24

Chapter 4

Habitat Requirements of Salmonids in Streams

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Habitat needs of salmon, trout, and char in streams vary with the season of the year and stage of the life cycle. The major life stages of most salmonid species are associated with different uses of fluvial systems: migration of maturing fish from the ocean (anadromous fishes), lakes, or rivers to natal streams; spawning by adults; incubation of embryos; rearing of juveniles; and downstream migration of juveniles to large-river, lacustrine, or oceanic rearing areas. We present information from the literature and from our own research on the range of habitat conditions for each life stage that allow the various species to exist. When possible, we attempt to define optimum and limiting conditions. Anadromous salmonids of the Pacific drainages of North America are our primary focus, but we have included information on other salmonids to illustrate the ranges of temperature, water velocities, depths, cover, and substrates preferred by salmon, trout, and char in streams. The scientific names of species identified by common names here are listed in the book's front matter.

Upstream Migration of Adults

Adult salmonids returning to their natal streams must reach spawning grounds at the proper time and with sufficient energy reserves to complete their life cycles. Stream discharges, water temperatures, and water quality must be suitable during at least a portion of the migration season. Native stocks of salmon, trout, and char that have evolved in stream systems with fluctuations in flow, turbidity, and temperature have often developed behaviors that enable survival despite the occurrence of temporarily unfavorable conditions. Native salmonids usually have sufficient extra time in their maturation, migration, and spawning schedules to accommodate delays caused by normally occurring low flows, high turbidities, or unsuitable temperatures. When upstream migration is not delayed, the fish in some stocks that migrate long distances arrive in the spawning areas 1–3 months before they spawn. Some stocks of fish that migrate short distances may not move into natal streams until shortly before spawning, but they must often wait in the ocean, lake, or river for flows or temperatures in the spawning streams to become suitable.

The flexibility in maturation and migration schedules observed in many stocks of native salmonids is not unlimited and has evolved for the specific environment

TABLE 4.1.—Water temperatures (Bell 1986) and depths and velocities (Thompson 1972) that enable upstream migration of adult salmon and trout.

Species of fish	Temperature range (°C)	Minimum depth (m)	Maximum velocity (m/s)
Fall chinook salmon	10.6–19.4	0.24	2.44
Spring chinook salmon	3.3–13.3	0.24	2.44
Summer chinook salmon	13.9–20.0	0.24	2.44
Chum salmon	8.3–15.6	0.18	2.44
Coho salmon	7.2–15.6	0.18	2.44
Pink salmon	7.2–15.6	0.18[a]	2.13
Sockeye salmon	7.2–15.6	0.18	2.13
Steelhead		0.18	2.44
Large trout		0.18	2.44
Trout		0.12[a]	1.22

[a] Estimate based on fish size.

of each stock. Natural or human-caused changes in the environment can be large enough to prevent fish from completing their maturation or migration to spawning areas; the proportion affected depends on the extent of the change. Transplanted stocks of fish may be less successful than native stocks in reproducing themselves if they do not possess the flexibility in migration timing required in their new environment.

Temperature

Salmon and trout respond to stream temperatures during their upstream migrations. Delays in upstream migration because natal streams were too warm have been observed for sockeye salmon (Major and Mighell 1966), chinook salmon (Hallock et al. 1970), and steelhead (Monan et al. 1975). Bell (1986) reported that Pacific salmon and steelhead have migrated upstream at temperatures between 3 and 20°C (Table 4.1).

Streams can be too cold as well as too warm for upstream-migrating salmonids. Cutthroat and rainbow trout have been observed waiting for tributaries to warm in spring before entering them to spawn. Adult steelhead that return from the sea in summer and autumn, and then spend the winter in inland rivers before spawning the following spring, overwinter in larger rivers downstream from their natal streams because the smaller headwater streams are often ice-choked during winter. We believe adult steelhead overwinter in the larger rivers because survival is higher there and the slightly higher temperatures in the rivers enable timely maturation (Reingold 1968).

Stream temperatures can be altered by removal of streambank vegetation, withdrawal and return of water for agricultural irrigation, release of water from deep reservoirs, and cooling of nuclear power plants. Unsuitable temperatures can lead to disease outbreaks in migrating and spawning fish, altered timing of migration, and accelerated or retarded maturation. Most stocks of anadromous salmonids have evolved with the temperature patterns of the streams they use for migration and spawning, and deviations from the normal pattern could adversely affect their survival.

Dissolved Oxygen

Reduced concentrations of dissolved oxygen (DO) can adversely affect the swimming performance of migrating salmonids. Maximum sustained swimming speeds of juvenile and adult coho salmon at temperatures of 10–20°C were reduced when DO dropped below air-saturation levels, and performance declined sharply when DO fell to 6.5–7.0 mg/L, at all temperatures tested (Davis et al. 1963). Swimming performance of brook trout declined similarly (Graham 1949). Low DO may also elicit avoidance reactions (Whitmore et al. 1960; Hallock et al. 1970), and may halt migration. Hallock et al. (1970) observed that adult migration ceased when DO fell below 4.5 mg/L, and did not resume until it exceeded 5 mg/L. Minimum DO recommended for spawning fish (at least 80% of saturation, and not even temporarily less than 5.0 mg/L) should provide the minimum needs of migrating salmonids.

Turbidity

Migrating salmonids avoid waters with high silt loads, or cease migration when such loads are unavoidable (Cordone and Kelley 1961). Bell (1986) cited a study in which salmonids did not move in streams where the suspended sediment concentration exceeded 4,000 mg/L (as a result of a landslide). Timing of arrival at spawning grounds by chinook salmon that migrate upstream during snowmelt runoff can vary by a month or more, depending on the concentration of suspended solids in rivers along their migration route (Bjornn 1978). In the lower Columbia River, the upstream migration of salmon may be retarded when secchi disk readings are less than 0.6 m (Figure 4.1).

High turbidity in rivers may delay migration, but turbidity alone generally does not seem to affect the homing of salmonids very much. In studies after the eruption of Mount St. Helens in 1980, Whitman et al. (1982) found that salmon preferred natal stream water without volcanic ash in an experimental flume, but that they recognized their natal streams despite the ash and attempted to ascend them. Quinn and Fresh (1984) reported that the rate of straying of chinook salmon to the Cowlitz River Hatchery was low and unaffected by the 1980 eruption, but that many coho salmon in the Toutle River, the Cowlitz River tributary most affected by the eruption, did stray to nearby streams in 1980 and 1981. Olfaction is a primary sense salmonids use for homing during upstream migration (Hasler and Larsen 1955; Hasler et al. 1978). Each stream may have a unique bouquet, and the extent to which that bouquet can be altered—by the addition of exotic chemicals, trans-basin diversions, and unnatural suspended sediments—without affecting the homing of salmonids is not known.

Barriers

Waterfalls, debris jams, and excessive water velocities may impede migrating fish. Falls that are insurmountable at one time of the year may be passed by migrating fish at other times when flows have changed. Stuart (1962) determined in laboratory studies that leaping conditions for fish are ideal when the ratio of height of falls to depth of pool below the falls is 1 : 1.25 (Figure 4.2). Given suitable conditions, salmon and steelhead can get past many obstacles that appear to be barriers. Both Jones (1959) and Stuart (1962) observed salmon jumping over

FIGURE 4.1.—Secchi disk visibility (broken line) and number of chinook salmon adults (solid lines) migrating up the Columbia River past Bonneville Dam during April and May of 1965, when high turbid flows interrupted the migration, and of 1966, when turbidities were low and the timing of migration was normal.
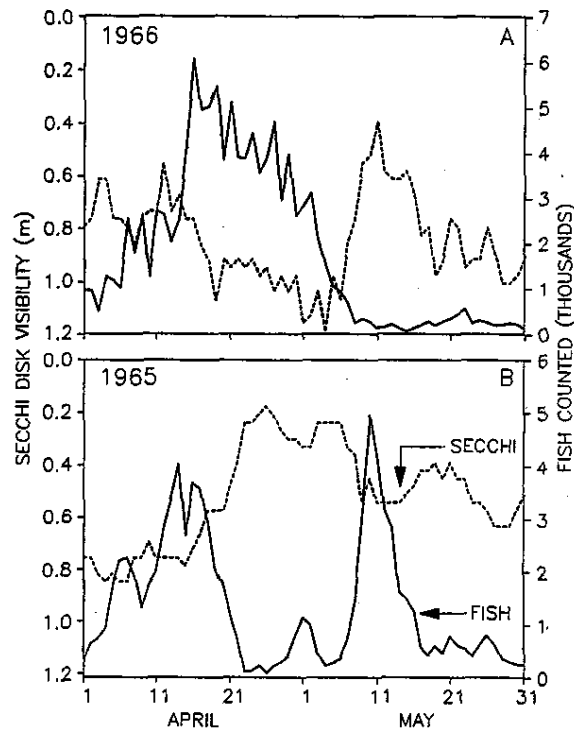
obstacles 2–3 m in height. Powers and Orsborn (1985) analyzed barriers to upstream-migrating fish in terms of barrier geometry, stream hydrology, and fish capabilities. They reported the abilities of salmon and trout to pass over barriers depended on the swimming velocity of the fish, the horizontal and vertical distances to be jumped, and the angle to the top of the barrier (Figure 4.3). Reiser and Peacock (1985) computed maximum jumping heights of salmonids on the basis of darting speeds; these heights ranged from 0.8 m for brown trout to more than 3 m for steelhead (Table 4.2).

The swimming abilities of fish are usually described in three categories of speed: cruising speed, the speed a fish can swim for an extended period of time, usually ranging from 2 to 4 body lengths/s; sustained speed, the speed a fish can maintain for a period of several minutes, ranging from 4 to 7 body lengths/s; and darting or burst speed, the speed a fish can swim for a few seconds, ranging from 8 to 12 body lengths/s (Watts 1974; Bell 1986; Table 4.2). According to Bell (1986), cruising speed is used during migration, sustained speed for passage through difficult areas, and darting speed for escape and feeding. Water velocities of 3–4 m/s approach the upper sustained swimming ability of large fish like salmon and steelhead.

Debris jams, whether natural or caused by human activities, can prevent or delay upstream migration. Chapman (1962b) cited a study in which a 75% decrease in number of spawning salmon in one stream was attributed to blockage by debris. On the other hand, many debris jams can be easily passed by fish and they often form pools and provide cover for fish. Removal of debris barriers
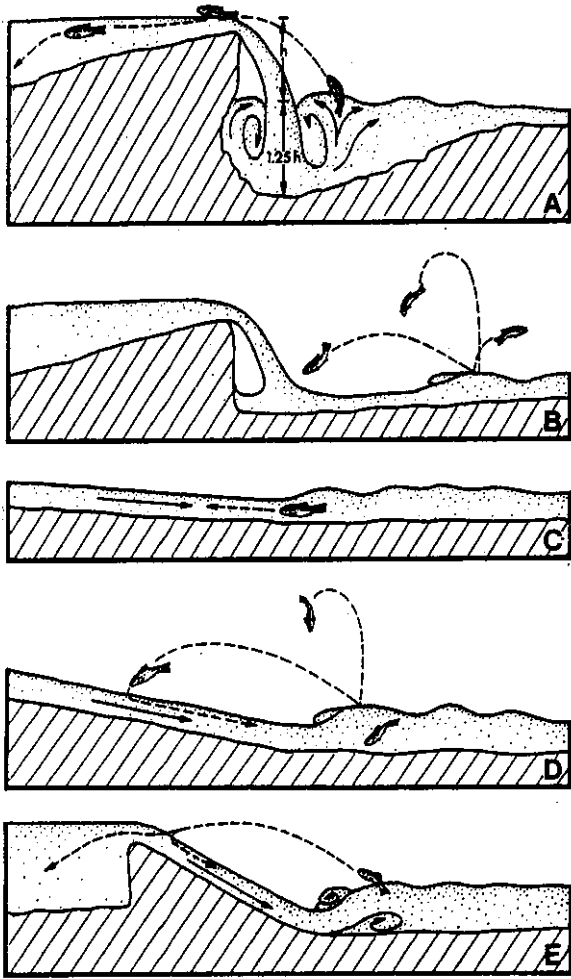
FIGURE 4.2.—Leaping ability of salmonids. (From Eiserman et al. 1975, diagrams drawn after Stuart 1962). (A) Falling water enters the pool at nearly a 90° angle. A standing wave lies close to the waterfall, where fish can use its upward thrust to leap the falls. Plunge-pool depth is 1.25 times the distance (h) from the crest of the waterfall to the water level of the pool. (B) The height of fall is the same as in A, but pool depth is less. The standing wave is formed too far from the ledge to be useful to leaping fish. (C) Flow down a gradual incline is slow enough to allow passage of ascending fish. (D) Flow over an incline steeper than fish can negotiate. Fish may even be repulsed in the standing wave at the foot of the incline. They sometimes leap futilely from the standing wave. (E) A shorter barrier with outflow over a steep incline may be ascended by some fish with difficulty.

should be done with care to avoid sedimentation of downstream spawning and rearing areas and loss of hydraulic stability.

