmon (*Oncorhynchus kisutch*) and other juvenile salmonids in the Coldwater River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46: 232-242.

Tautz, A. F., and C. Groot. 1975. Spawning behavior of chum salmon (*Onchorhynchus keta*) and rainbow trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 32: 633-642.

Thurrow, R.F., and J.G. King. 1994. Attributes of Yellowstone cutthroat trout redds in a tributary of the Snake River, Idaho. Transactions of the American Fisheries Society 123: 37-50.

Tripp, D. 1986. Using large organic debris to restore fish habitat in debris-torrented streams. British Columbia Ministry of Forests. Land Management Report 47.

Tripp, D. 1994. The use and effectiveness of the Coastal Fisheries / Forestry Guidelines in selected forest districts in British Columbia. Contract report for the Ministry of Forests. 86 p.

Tschaplinski, P.J., and G.F. Hartman. 1983. Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. Canadian Journal of Fisheries and Aquatic Sciences 40: 452-461.

van den Berghe, E.P., and M.R. Gross. 1984. Female size and nest depth in coho salmon (*Onchorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 41: 204-206.

van den Berghe, E.P., and M.R. Gross. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho: *Onchorhynchus kisutch*). Evolution 43: 125-140.

Wankowski, J. W. J., and J. E. Thorpe. 1979. Spatial distribution and feeding in Atlantic salmon, *Salmo salar* L. juveniles. Journal of Fish Biology 14: 239-247.

Ward, B. R., and P. A. Slaney. 1979. Evaluation of in-stream enhancement structures for the production of juvenile steelhead trout and coho salmon in the Keogh River: progress 1977 and 1978. British Columbia Ministry of Environment. Fisheries Technical Circular 45: 47 p.

Ward, B. R., and P. A. Slaney. 1993. Habitat manipulations for rearing of fish in British Columbia. Pages 142-148 *in* G. Shooner and S. Asselin, [eds.] Le développement du saumon Atlantique au Québec: connaître règles du jeu pour réussir. Colloque internaltional de la Fédération québecoise pour le saumon atlantique. Québec, PQ.

Witzel, L. D., and H. R. MacCrimmon. 1983. Redd-site selection by brook trout and brown trout in southwestern Ontario streams. Transactions of the American Fisheries Society 112: 760-771.

Young, M. K., W. A. Hubert, and T. A. Wesche. 1989. Substrate alteration by spawning brook trout in a southeastern Wyoming stream. Transactions of the American Fisheries Society 118: 379-385.