Streamflow

Fish migrating upstream must have streamflows that provide suitable water velocities and depths for successful upstream passage. A variety of techniques have been used to estimate the flows required for migrating fish. Baxter (1961) reported that salmon needed 30–50% of the average annual flow for passage through the lower and middle reaches in Scottish rivers and up to 70% for passage up headwater streams. Thompson (1972) developed a procedure for estimating minimum flows required for migrating fish on the basis of minimum depth and maximum velocity criteria (Table 4.1) and measurements in critical stream reaches, usually shallow riffles. Stream discharges that provide suitable depths and velocities for upstream passage of adults can be estimated by the techniques he described (Thompson 1972):
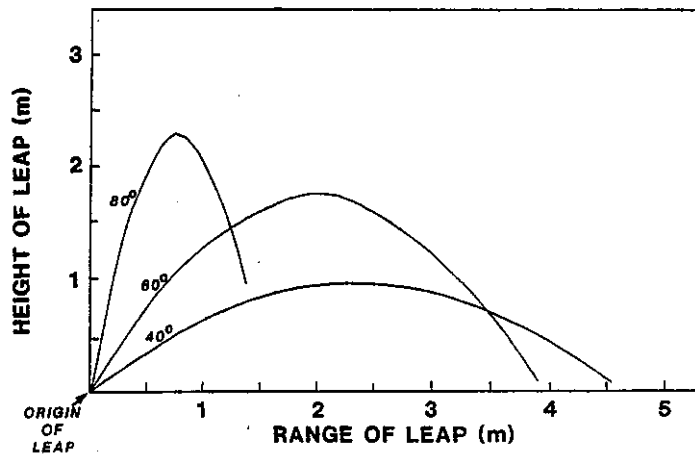
FIGURE 4.3.—Leaping curves for chinook, coho, and sockeye salmon swimming with a maximum burst speed of 6.8 m/s and jumping at various angles. (Adapted from Powers and Orsborn 1985.)

. . . shallow bars most critical to passage of adult fish are located and a linear transect marked which follows the shallowest course from bank to bank. At each of several flows, the total width and longest continuous portion of the transect meeting minimum depth and maximum velocity criteria are measured. For each transect, the flow is selected that meets the criteria on at least 25% of the total transect width and a continuous portion equaling at least 10% of its total width.

The mean selected flow from all transects is recommended as the minimum flow for passage.

Sautner et al. (1984) reported that passage of chum salmon spawners through sloughs and side channels of the Susitna River, Alaska, depended primarily on water depth, length of the critical stream reach, and size of substrate particles. Fish could successfully pass any stream reach of reasonable length if the depth was greater than 0.12 m when substrate particles averaged larger than 7.6 cm in diameter, or if the depth was greater than 0.09 m when particles were less than 7.6 cm.

TABLE 4.2.—Swimming (Bell 1986) and jumping abilities (Reiser and Peacock 1985) of average-size adult salmonids.

Taxon	Swimming speed (m/s)			Maximum jumping height (m)
	Cruising	Sustained	Darting	
Chinook salmon	0–1.04	1.04–3.29	3.29–6.83	2.4
Coho salmon	0–1.04	1.04–3.23	3.23–6.55	2.2
Sockeye salmon	0–0.98	0.98–3.11	3.11–6.28	2.1
Steelhead	0–1.40	1.40–4.18	4.18–8.08	3.4
Trout	0–0.61	0.61–1.95	1.95–4.11	
Brown trout	0–0.67	0.67–1.89	1.89–3.87	0.8

Spawning

Substrate composition, cover, water quality, and water quantity are important habitat elements for salmonids before and during spawning. The number of spawners that can be accommodated in a stream is a function of the area suitable for spawning (suitable substrate, water depth, and velocity), area required for each redd, suitability of cover for the fish, and behavior of the spawners. Cover is important for species that spend several weeks maturing near spawning areas.

The amount of suitable stream substrate for spawning varies with the size (order) of the stream and species of salmonid using it, as Boehne and House (1983) learned from study of two coastal and two Cascade Range watersheds in Oregon. First-order streams (small headwater streams without tributaries) were not used by salmonids. Less than half the second-order streams (streams resulting from the junction of two or more first-order streams) were used by salmonids; those that were contained nonanadromous cutthroat trout. Most of the third-order streams (steams resulting from the junction of two or more second-order streams) in the coastal watersheds, but only 37% of those in the Cascade Range drainages, were used by cutthroat trout. The larger anadromous steelhead, coho salmon, and chinook salmon spawned in a few third-order streams, but most were found in fourth- and fifth-order streams. As stream order increased, gradient decreased but stream length, width, and depth increased. The amount of spawning gravel per kilometer of stream was greatest in fourth-order coastal watersheds and fifth-order Cascade Range watersheds. Platts (1979b) found similar relations between stream size (order) and use of the streams by fish in an Idaho drainage.
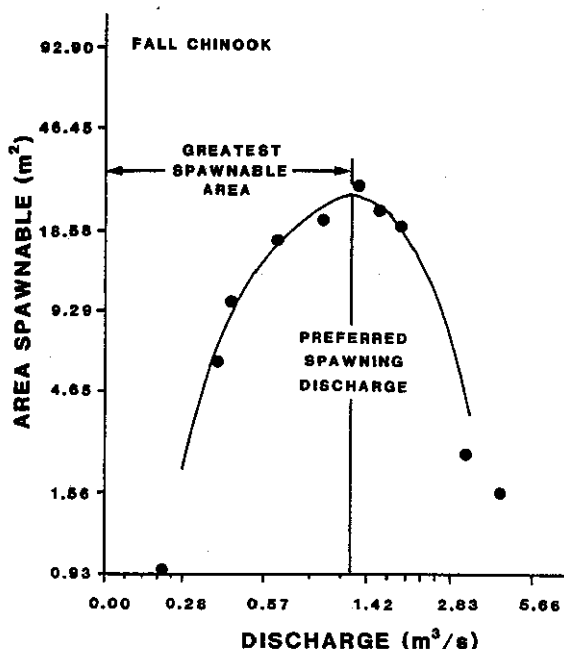
Streamflow

Streamflow regulates the amount of spawning area available in any stream by regulating the area covered by water and the velocities and depths of water over the gravel beds. D. H. Fry (in Hooper 1973) summarized the effect of discharge on the amount of spawning area in a stream.

> As flows increase, more and more gravel is covered and becomes suitable for spawning. As flows continue to increase, velocities in some places become too high for spawning, thus cancelling out the benefit of increases in usable spawning area near the edges of the stream. Eventually, as flows increase, the losses begin to outweigh the gains, and the actual spawning capacity of the stream starts to decrease. If spawning area is plotted against streamflow, the curve will usually show a rise to a relatively wide plateau followed by a gradual decline.
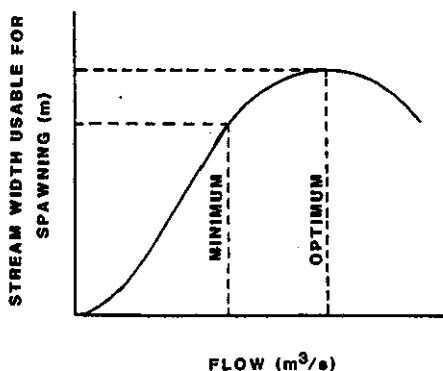
Relations between flow and amount of suitable spawning area have been assessed or predicted by methods based primarily on measurements of water depths and velocities in areas with suitable substrate. Collings (1972, 1974) used a process of depth and velocity contouring to determine the area suitable for spawning at a given discharge. Thompson (1972) quantified the width of the stream at cross-channel transects on spawning bars that met minimum criteria of depth (18 cm) and velocity (0.3–3.0 m/s) at different flows. When measurements have been taken over a wide range of flows, a graph can be plotted of flow versus suitable spawning areas (Figure 4.4) or usable width (Figure 4.5). A method

FIGURE 4.4.—Usable-area technique for selecting preferred spawning discharge, North Nemah River. (From Collings 1972.)

FIGURE 4.5.—Usable-width technique for determining spawning flow. (From Thompson 1972.)

similar to that used by Waters (1976), termed the instream flow incremental methodology (IFIM), was developed by U.S. Fish and Wildlife Service personnel to estimate the amount of suitable habitat (for spawning, in this instance); the method relates variations in a stream's water velocity, depth, substrate, and other variables to use of the stream by fishes (Stalnaker and Arnette 1976b; Bovee 1978, 1982, 1986; Bovee and Milhous 1978; Trihey and Wegner 1981). An IFIM analysis results in an index of suitable habitat (weighted usable area, WUA) for a range of streamflows (Figure 4.6). Wesche and Rechard (1980) and EA Engineering, Science and Technology, Inc. (1986) reviewed and evaluated a variety of methods that could be used for estimating the quantity and quality of spawning habitat for salmonids.
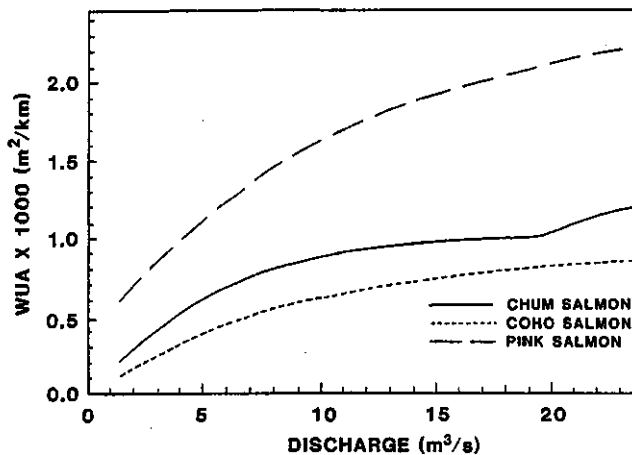
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FIGURE 4.6.—Relation of available chum, coho, and pink salmon spawning habitat (weighted usable area, WUA) to streamflow, Upper Tunnel Creek. (From Reiser and Ramey 1984.)

Temperature

Timing of salmonid spawning has likely evolved in response to water temperatures in each stream before, during, and after spawning, and, in some streams, to the occurrence of flows that allow upstream migration of maturing adults. Salmonids have spawned when water temperatures have ranged from 1.0 to 20.0°C, but the favorable range of temperatures for spawning is much narrower (Table 4.3). In British Columbia (Shepherd et al. 1986b), salmon were observed spawning over a wide range of temperatures, but most of the pink, chum, and

TABLE 4.3.—Recommended temperatures for spawning and incubation of salmonid fishes (Bell 1986).

Species	Temperature (°C)[a]	
	Spawning	Incubation[a]
Fall chinook salmon	5.6–13.9	5.0–14.4
Spring chinook salmon	5.6–13.9	5.0–14.4
Summer chinook salmon	5.6–13.9	5.0–14.4
Chum salmon	7.2–12.8	4.4–13.3
Coho salmon	4.4–9.4	4.4–13.3
Pink salmon	7.2–12.8	4.4–13.3
Sockeye salmon	10.6–12.2	4.4–13.3
Kokanee	5.0–12.8	
Steelhead	3.9–9.4	
Rainbow trout	2.2–20.0	
Cutthroat trout	6.1–17.2	
Brown trout	7.2–12.8[b]	

[a] The higher and lower values are threshold temperatures beyond which mortality increases. Eggs survive and develop normally at lower temperatures than indicated, provided initial development of the embryo has progressed to a stage that is tolerant of cold water.
[b] From Hunter (1973).

sockeye salmon spawned in water of 8–13°C, chinook salmon in water of 10–17°C, and coho salmon in water of less than 10°C (mode, 5–6°C).

Each native fish stock appears to have a unique time and temperature for spawning that theoretically maximizes the survival of their offspring. Temperatures before and during spawning must allow the spawners to survive and deposit their eggs, but temperatures during incubation of the embryos (which regulates timing of juvenile emergence from the redd) may be the primary evolutionary factor that has determined the time of spawning (Heggberget 1988). In the case of fall spawners, newly spawned embryos must reach a critical stage of development before the water becomes too cold (Brannon 1965), and emergence of fry must occur at a suitable time during the following spring (Sheridan 1962a; Miller and Brannon 1982; Godin 1982; Burger et al. 1985; Heggberget 1988). Spring spawners must not spawn before the water has warmed sufficiently to permit normal development of embryos, but there may be a survival advantage for the fish to spawn as early as possible to allow the offspring to emerge and grow before the onset of winter. Support for the latter hypothesis can be found in Idaho streams, where steelhead usually spawn before the peak of the snowmelt runoff in spring (thereby risking destruction of their redds by the high flows) rather than after the peak, which would delay the emergence of their offspring until late summer.

Areas with upwelling groundwater have been selected as spawning areas by salmonids such as chum salmon, brown trout, and brook trout (Benson 1953; Bakkala 1970; Witzel and MacCrimmon 1983; Vining et al. 1985). Use of areas with groundwater flow may have survival advantages if the water quality (suitable temperatures and dissolved gases, and lack of damaging heavy metals and sediments) in such areas is more suitable than in areas without groundwater.

Space

The amount of space required by salmonids for spawning depends on the size and behavior of the spawners and the quality of the spawning area. Large fish make large redds; tolerance of nearby fish varies by species; and poor-quality spawning areas may force females to make several redds. Redds range in size from 0.6 m² to more than 10 m² for anadromous salmonids, and from 0.09 m² to 0.9 m² for smaller nonanadromous trout and salmon (Table 4.4).

Many salmonids prefer to spawn in the transitional area between pools and riffles (Hazzard 1932; Hobbs 1937; Smith 1941; Briggs 1953; Stuart 1953). Tautz and Groot (1975) reported that chum salmon spawned in an accelerating flow, such as that found at a pool–riffle transition. By placing crystals of potassium permanganate on the gravel surface, Stuart (1953) demonstrated the presence of downwelling currents in these transitional areas (Figure 4.7) and noted that the gravel there was easy to excavate and relatively free of silt and debris. Vaux (1962, 1968) reported that downwelling currents normally occurred in areas where the streambed was convex (such as the pool–riffle transition), and upwelling currents occurred in concave areas (such as the downstream end of a riffle).

The density of redds in streams depends on the amount of stream area suitable for spawning, the number and size of spawners, and the area required for each redd. In two Lake Michigan tributaries with alternating pool–riffle habitat, the densities of spawning chinook salmon ranged from about 80 to 250 fish per hectare of stream area (Carl 1984). The average velocities at the preferred spawning sites in the two streams

TABLE 4.4.—Average area of salmonid redds and area recommended per spawning pair of fish in channels.

| Species	Average area of redd (m²)	Area recommended per spawning pair[a] (m²)	Source
Chinook salmon	9.1–10.0		Neilson and Banford (1983)
Spring chinook salmon	3.3	13.4	Burner (1951)
Spring chinook salmon	6.0		Reiser and White (1981a)
Fall chinook salmon	5.1	20.1	Burner (1951)
Summer chinook salmon	5.1	20.1	Burner (1951)
Summer chinook salmon	9.4		Reiser and White (1981a)
Coho salmon	2.8	11.7	Burner (1951)
Chum salmon	2.3	9.2	Burner (1951)
Sockeye salmon	1.8	6.7	Burner (1951)
Pink salmon	0.6	0.6	Hourston and MacKinnon (1957)
Pink salmon	0.6–0.9		Wells and McNeil (1970)
Steelhead	5.4		Orcutt et al. (1968)
Steelhead	4.4		Hunter (1973)
Steelhead	4.4		Reiser and White (1981a)
Rainbow trout	0.2		Hunter (1973)
Cutthroat trout	0.09–0.9		Hunter (1973)
Brown trout	0.5		Reiser and Wesche (1977)

[a] Modified from Clay (1961).
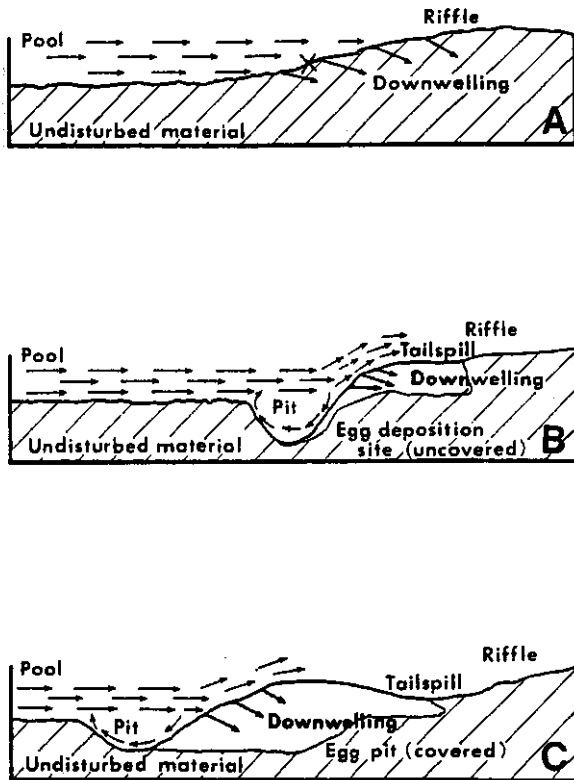
FIGURE 4.7.—Longitudinal sections of a spawning area. (From Reiser and Wesche 1977.) (A) Convexity of the substrate at the pool–riffle transition induces downwelling of water into the gravel. The area likely to be used for spawning is marked with a ×. (B) Redd construction results in negligible currents in the pit (facilitating egg deposition) and increased currents over and through (downwelling) the tailspill. (C) Egg-covering activity results in the formation of a second pit upstream, which may also be used for spawning. Increased permeability and the convexity of the tailspill substrate induces downwelling of water into the gravel, creating a current past eggs. The current brings oxygen to the eggs and removes metabolic wastes.

were 0.42 m/s and 0.50 m/s—similar to those reported by Burner (1951) in the Toutle River, Washington. In the Nechako River, British Columbia, Neilson and Banford (1983) reported that the area of chinook salmon redds averaged 9.1 and 10.0 m^2 and that densities were 1 redd per 235 m^2 and 1 per 112 m^2 in two areas with water depths of at least 0.45 m (the shallowest water in which redd construction was seen). Water depth in the deepest part (pit) of 47 completed redds was 0.46–1.20 m (mean, 0.87 m). Water velocity over the pit of the redds was 15–100 cm/s (mean, 56 cm/s). In a small Oregon coastal tributary, coho salmon constructed 1.7 redds per female and produced a density of 194 redds per hectare of stream (R. A. House, U.S. Bureau of Land Management, unpublished data).

The number of redds that can be built in a stream depends on the amount of suitable spawning habitat and the area required per spawning pair of fish (Reiser and Ramey 1984, 1987; IEC Beak 1984; Reiser 1986). The area suitable for spawning (defined by water depth, velocity, and size of substrate) is usually less than the total area of gravel substrate in the stream, and spatial requirements for each spawning pair may exceed the area of a completed redd. Surface areas of redds can be readily measured, but the spatial requirement for each spawning pair may require additional information such as area of suitable spawning habitat, number of spawners in a given area, and the size and behavior of spawners. Burner (1951) suggested that a conservative estimate of the number of salmon a stream could accommodate could be obtained by dividing the area suitable for spawning by four times the average area of a redd.

In an Oregon stream, gravel substrate made up 25% of the total stream area, but only 30% of that gravel substrate was suitable for spawning by coho salmon (R. A. House, unpublished data). The main stem of the Tucannon River in southeastern Washington contained nearly 200,000 m^2 of gravel substrate (D. W. Kelley and Associates 1982); however, only a small fraction of the river bed was suitable for anadromous fish spawning in the judgment of one of us (T.C.B.), who surveyed 9,000 linear meters of the river and estimated that 3,200 salmon or steelhead redds could be constructed without serious superimposition of redds. If the total area of gravel substrate in the stream (200,000 m^2) had been divided by the average size of salmon or steelhead redds (about 5 m^2), the capacity of the river would have been erroneously estimated to be about 40,000 redds. If Burner's (1951) formula (four times the average redd area) had been used, the estimate would be about 10,000 redds. Much of the river was unsuitable for spawning because water depths and velocities were outside the range acceptable to spawning salmon.

Water Depth and Velocity

Preferred water depths and velocities for various spawning salmonids have been determined from measurements of water depth and velocity at redds (Cope 1957; Sams and Pearson 1963; Orcutt et al. 1968; Thompson 1972; Hooper 1973; Hunter 1973; Smith 1973; Reiser and Wesche 1977; Reiser and White 1981a; Neilson and Banford 1983; Shepherd et al. 1986b). Water depths measured at redd sites varied with species and size of fish and ranged from 6 to 300 cm. In general, the water was at least deep enough to cover the fish during spawning; large salmon required 15–35 cm and smaller trout 6–10 cm (Table 4.5). Many fish spawned in water deeper than necessary to submerge them, but it is not known if the fish preferred the greater depths or were merely using what was available. Water

TABLE 4.5.—Water depth, velocity, and substrate size criteria for anadromous and other salmonid spawning areas.

Species	Depth (cm)	Velocity (cm/s)	Substrate size (cm)	Source
Fall chinook salmon	≥24	30–91	1.3–10.2[a]	Thompson (1972)
Spring chinook salmon	≥24	30–91	1.3–10.2[a]	Thompson (1972)
Summer chinook salmon	≥30	32–109	1.3–10.2[a]	Reiser and White (1981a)
Chum salmon	≥18	46–101	1.3–10.2[a]	Smith (1973)
Coho salmon	≥18	30–91	1.3–10.2[b]	Thompson (1972)
Pink salmon	≥15	21–101	1.3–10.2[a]	Collings (1974)
Sockeye salmon	≥15	21–101[b]	1.3–10.2[a]	[b]
Atlantic salmon	≥25	25–90		Beland et al. (1982)
Kokanee	≥6	15–73		Smith (1973)
Steelhead	≥24	40–91	0.6–10.2[c]	Smith (1973)
Rainbow trout	≥18	48–91	0.6–5.2	Smith (1973)
Cutthroat trout	≥6	11–72	0.6–10.2	Hunter (1973)
Brown trout	≥24	21–64	0.6–7.6[c]	Thompson (1972)

[a] From Bell (1986).
[b] Estimated from criteria for other species.
[c] From Hunter (1973).

velocities at the redd sites ranged from 3 to 152 cm/s, but most were from 20 to 100 cm/s (Table 4.5).

Measurements of depth and velocity were usually taken at the upstream edge of the redd because that point most closely approximated conditions before the redd was constructed and reflected the depths and velocities selected by the fish. Two locations in the water column have been used for making estimates of preferred velocity: 0.6 × depth from the surface to the streambed, and nose velocity (which approximates the location of the fish close to the bed surface). Most velocity criteria have been developed for 0.6 × depth. The ranges of preferred depths and velocities have been defined in a variety of ways. Thompson (1972) used the depths and velocities within a 90–95% confidence interval. Hunter (1973) used the middle 80–90% of the measurements. Smith (1973) used a two-sided tolerance limit within which there was 95% confidence that 80% of the measurements would occur within a normal distribution. Others have simply listed the ranges of depth and velocity measured.

More recently, investigators have developed a series of index curves to depict the suitability of selected variables for different species of fish and life history stages (Figure 4.8). Such curves, used primarily in IFIM, have usually been developed from empirical measurements of depth, velocity, and substrate at the redd site. The curves were based on the assumption that fish select areas in a stream with optimal combinations of physical and hydraulic conditions. The development and limitations of these types of curves were discussed by various investigators (Bovee and Cochnauer 1977; Waters 1976; Baldridge and Amos 1982; Bovee 1982, 1986; Theilke 1985; EA Engineering, Science and Technology, Inc. 1986).

Substrate

The suitability of gravel substrate for spawning depends mostly on fish size; large fish can use larger substrate materials than can small fish. Bell (1986) stated that substrate for anadromous salmon and trout should range from 1.3 to 10.2 cm

5314

FIGURE 4.8.—Suitability index curves for average substrate particle size and temperature, and use curves for mean current velocity in the water column and water depth, in a spawning area used by chinook salmon. Solid line indicates spawning, dashed line incubation. (Redrawn from Raleigh et al. 1986.)
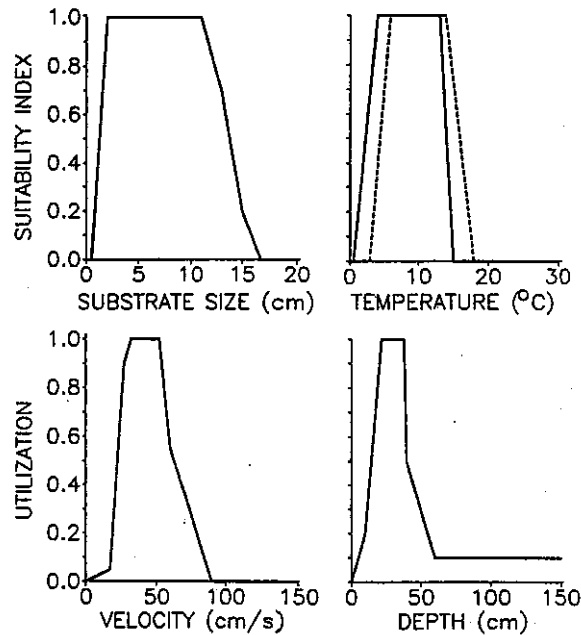
in diameter (Table 4.5). For smaller fish, other investigators have recommended that the materials not exceed 5.2 or 7.6 cm, depending on size of the fish. The criteria presented above are in general agreement with the sizes of substrate particles found in redds (Orcutt et al. 1968; Hooper 1973; Hunter 1973; Smith 1973; Reiser and Wesche 1977). Salmon have been observed spawning in areas with substrate particles larger than 30 cm, but most often in areas where the majority of particles were smaller than 15 cm (Shepherd et al. 1986b).

To determine the composition of substrate used by salmonids, investigators have collected substrate samples from active redds or known spawning areas and graded them through a series of sieves (Burner 1951; Cope 1957; Warner 1963; Orcutt et al. 1968; Hunter 1973; Reiser and Wesche 1977; Tagart 1976; Corley and Burmeister 1979; Huntington 1985). In such studies, various techniques have been used for the collection of substrate materials (McNeil and Ahnell 1964; Tagart 1976; Walkotten 1976; Platts and Penton 1980; Lotspeich and Everest 1981) and for their characterization (Platts et al. 1979b; Lotspeich and Everest 1981; Shirazi and Seim 1981; Tappel and Bjornn 1983). The particle makeup of redds or spawning areas has been characterized by the proportions within specified size ranges (Tappel and Bjornn 1983), the geometric mean particle diameter (dg: Shirazi and Seim 1981), and the Fredle index (Fi: Lotspeich and Everest 1981).

Substrates used in artificial spawning channels represent the particle sizes best suited for selected species in the judgment of those who designed the channels. Gravel from 2 to 10 cm in diameter was used in the Robertson Creek (British Columbia) spawning channels for pink, coho, and chinook salmon (Lucas 1960). Gravel from 0.6 to 3.8 cm was used in the Jones Creek (British Columbia) spawning channel for anadromous fish (MacKinnon et al. 1961). The Tehama–Colusa spawning channels in California, designed primarily for chinook salmon,

contained gravel 1.9–15.2 cm in diameter (Pollock 1969). Bell (1986) stated that, in general, up to 80% of the substrate in artificial spawning channels should be gravel with diameters of 1.3–3.8 cm; the balance should be of sizes up to 10.2 cm.

Cover

Cover for salmonids waiting to spawn or in the process of spawning can be provided by overhanging vegetation, undercut banks, submerged vegetation, submerged objects such as logs and rocks, floating debris, deep water, turbulence, and turbidity (Giger 1973). Cover can protect fish from disturbance and predation and also can provide shade. Some anadromous fish—chinook salmon and steelhead, for example—enter freshwater streams and arrive at the spawning grounds weeks or even months before they spawn. If the holding and spawning areas have little cover, such fish are vulnerable to disturbance and predation over a long period. Nearness of cover to spawning areas may be a factor in the selection of spawning sites by some species. In three studies, for example, brown trout selected spawning areas that were adjacent to undercut banks and overhanging vegetation (Johnson et al. 1966; Reiser and Wesche 1977; Witzel and MacCrimmon 1983).

Incubation

Although incubation is inextricably tied to spawning, the habitat requirements of embryos during incubation are different from those of spawning adults and thus warrant a separate discussion. When an adult fish selects a spawning site, it is also selecting the incubation environment. Successful incubation of embryos and emergence of fry, however, depend on many extragravel and intragravel chemical, physical, and hydraulic variables: DO, water temperature, biochemical oxygen demand (BOD) of material carried in the water and deposited in the redd, substrate size (including the amount of fine sediment), channel gradient, channel configuration, water depth (head) above the redd, surface water discharge and velocity, permeability and porosity of gravel in the redd and surrounding streambed, and velocity of water through the redd. Chapman (1988) reviewed the literature and discussed the primary factors involved in the incubation of salmonid embryos.

The relations between number of spawners, eggs deposited in redds, and juveniles that emerge from the redds take a variety of forms, depending on the species, life history, stream, and incubation conditions. The number of eggs deposited may increase linearly with the number of spawners as long as the amount of suitable spawning area is not limiting, but level off when suitable habitat becomes in short supply. Usually the number of fry emerging is directly related to the number of eggs deposited; if these two numbers are plotted against each other, differences in the linear slope between areas or streams probably reflect differing qualities of the incubation environment. Some species such as pink or chum salmon occasionally aggregate in extraordinarily large numbers on limited spawning grounds; if redds are superimposed and high egg densities result in oxygen depletion and poor incubation conditions, the number of emerging fry could be inversely related to the number of spawners.

Substrate

Streambed particles in the redd at the end of spawning, and organic and inorganic particles that settle into the redd and surrounding substrate during incubation, affect the rate of water interchange between the stream and the redd, the amount of oxygen available to the embryos, the concentration of embryo wastes, and the movement of alevins (especially when they are ready to emerge from the redd). During redd construction and spawning, the spawners displace streambed particles, deposit eggs and sperm in one or several pockets (Hawke 1978; Chapman 1988), and then cover the embryos with hydraulically displaced particles. During this process, fine sediments and organic materials in the stream substrate tend to be washed downstream; consequently the redd environment is as favorable for the embryos immediately after construction as it will ever be. Conditions for embryos within redds may change little or greatly during incubation depending on weather, streamflows, spawning by other fish in the same area at a later time, and fine sediments and organic materials transported in the stream.

Redds may be disturbed by late-spawning fish constructing redds, or by floods that displace the streambed containing the redd. Redds that remain intact during incubation may become less suitable for embryos if inorganic fine sediments (Figure 4.9) and organic materials are deposited in the interstitial spaces between the larger particles. The fine particles impede the movement of water and alevins in the redd, and the organic material (or the microbe community on it) consumes oxygen during decomposition; if the oxygen is consumed faster than the reduced intragravel water flow can replace it, the embryos or alevins will asphyxiate.

The redd construction process reduces the amounts of fine sediments and organic matter in the pockets where eggs are deposited (McNeil and Ahnell 1964; Ringler 1970; Everest et al. 1987a). If fine sediments are being transported in a stream either as bedload or in suspension, some of them are likely to be deposited in the redd. The amount of fine sediment deposited and the depth to which it intrudes depend on the size of substrate in the redd, flow conditions in the stream, and the amount and size of sediment being transported (Cooper 1965; Beschta and Jackson 1979). In general, intrusion into the redd increases as particle size decreases. When fine sediments are large relative to the spaces (pores) between gravel particles in the redd, they may only settle into the surface layer of the redd, where they can block other sediments from the deeper egg pockets (Hobbs 1937; Beschta and Jackson 1979; Chapman 1988). Under certain conditions, a layer of fine sediments may form above the egg pocket during redd construction or later. Such a layer can be beneficial (if it prevents deposition of fine organic or inorganic materials in the pocket), detrimental (if it impedes emergence of the alevins), or both. Deposition of fine sediments in redds may reduce survival more if it occurs early rather than late in the incubation period (Wickett 1954) because young embryos take up oxygen less efficiently than advanced embryos (Shaw and Maga 1943; Reiser and White 1988).

Depth of the egg pockets below the surface of the streambed varies with the size of fish and the size of streambed material. Large fish like chinook salmon may dig as deep as 43 cm below the streambed surface, but average pocket depths are in the 20- to 30-cm range (Hobbs 1937; Hawke 1978; Chapman 1988). The egg pockets of smaller fish tend to be closer to the streambed surface. Hawke (1978)
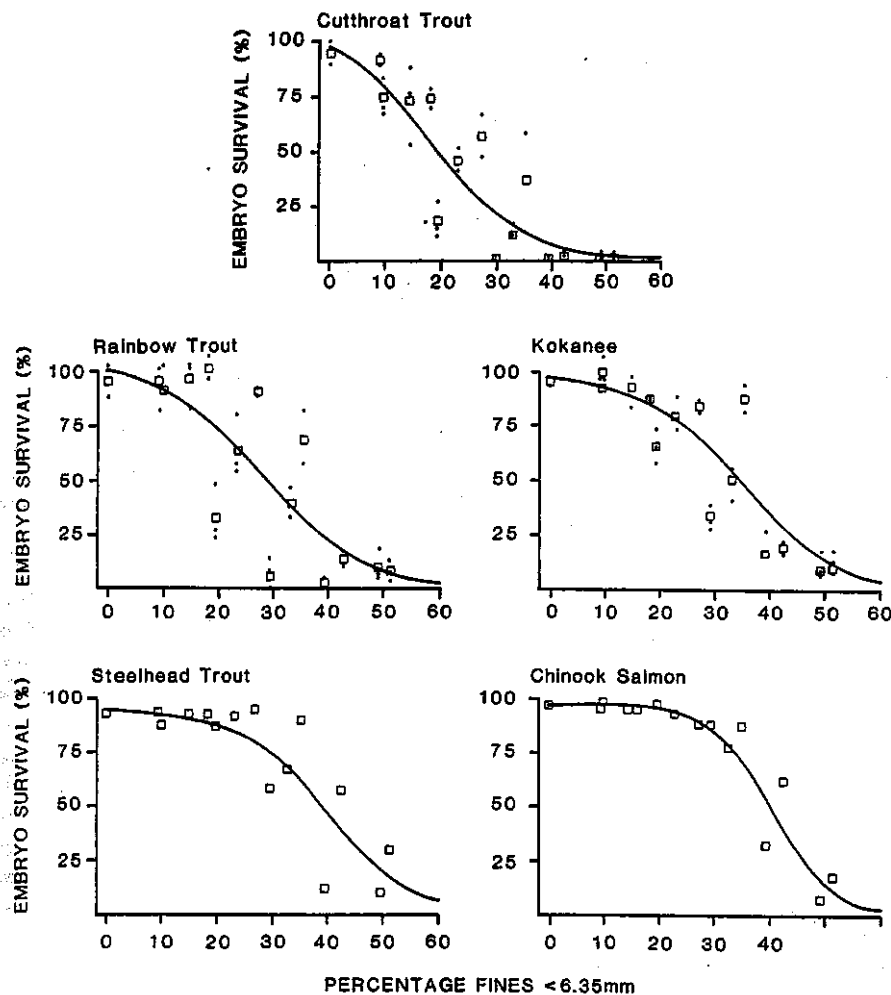
FIGURE 4.9.—Relation between embryo survival and percentage of substrate particles smaller than 6.35 mm for several salmonid species. Chinook salmon and steelhead data are from Tappel and Bjornn (1983); the others are from Irving and Bjornn (1984). Curves were fitted to the data by exponential equations. Squares indicate mean values and dots denote individual replicates.

and Everest et al. (1987a) found that the eggs tended to be near the bottom of the pocket and adjacent to the undisturbed streambed at the bottom of the redd.

During incubation, sufficient water must circulate through the redd as deep as the egg pocket to supply the embryos with oxygen and carry away waste products. Circulation of water through redds is a function of the porosity (ratio of pore space to total volume of redd) of the particles in the redd, hydraulic gradient at the redd, and temperature of the water. Porosity is highest in newly constructed redds and declines during the incubation period as the interstitial spaces acquire fine sediments. The hydraulic gradient through a redd is enhanced by the mounded tailspill created during construction (Figure 4.7). Permeability (ability of
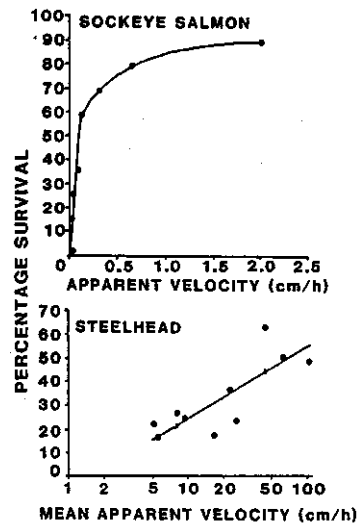
FIGURE 4.10.—Relations between rate of flow of water through a gravel bed and the survival of eyed sockeye salmon eggs (redrawn from Cooper 1965) and steelhead embryos (from Coble 1961).

particles in the redd to transmit water per unit of time) and apparent velocity (volume of water passing through a given area of redd per unit of time) are two commonly used measures of the suitability of a redd for successful incubation of salmonid embryos (Wickett 1954, 1958; Pollard 1955; Terhune 1958; Coble 1961; Vaux 1968). When the permeability and apparent velocity of water in the redd have been too low, reduced embryo survival has been measured for sockeye salmon (Pyper in Cooper 1965), steelhead (Coble 1961), chinook salmon (Gangmark and Bakkala 1960), pink salmon (Wickett 1958), and coho salmon and steelhead (Phillips and Campbell 1961). Survival of embryos decreases as apparent velocities (an indication of the amount of DO reaching the embryos) decrease (Figure 4.10).

Interchange of water between a stream and its streambed particles (Figure 4.7) has been repeatedly demonstrated (Stuart 1953; .Sheridan 1962b; Vaux 1962; Cooper 1965). Sheridan (1962b) showed that groundwater in salmon spawning areas in southeast Alaska contains little oxygen, and that the oxygen content of intragravel water decreases with gravel depth. He concluded that the major source of oxygen in intragravel water was the interchange of that water with the surface flow. Cooper (1965) used dyes to demonstrate the influence of streambed configuration on intragravel flow patterns (Figure 4.11). Wells and McNeil (1970) attributed the high intragravel DO in Alaskan pink salmon spawning beds to high permeability of the substrate and to stream gradient. McNeil and Ahnell (1964) reported high permeabilities (>24,000 cm/h) in salmon spawning areas when sands and silts smaller than 0.84 mm made up less than 5% of the particles, and lower permeabilities (<1,300 cm/h) when they made up more than 15%. In sloughs of the Susitna River in central Alaska, Vining et al. (1985) noted that DO concentrations in intragravel water were consistently lower than in surface waters; in the main channel, however, differences in DO concentrations between surface and intragravel waters were slight.

Apparent velocity of water in redds may increase or decrease with the .depth (and quantity) of the surface water (Reiser and White 1981a). Early evidence of
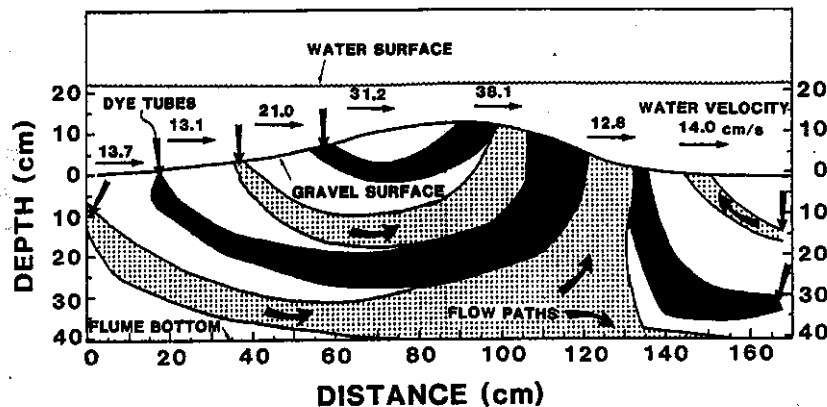
FIGURE 4.11.—Water flow through homogeneous gravel in a flume with a surface similar to that of a new salmon redd. Shadings indicate dispersions of injected dyes. (Redrawn from Cooper 1965.)

this was reported by Wickett (1954), who found a direct relation between gage-height readings in a stream and subsurface flow. Chapman et al. (1982) also observed decreases in apparent velocity when flow decreased from 1,982 to 1,019 m³/s in the Columbia River.

Salmonid embryos have survived dewatering of redds when the dewatering occurred before hatching, temperatures were kept within a suitable range, fine sediment concentrations did not impede air flow, and humidity was maintained near 100% in the redds (Reiser and White 1981b, 1983; Becker et al. 1982; Stober et al. 1982; Becker and Neitzel 1985; Neitzel and Becker 1985). In a moist environment, unhatched embryos are able to get the oxygen they need from air in the redds (Figure 4.12). Several examples have been reported. Hobbs (1937) found that 80% of the brown trout eggs he observed were still alive in redds that had had no surface flow for 5 weeks, and Hardy (1963) found similar results in brown trout redds after 2–5 weeks of dewatering. Chinook salmon embryos survived in redds that had been dewatered for 3 weeks (Hawke 1978). Steelhead and chinook salmon embryos tolerated 1–5 weeks of dewatering (water flowed through the gravel 10 cm below the eggs) with no significant reduction in survival to hatching, alevin quality, growth rate, or quality of emerged fry (Reiser and White 1983). Survival through hatching of dewatered eggs of chinook, chum, pink, and coho salmon and steelhead was high during a study by Stober et al. (1982). Chinook salmon embryos survived 24 h of dewatering when relative humidity was kept at 100%, but all died if humidity was lowered to 90% (Neitzel and Becker 1985).

In streams with substantial groundwater inflows, DO concentrations and flow patterns of intragravel water may not relate in the usual way to substrate composition and permeability (Hansen 1975; Sowden and Power 1985). Upwelling areas are reportedly favored for spawning by chum, sockeye (Lister et al. 1980; Wilson 1984; Vining et al. 1985), and pink salmon (Krueger 1981). Embryo incubation is improved because upwelling reduces the chances that embryos will become dewatered or frozen, provides a stable incubation environment, and increases the water exchange rate past the embryos, thereby enhancing the
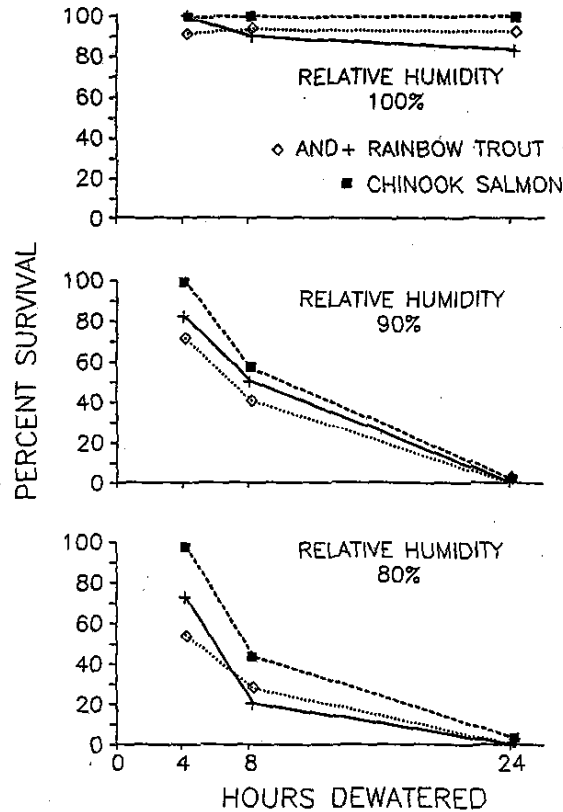
FIGURE 4.12.—Percent survival for dewatered embryos of rainbow trout and chinook salmon under conditions of reduced relative humidity. (From Becker et al. 1986.)

replenishment of DO (if the upwelling water has sufficient amounts) and removal of metabolic waste (Vining et al. 1985).

Egg densities in natural redds are relatively low compared to those in artificial culture facilities; they typically do not affect embryo and alevin survival unless the incubation environment is of marginal quality. If a large chinook salmon deposited 5,000 eggs in a single redd that covered 10 m^2, the density in that redd would be 500 eggs/m^2. However, the density in the actual egg pocket or pockets would be higher, perhaps as high as 2,000–5,000 eggs/m^2 if most of the eggs were deposited in one or two pockets. McNeil (1969) reported that production of pink salmon fry approached 500 fry/m^2 of spawning area when egg deposition was 2,000–3,000 eggs/m^2. In shallow matrix incubators, Kapuscinski and Lannan (1983) found that chum salmon could be incubated at densities as high as 43,000 eggs/m^2 without sacrificing quality of the fry produced.

Once incubation is complete and the alevins are ready to emerge from the redd and begin life in the stream, they must move from the egg pocket up through interstitial spaces to the surface of the streambed. Nunan and Noakes (1985) concluded that emergence of salmonid alevins was a response primarily to gravitational cues rather than to light or intragravel water flow. Emergence can be a problem if the interstitial spaces are not large enough to permit passage of the alevins. In laboratory studies, alevins of chinook salmon and steelhead (Bjornn
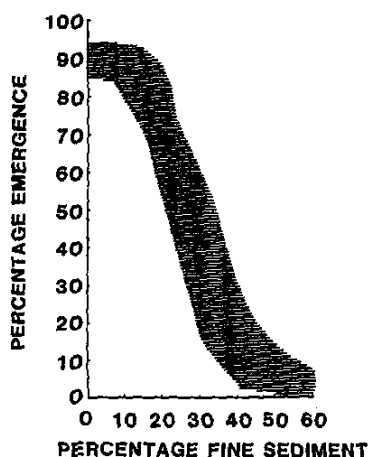
FIGURE 4.13.—Percentage emergence of swim-up fry placed in gravel–sand mixtures in relation to the percentage of sediment smaller than 2–6.4 mm in studies by Bjornn (1968), Phillips et al. (1975), Hausle and Coble (1976), and McCuddin (1977). The stippled area includes data from eight tests on brook trout, steelhead, and chinook and coho salmon.

1968) and coho salmon and steelhead (Phillips et al. 1975) had difficulty emerging from gravel-filled troughs when the percentage of fine sediments exceeded 30–40% by volume (Figure 4.13). Particle sizes that reduce embryo survival and impede emergence have been defined as those less than 6.4 mm (Bjornn 1968; McCuddin 1977), less than 4.6 mm (Platts et al. 1979b), less than 3.3 mm (Koski 1966), less than 2.0 mm (Hausle and Coble 1976), and less than 0.84 mm (McNeil and Ahnell 1964; Hall and Lantz 1969; Cloern 1976; Tagart 1976). Witzel and MacCrimmon (1981) tested rainbow trout in vertical-flow incubators filled with particles of 2, 4, 8, 16, and 26.5 mm, and found that emergence was impeded when particles were less than 8 mm in diameter. Stowell et al. (1983) defined the harmful size range of particles as those less than 6.4 mm, when at least 20% were less than 0.84 mm in diameter. As we previously mentioned, the particle size composition of redds can be characterized in numerous ways (Platts et al. 1979b; Lotspeich and Everest 1981; Shirazi and Seim 1981; Tappel and Bjornn 1983).

Fine sediments that impede intragravel flow and alevin movements may also affect the size of emergent fry (Koski 1966, 1981; Phillips et al. 1975; Tappel and Bjornn 1983; Tagart 1984; MacCrimmon and Gots 1986) and the time of emergence (Koski 1966, 1975; MacCrimmon and Gots 1986), but such effects were not seen in all studies (Hausle and Coble 1976; McCuddin 1977). Silver et al. (1963) reported that the size of newly emerged steelhead and chinook salmon depended on apparent velocities, even at velocities as high as 740–1,350 cm/h. Shumway et al. (1964) found that reduced velocities (3–10 cm/h) resulted in decreased size of fry at all DO levels tested (2.5–11.5 mg/L), and that hatching was delayed at low DO concentrations.

Dissolved Oxygen

Critical concentrations of DO that barely satisfy respiratory demands have been experimentally determined for salmonid embryos at different developmental stages (Table 4.6). Alderdice et al. (1958) found that embryos generally were most sensitive to hypoxial conditions during the early stages of development, when they had received 200–390 temperature units (a temperature unit is one degree

TABLE 4.6.—Critical levels of dissolved oxygen (DO; minimum that satisfies respiratory demand) for salmonid embryos at various stages of development.

Species	Stage of development	Age (d)	Critical DO (mg/L)
Chum salmon	Pre-eyed	0	0.72
(Wickett 1954)	Pre-eyed	5	1.67
	Pre-eyed	12	1.14
	Faintly eyed	85	3.70
Chum salmon		<1	0.72[a]
(Alderdice et al.		<1	1.67[a]
1958)		4	1.14[a]
		12	3.96
		16	3.70[a]
		27	5.66
		35	6.60
	Nearly hatching	45	7.19
Atlantic salmon	Died		0.76
(Lindroth 1942)	Nearly hatching		5.80
	Hatching		10.00
Atlantic salmon	Eyed	25	3.1
· (Hayes et al. 1951)	Hatching	50	7.1

[a] From Wickett (1954).

above zero for one day). Wickett (1954) showed that larval development during the early stage of development depended wholly on diffusion for satisfying oxygen requirements. Once the circulatory system is functional, oxygen transfer to the embryo becomes more efficient.

Embryos may survive when DO concentrations are below saturation (but above the critical level), but their development often deviates from normal. Doudoroff and Warren (1965) found that when DO was below saturation throughout development, embryos were smaller than usual and that hatching was either delayed or premature. Alderdice et al. (1958) showed that low DO concentrations in the early stages of development of chum salmon delayed hatching and increased

FIGURE 4.14.—Relation between mean length of steelhead sac fry when hatched and dissolved oxygen concentration at which the embryos were incubated, for several water velocities during incubation and a temperature of 9.5°C. (From Silver et al. 1963.)
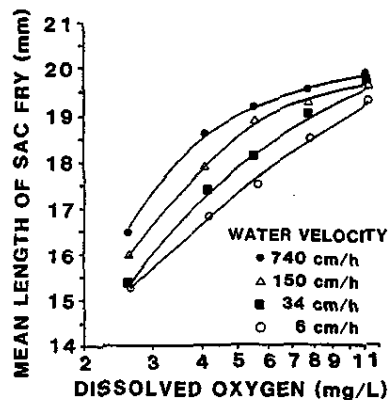
TABLE 4.7.—Characteristics of sockeye salmon alevins at hatching after embryos were incubated in water at three oxygen concentrations. (From Brannon 1965.)

Characteristic	O₂ concentration (mg/L)		
	3.0	6.0	11.9
Temperature units[a] to 50% hatching	670	670	670
Length (mm)	16.3	18.6	19.7
Yolk-sac shape	Spherical	Longitudinal	Longitudinal
Pigmentation	Lightly on head	On head and starting on back	On head and back
Visibility of the dorsal and anal fin rays	Not visible	Distinguishable	Readily visible
Caudal fin development	Forming	Forming	Well advanced

[a] Degree-days above 0°C.

the incidence of morphological anomalies. Silver et al. (1963) reported that newly hatched steelhead and chinook salmon alevins were smaller and weaker when they had been incubated as embryos at low and intermediate DO concentrations than when they were incubated at higher concentrations (Figure 4.14). Shumway et al. (1964) found that reduced DO lengthened the incubation period of coho salmon embryos, which hatched into smaller alevins than normal. Brannon (1965) found differences in length and other anatomical features among newly hatched sockeye salmon fry that had developed at three DO levels (Table 4.7); however, weights of the emergent fry were similar among treatment groups.

In field studies, survival of steelhead embryos (Coble 1961) and coho salmon embryos (Phillips and Campbell 1961) was positively correlated with intragravel DO in redds (Figure 4.15). Phillips and Campbell (1961) concluded that intragravel DO must average 8 mg/L for embryos and alevins to survive well. Stober et al. (1982) and Fast and Stober (1984) reported that newly hatched alevins in the gravel are able to detect oxygen gradients and migrate to areas containing more DO.

Intragravel DO concentrations are functions of many factors: water temperature, surface and intragravel water interchange, apparent velocity of water flow in
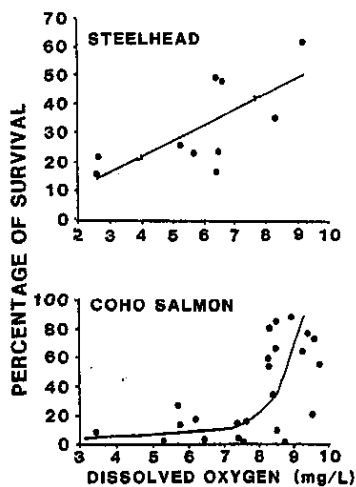

FIGURE 4.15.—Relation between dissolved oxygen concentration and survival of steelhead embryos (from Coble 1961) and coho salmon embryos (Phillips and Campbell 1961) in natural redds.

the redd, permeability of the substrate, and oxygen demand of organic material in the redd, among others. Hall and Lantz (1969), Ringler and Hall (1975), and Moring (1975a) reported that intragravel DO concentrations were reduced in some Oregon streams after adjacent areas had been logged. They attributed such reductions to elevated stream temperatures after removal of the riparian canopy and to increased concentrations of fine sediment that reduced substrate permeability and apparent velocity. Tagart (1976) and Reiser and White (1981b) found direct relations between DO and permeability and inverse relations between DO and percentage of fines in stream substrates. Coble (1961) generalized his experience with this subject by stating that when apparent water velocities are low, DO is low; when they are high, DO is usually high.

All streams transport particulate and dissolved organic matter. The amount transported and the timing of transport varies with the productivity of the stream, the source and type of organic matter, and streamflow (Fisher and Likens 1973; Hobbie and Likens 1973; Liaw and MacCrimmon 1977; Naiman and Sibert 1978; Bilby and Likens 1979; Dance et al. 1979; Naiman and Sedell 1979). Organic matter that settles into redds can reduce the DO concentration as it decomposes; the extent of oxygen depletion depends on the amount and type of organic debris (Hargrave 1972) and the chemical, physical, and hydraulic characteristics (DO content, temperature, permeability, and reaeration capability) of the stream and its substrate. Excessive recruitment of organic material to a stream can result in reduced DO concentrations and intragravel water flow, leading to reduced survival of incubating embryos (Olssen and Persson 1986).

Although DO concentrations required for successful incubation depend on both species and developmental stage, we recommend that concentrations should be at or near saturation, and that temporary reductions should drop to no lower than 5.0 mg/L, for anadromous salmonids. Apparent velocities of water flowing through redds also must be maintained at acceptable rates because high DO alone does not guarantee optimum embryo development. In redds with similar DO concentrations, but different apparent velocities, embryonic development may be better in the redds with the higher rate of water exchange (Coble 1961). Mathematical models have been developed to estimate apparent velocity in redds (Bovee and Cochnauer 1977) and to assess transfer of DO between the stream and substrate (Chevalier and Carson 1985), concentrations of intragravel DO (Chevalier and Murphy 1985), salmonid egg respiration (Carson 1985), and fry emergence (Miller 1985).

Temperature

Water temperature during incubation affects the rate of embryo and alevin development and the capacity of water for dissolved oxygen, and (beyond certain limits) survival of the young fish. There are upper and lower temperature limits (thresholds) for successful incubation of salmonid eggs (Table 4.3). In general, the higher the temperature (within the acceptable range), the faster the rate of development and the shorter the incubation period and time to emergence. The amount of time required for embryos to hatch and for alevins to emerge from redds varies by species and perhaps by location. For example, time to 50% hatch for Pacific salmon species ranges from 115 to 150 d at 4°C and from 35 to 60 d at 12°C; coho salmon require the least time and sockeye salmon the most (Alderdice
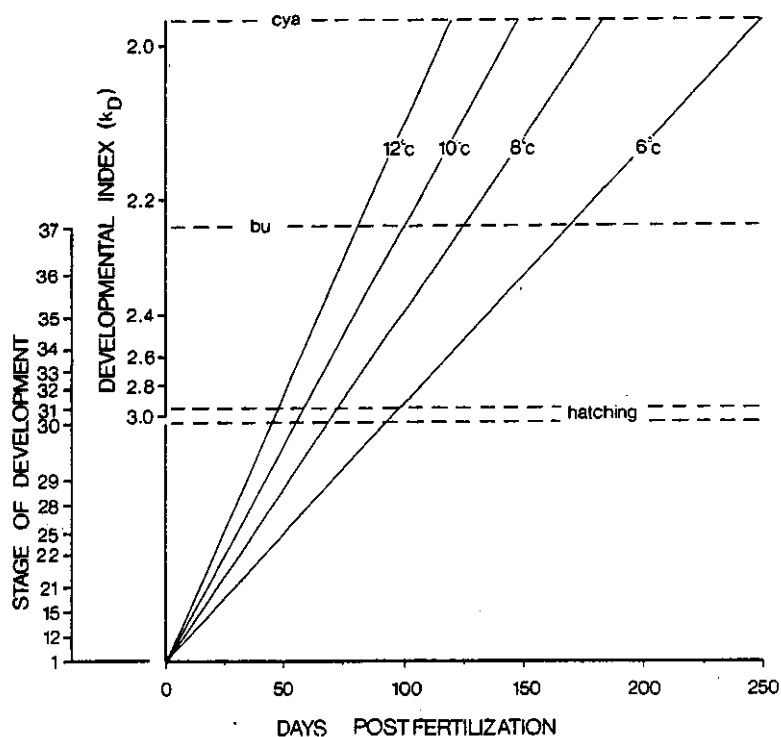
FIGURE 4.16.—Effect of temperature on the development of chinook salmon according to Vernier's (1969) stages of development and Bams's (1970) developmental index (k_D) in a graph from Heming (1982). In the graph, bu = button-up stage of development and cya = complete yolk absorption.

and Velsen 1978; Tang et al. 1987; Velsen 1987). Steelhead and rainbow trout require about 85 d at 4°C and 26 d at 12°C to reach 50% hatch. Heming (1982) graphed stage of development against time (Figure 4.16) for chinook salmon raised experimentally at several temperatures; from these graphs, he estimated emergence at 192 d at 6°C and 85 d at 12°C, about twice the time to 50% hatch. In field studies on the Columbia River, Chapman et al. (1982) found that Heming's curves were reasonable predictors of the time chinook salmon fry emerge. Time to hatch for lake trout is similar to that of chinook salmon, 80–90 d at 6°C (Dwyer 1987).

In many streams in which salmonids spawn, winter temperatures are lower than the 4.4°C minimum recommended for incubation in Table 4.3, but the eggs develop normally because spawning and initial embryo development occur when temperatures are within the suitable range. Combs and Burrows (1957) and Combs (1965) reported that pink and chinook salmon embryos could tolerate long periods of low temperature if the initial temperature was above 6.0°C and embryogenesis had proceeded to a critical developmental stage before the onset of lower water temperatures. Combs and Burrows (1957) believed that salmon produced from eggs deposited in water colder than 4.5°C would be less viable than fish produced from eggs spawned in warmer water. Wangaard and Burger (1983) reported 3.4°C as the temperature below which some newly spawned chum and pink salmon

embryos would be killed. Bailey and Evans (1971) defined the lower threshold temperature for pink salmon embryos as 4.5°C. In a summarization of available data, Velsen (1987) reported high mortalities for all Pacific salmon and steelhead when water temperatures were lower than 2–3°C after fertilization. Jungwirth and Winkler (1984) reported that embryos of fall-spawning fishes develop more slowly at any temperature, and have lower upper lethal incubation temperatures, than progeny of spring spawners. Incubation temperatures can also affect the size of newly hatched alevins. When Beacham and Murray (1985) incubated chum salmon eggs at temperatures of 4, 8, and 12°C, the newly hatched alevins incubated at 4°C were the longest, and those at 12°C were the heaviest, but there was no difference in size at emergence. Reiser and White (1981b) observed similar early differences among chinook salmon, which then reached equivalent sizes after 57 d of rearing.

Intragravel water temperatures are influenced by temperatures of the surface water, the thermal mass of the substrate, and the interchange rate of surface and intragravel water. Ringler and Hall (1975) observed that temperatures of intragravel water reached diurnal maxima 2–6 h after those of surface waters in an Oregon stream. Chapman et al. (1982) observed temperature lags of 2–8 h between surface and intragravel waters. There are seasonal as well as daily differences: intragravel water temperatures often are lower than surface water temperatures during summer, and higher during winter (Shepherd et al. 1986a). When salmonids spawn in areas close to groundwater inflows (Hansen 1975; Witzel and MacCrimmon 1983; Wilson 1984; Vining et al. 1985), embryos experience reduced extremes in water temperatures than they would otherwise.

Incubating embryos and alevins can be killed when frazil or anchor ice forms in streams and reduces water interchange between the stream and the redd. Anchor ice normally forms in shallow water typical of spawning areas and may completely blanket the substrate. Ice dams may impede flow or even dewater spawning areas. When such dams melt, the released water may, floodlike, displace the streambed and scour the redds. In an experiment by Reiser and Wesche (1977), eggs placed in plastic-mesh boxes 15 cm below the surface of the streambed completely froze even though the stream above was more than 13 cm deep. Anchor ice had formed at least twice during the incubation period. Neave (1953) and McNeil (1966b) also reported that embryo survival was poor at freezing temperatures.

Rearing in Fresh Water

The abundance of juvenile salmon, trout, and char in streams is a function of many factors, including abundance of newly emerged fry, quantity and quality of suitable habitat, abundance and composition of food, and interactions with other fish, birds, and mammals. Fausch et al. (1988) reviewed many of the models developed in recent years to predict the abundance of fish in streams from habitat variables. We next discuss variables of habitat quantity and quality, and where possible, list the preferences of juvenile salmonids.

The abundance of older fish generally increases as the abundance of juveniles increases until an upper limit (here termed carrying capacity) is reached. We believe that the relation between the seeding level—the number of young fish emplaced in a stream by adult fish or humans—and the abundance of older fish is
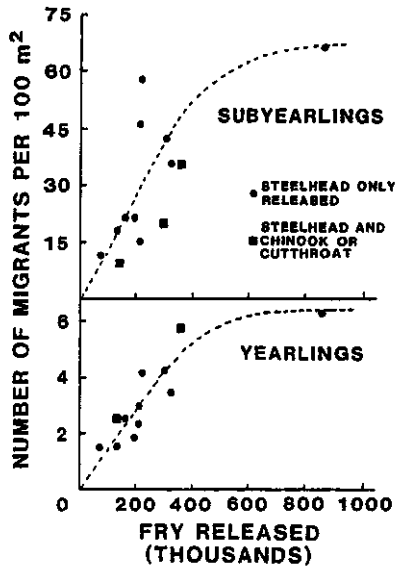
FIGURE 4.17.—Relation between the number of steelhead fry released in Big Springs Creek, Idaho, and the number of subyearling and yearling rainbow trout and steelhead per 100 m² that migrated from the stream. Each point represents one of the 1962–1974 year-classes (1962–1973 for yearlings); curves were fitted by inspection. (From Bjornn 1978.)

asymptotic for most salmonids that spend an extended period in streams. At relatively low seeding levels, environmental conditions that set the carrying capacity of a stream for a given age group of fish will place little constraint on the abundance of juveniles and older fish. As spawner abundance (or stocking) approaches that needed for full seeding, the biotic or physical factors that set the carrying capacity come into full play. Habitat variables we discuss here may set the carrying capacity of streams for salmonid fishes, but interactions among many of the relevant physical and biotic variables have not been well defined. In addition, variables that are important in one stream or season may be relatively unimportant in another.

Changes in spawner abundance and variation in the success of incubation and emergence affect the number of young fish entering a stream. Changes in the abundance of newly emerged fry can result in large or insignificant changes in abundance of older fish, depending on the shape of the reproduction curve and actual fry abundance. In two productive Idaho streams, the abundance of older steelhead was primarily a function of the number of newly emerged juveniles placed in the stream at seeding rates up to about 6 fish/m² (Bjornn 1978) (Figure 4.17). When steelhead were stocked at a rate of 12/m² in Big Springs Creek (right-most point in Figure 4.17), no more subyearlings or yearlings were produced than when 6/m² were stocked—evidence that the carrying capacity had been reached. In the Lemhi River, about the same number of steelhead smolts were produced (75,000–80,000) from releases of 2.5 and 4.6 million newly emerged juveniles—additional evidence that carrying capacity had been achieved. The carrying capacity for chinook salmon in the Lemhi River was not reached during 12 years of study in which natural egg-deposition rates ranged from 2 to 8/m² (Figure 4.18).

In less-productive Idaho streams, seeding rate (abundance of spawners) was the main factor regulating the abundance of juvenile steelhead (Figure 4.19) and chinook salmon when spawner abundance was relatively low. In Marsh Creek,
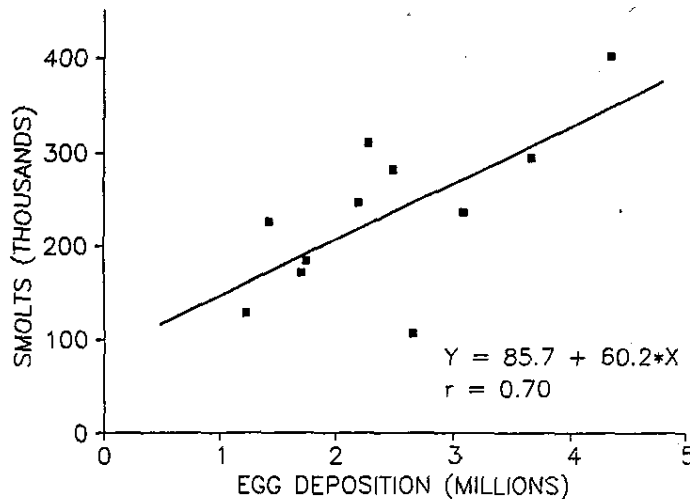
FIGURE 4.18.—Egg deposition (X) by adult chinook salmon in the upper Lemhi River, Idaho, and number of smolt-sized fish (Y) that later migrated past the Lemhi River weir during fall, winter, and spring, 1963–1973. (From Bjornn 1978.)

one of the relatively unproductive streams, the density of juvenile chinook salmon, monitored irregularly over 12 years, was related to spawner abundance over a nearly 20-fold range (Figure 4.20). Sekulich (1980) presented evidence that the summer carrying capacity for naturally produced salmon in the relatively unproductive streams was 2–3 g/m^2, lower than the carrying capacity of at least 13 g/m^2 in the relatively productive Lemhi River (Bjornn 1978). In Pacific coast streams, the biomass of coho salmon averaged 2–3 g/m^2 in several studies (Cederholm and Reid 1987).

The number of chinook salmon smolts produced in two Lake Michigan tributaries with alternating pool–riffle habitats was independent of the threefold difference in spawner densities that occurred in 2 years of study (Carl 1984). Even at their lower density, spawners apparently seeded the rearing area fully (about 80 spawners per hectare, 0.7–2.9 newly emerged fish per square meter).

For a given level of seeding, what factors in the stream environment regulate abundance or set the carrying capacity for juvenile salmonids? Density-independent environmental factors (amount of suitable habitat, quality of cover, productivity of the stream, and certain types of predation) set an upper limit on the abundance of juveniles, and the population is held to that level by interactions that function in a density-dependent fashion (competition and some types of predation). Carrying capacity, and hence fish production, may vary yearly if controlling habitat components, such as streamflow, vary widely from year to year at critical periods such as late summer (Smoker 1955). The carrying capacity of a stream may also vary with the season, differing, for example, between winter and summer (Bjornn 1978), and it may differ for the various life stages of fish.

Environmental factors can affect the distribution and abundance of juvenile salmonids throughout a stream or drainage or within specific segments of streams.
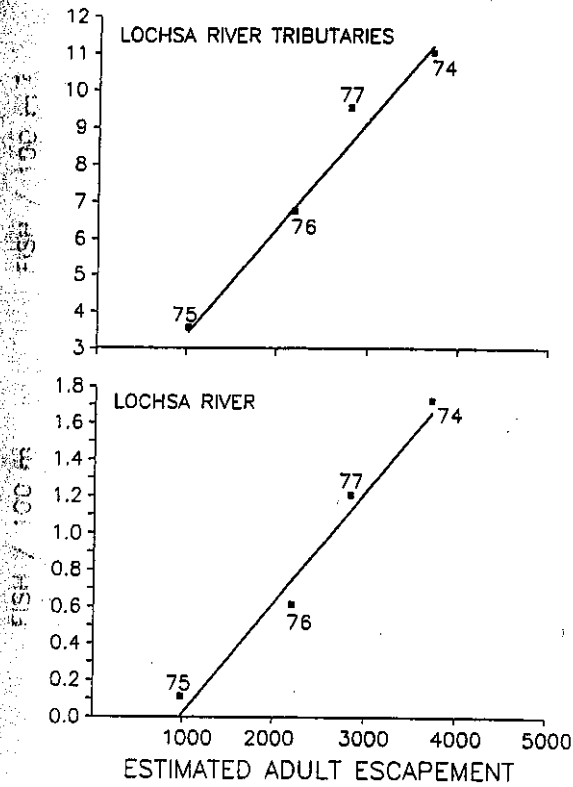
FIGURE 4.19.—Observed density of age-1 steelhead in relation to estimated number of adults returning to the Lochsa River and its tributaries, Idaho, 1974–1977. (Redrawn from Mabbott 1982.)

Temperature, productivity, suitable space, and water quality (turbidity, DO, etc.) are examples of variables that regulate the general distribution and abundance of fish within a stream or drainage. Factors to which fish respond at specific locations in a stream are velocity, depth, substrate, cover, predators, and competitors. Fish often spawn in limited parts of a drainage (sometimes in ephemeral streams), but
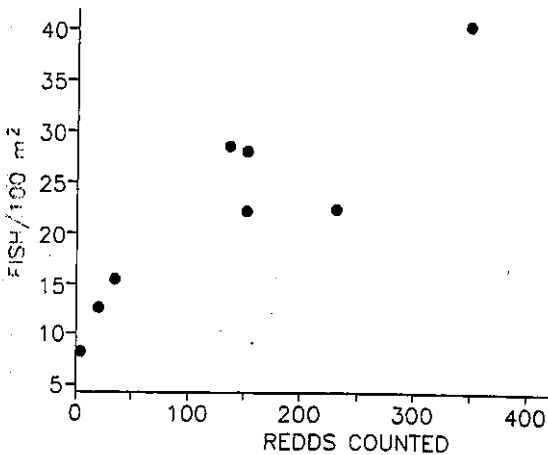

FIGURE 4.20.—Relation between chinook salmon redds counted and density of age-0 juveniles the following summer in an Idaho stream. (Authors' original data.)

5330

the juveniles spread out and occupy most of the areas that are suitable and accessible (Everest 1973; Leider et al. 1986).

All of the general factors must be within suitable ranges for salmonids during the time they use a stream segment; otherwise, no fish will be present and there will be no concern about site-specific factors. Rarely, if ever, are most factors optimum for salmonid production. Often some factors may be near optimum while others are suboptimum but still in a suitable range.

Temperature

Salmonids are coldwater fish with definite temperature requirements during rearing. Water temperature influences the metabolism, behavior, and mortality of fish and the other organisms in their environment (Mihursky and Kennedy 1967). Although fish may survive at temperatures near the extremes of the suitable range, growth is reduced at low temperatures—because all metabolic processes are slowed—and at high temperatures—because most or all food must be used for maintenance. Many salmonids change behavior with increases or decreases in temperature.

Normal water temperatures in salmonid streams vary daily, seasonally, annually, and spatially. Humans have altered temperature patterns by changing riparian zone vegetation, diverting water, building reservoirs, and discharging hot water from power plants. Alterations of natural light and temperature patterns in streams can be beneficial or detrimental, depending on the situation, but the consequences of marked changes in the temperature regime of a stream are not fully understood. Small streams in dense forests of the Pacific Northwest, for example, might be too cold in summer for maximum growth of salmonids (Chapman and Knudsen 1980), but warming the stream by altering the riparian vegetation (Gray and Edington 1969; Narver 1972a; Moring 1975a; Moring and Lantz 1975; Murphy et al. 1981; Johnson et al. 1986; Murphy et al. 1986; Beschta et al. 1987) might not enhance growth unless food abundance can satisfy the increase in fish metabolism and other needs of the fish are met (Brett et al. 1969; Hughes and Davis 1986; Hartman et al. 1987; Holtby 1988a). Care must be taken to avoid unwanted warming of downstream waters and excessive loss of cover (both overhead bank and instream) that may be important in winter as well as in summer (Murphy et al. 1986). In many large streams, temperatures become too warm for salmonids in summer for a variety of reasons, including excessive exposure to the sun.

Temperatures that can be tolerated by fishes have been defined and determined in two ways (Brett 1952; Becker and Genoway 1979): slow heating of fish (to reveal the critical thermal maximum, CTM), and abrupt transfer of fish between waters of different temperature (to show the incipient lethal temperature, ILT). In general, upper lethal temperatures determined by the CTM procedure tend to be higher than those established with the ILT technique. The upper ILT for anadromous Pacific salmon, Atlantic salmon, trout, and char range from about 23 to 29°C, depending on species and acclimation temperature (selected examples are in Table 4.8). Half of the upper lethal values presented in Table 4.8 were taken from Brett (1952), who acclimated fish at 20°C and used 50% mortality at 1,000 min as the end point. Lee and Rinne (1980) reported CTM values of 29–30°C for hatchery stocks of rainbow, brown, and brook trout stocked in Arizona and two

TABLE 4.8.—Lower lethal, upper lethal, and preferred temperatures (°C) for selected species of salmon, trout, and char based on techniques to determine incipient lethal temperatures (ILT) and critical thermal maxima (CTM).

Species	Lethal temperature (°C)		Preferred temperature (°C)	Source	Technique
	Lower lethal[a]	Upper lethal[b]			
Chinook salmon	0.8	26.2	12–14	Brett (1952)	ILT
Coho salmon	1.7	26.0	12–14	Brett (1952)	ILT
		28.8[c]		Becker and Genoway (1979)	CTM
Sockeye salmon	3.1	25.8	12–14	Brett (1952)	ILT
Chum salmon	0.5	25.4	12–14	Brett (1952)	ILT
Steelhead	0.0	23.9	10–13	Bell (1986)	
Rainbow trout		29.4		Lee and Rinne (1980)	CTM
		25.0		Charlon et al. (1970)	ILT
Brown trout		29.9		Lee and Rinne (1980)	CTM
		26.7		Brett (1952)	ILT
Gila trout		29.6		Lee and Rinne (1980)	CTM
Apache trout		29.4		Lee and Rinne (1980)	CTM
Brook trout		29.8		Lee and Rinne (1980)	CTM
		25.8		Brett (1952)	ILT
			14–16	Graham (1949)	
Cutthroat trout	0.6	22.8		Bell (1986)	
Atlantic salmon		27.1		Brett (1952)	ILT
		27.8		Garside (1973)	ILT
Lake trout		25.0		Brett (1952)	ILT

[a] Acclimation temperature was 10°C; no mortality occurred in 5.500 min.
[b] Acclimation temperature was 20°C unless noted otherwise; 50% mortality occurred in 1,000 min.
[c] Acclimation temperature was 15°C.

native trouts (Gila trout and Apache trout) when these fish were acclimated at 20°C and subjected to a temperature change rate of 1.2°C/h. Although some salmonids can survive at relatively high temperatures, most are placed in life-threatening conditions when temperatures exceed 23–25°C, and they usually try to avoid such temperatures by moving to other areas.

Lower lethal temperatures for salmonids depend somewhat on previous acclimation (Brett 1952) but they probably are no lower than −0.1°C (Brett and Alderdice 1958). Temperatures in the range of 1 to 4°C can be lethal if fish acclimated in warmer water are transferred abruptly into the cold water. Under natural conditions, fish are not subjected to cold water (<4°C) without prior acclimation in gradually decreasing temperatures, and thus lower lethal temperatures for most species are near 0°C.

Daily summer temperatures can fluctuate more than 15°C in small streams with flows less than 1 m³/s and little or no shade (Meehan 1970; Bjornn 1978).

Temperatures can increase rapidly in a short distance under direct sunlight: 6°C in 1,000 m within a stream flowing at about 1.4 m³/s in central Idaho, for example (Bjornn et al. 1968). As stream size and water mass increase, daily temperatures of streams fluctuate less and tend to reflect the local climate near the stream.

Many populations of native salmonids respond to natural temperature patterns in streams by moving upstream or downstream when water temperatures become unsuitable. Fish may use a section of stream during one season of the year, but move to other sections at other seasons because temperatures become unsuitable. Salmonids may not always avoid unsuitable temperatures, however, especially if the temperatures change rapidly and are not part of the normal pattern in which the fish evolved. Munson et al. (1980) found that rainbow trout accustomed to feeding in a certain location continued to enter the area after temperatures had been changed to a lethal level.

In small streams where daily maximum temperatures approach upper incipient lethal values, salmonids can thrive if the temperature is high for only a short time and then declines well into the optimum range. In an Idaho stream with daily maximum temperatures up to 24°C that lasted less than 1 h and minimums of 8–12°C, juvenile chinook salmon and steelhead maintained high densities and grew normally (Bjornn 1978). In larger Idaho streams where summer maximum temperatures were 24–26°C, but the minimums were relatively high (15–16°C), most young salmon and trout moved upstream or into tributaries where temperatures were lower (Mabbott 1982).

As water temperatures in temperate-zone streams decline in autumn, salmonids change behavior from mostly feeding and defending territory to hiding and schooling. The winter behavior patterns appear to us to be motivated by security. Fish that were curious and easily approached by divers in summer become wary and often dart from view in winter. Winter water temperatures in streams can range from freezing to relatively moderate, according to geographic and ground-water influences. Temperatures in coastal streams often are moderated by maritime climates. Inland, streams can become filled with flow ice, anchor ice, and ice jams during extreme cold spells. The temperature at which the change in behavior occurs apparently varies by species. Chapman and Bjornn (1969) reported that most of the steelhead and chinook salmon juveniles they tested in winter were visible above the substrate at 6°C but hid at 4°C (Figure 4.21). In a British Columbia stream, juvenile coho salmon and steelhead began shifting to winter positions at about 7°C (Bustard and Narver 1975a). Gibson (1978) found that Atlantic salmon began entering the interstitial spaces of rubble substrate in autumn when water temperatures dropped to 10°C, and most had disappeared at 9°C.

The response of salmonids to the lower temperatures that occur in autumn and winter in temperate streams can vary by species and size of fish. Small fish (<15–20 cm) tend to hide in interstitial spaces in the substrate of streams, or in other forms of cover if available, and may move to shallower water (Bustard and Narver 1975a; Gibson 1978), whereas larger fish may join together in schools and move long distances to find suitable winter habitat. In the Lemhi River drainage, Idaho, a large fraction of the young chinook salmon and steelhead moved downstream from rearing areas after their first summer (Bjornn 1971). The chinook salmon moved down into the Salmon River and even the Snake River
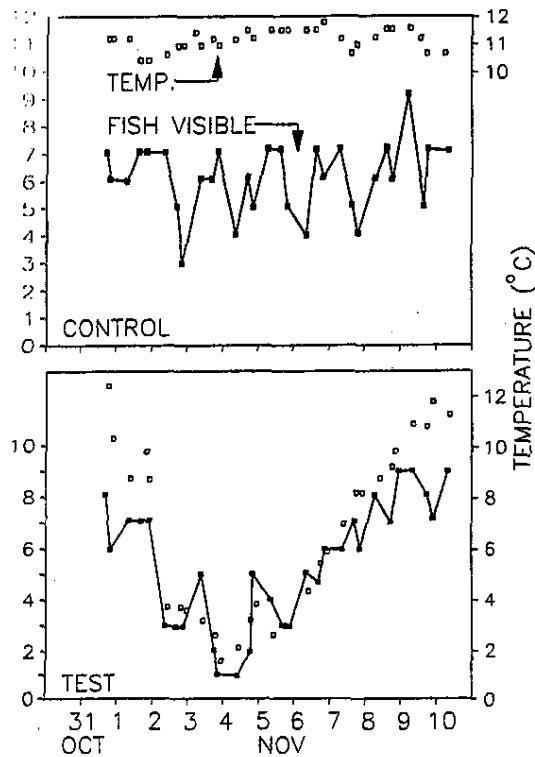
FIGURE 4.21.—Water temperature and number of age-0 steelhead visible above the substrate in test and control vats. (From Chapman and Bjornn 1969.)

(50–200 km) to spend the winter before continuing to the ocean as smolts the following spring. The steelhead moved downstream out of a tributary with a high summer carrying capacity (at least 12 g/m²) but a lower winter carrying capacity, and spent the winter, the next summer, and the following winter in the larger stream before going to the ocean the following spring. Both the chinook salmon and steelhead moved downstream in response to low winter temperatures and a lack of winter cover. Fish migrating downstream in the fall ceased moving when placed in channels with large rock piles (which contained interstitial spaces used in winter) but continued moving downstream when placed in channels without the rock piles (Bjornn and Morrill 1972). In contrast, few juvenile cutthroat trout moved downstream in autumn in tributaries of other Idaho streams where densities were lower (2.1 g/m²) and adequate amounts of suitable winter cover were apparently present (Mauser 1972). On sunny autumn days, the cutthroat trout could be seen in the stream in the afternoon when temperatures approached the daily high (8–10°C), but were not visible in the morning when temperatures were low (3–5°C).

Larger fish that may not be able to use voids in the substrate to hide in winter have been observed joining together in large schools (600 fish) and in some cases moving long distances in fall and spring. In the Coeur d'Alene River of Idaho, Lewynsky (1986) counted fish along transects throughout the summer, fall, and winter; in winter, larger (>20 cm) cutthroat trout moved from dispersed summer feeding stations throughout the river to a few large pools, where they became

much more wary and difficult to approach. The extent of seasonal movements of fish in response to temperature is illustrated by migrations of cutthroat and bull trout more than 100 km downstream in autumn and back upstream in spring and early summer in the Salmon River, Idaho (Bjornn and Mallet 1964). Winter temperatures and ice conditions apparently were unsuitable in the upper portions of the Middle Fork drainage and most of the fish larger than 15 cm moved. Temperatures in the main-stem rivers became marginal in summer for salmonids.

Temperature is one of the factors that contribute to quality of habitat for fish. If temperature is in a tolerable range for the fish, the question of optimum temperature becomes pertinent. Optimum temperature could be defined in relation to a variety of population or individual variables, including temperature preference, growth, efficiency of converting food to tissue, standing crops, and swimming performance. When Brett (1952) placed five species of Pacific salmon in a vertical temperature gradient, they all tended to congregate in the 12–14°C stratum.

Optimum temperatures, measured in terms of fish growth rate and food conversion efficiency, vary with the amount of food available. Brett et al. (1969) reported that growth of yearling sockeye salmon was highest at about 5°C when the daily ration (percent of body weight) available was 1.5%, but shifted to about 15°C when the ration was 6%. At highest temperatures, the growth rate declined regardless of food abundance. Food conversion efficiency peaked at 8–11°C (Brett et al. 1969)—lower than the 15°C associated with maximum growth, optimum metabolic scope for activity, greatest tolerance of oxygen debt, and maximum sustained swimming speed (Brett 1964). After tests with Atlantic salmon, Dwyer and Piper (1987) reported that maximum growth with unlimited food was attained at 16–19°C, but that growth efficiency was highest at 10–16°C.

Similar relations—with variations in the optimum temperature or temperature range—probably exist for other species. The optimum temperature for brook trout, for example, appears to be 14–16°C. Graham (1949), as reported in Mihursky and Kennedy (1967), listed 14–16°C as the temperature preferendum for brook trout, and Beamish (1964) gave 15°C as the temperature for maximum spontaneous activity. Dwyer et al. (1983) reported that brook trout grew most efficiently at 10 and 13°C. Jensen and Johnsen (1986) presented evidence that stocks of fish may be able to adapt to temperatures that might otherwise make their existence unlikely.

Brett et al. (1958) reported that the optimum temperature for sustained swimming was 15°C for sockeye and 20°C for coho salmon (Figure 4.22), and that maximum sustained swimming speeds at these temperatures were 35 and 30 cm/s, respectively. Sustained swimming performance was reduced to about 12 cm/s for sockeye salmon and to 6 cm/s for coho salmon at temperatures near 0°C. Davis et al. (1963) also found that the maximum sustained swimming speed of underyearling coho salmon was higher at 20°C than at 15 or 10°C. In a study of the critical swimming speeds of yearling rainbow trout as a measure of temperature preference, Schneider and Connors (1982) found no significant differences at 10, 15, or 20°C, but swimming performance was reduced at 25°C. The 25°C test temperature was 2°C less than the ILT measured for rainbow trout by Charlon et al. (1970).

The effect of water temperature on fish behavior and the regulation of densities in streams is not well understood, but there is some evidence that densities or
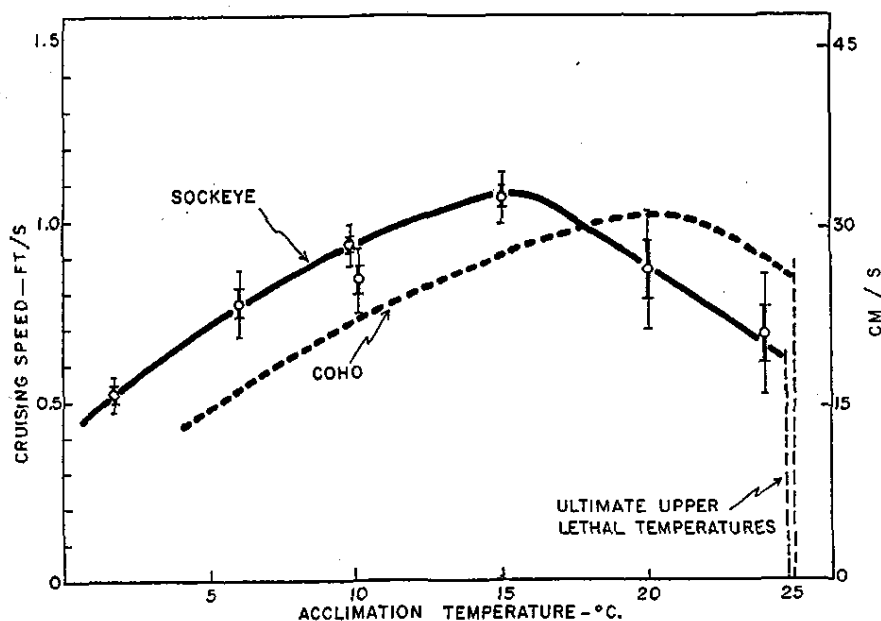
FIGURE 4.22.—Variation in cruising speed among temperature-acclimated underyearling sockeye and coho salmon, adjusted to common mean lengths of 6.9 cm and 5.4 cm, respectively. The fish were cultured under similar conditions and were 4 to 6 months of age. The sockeye salmon data are means (circles), standard errors (heavy vertical bars), and standard deviations. (From Brett et al. 1958.)

even production of fish may be less at high (but suitable) temperatures than at lower ones. In laboratory stream studies, Hahn (1977) found that twice as many steelhead fry remained in channels with daily temperature fluctuations of 8–19°C or a constant temperature of 13.5°C than in a channel held at a constant 18.5°C. At constant 8.5°C, the density of fish was twice that found in channels held at 13.5°C. Hughes and Davis (1986), who studied coho salmon and steelhead in laboratory streams, concluded that a moderate (4°C) increase in temperature could decrease the productivity of streams for those species when food is limiting. Glova (1986) found that habitat use by juvenile coho salmon and cutthroat trout in summer, when temperatures were 13°C, was different from that in winter, when temperatures were colder. When tested separately in summer, most fish of both species took up residence in pools, but, when tested together, most of the coho salmon stayed in pools and cutthroat trout remained in riffles. In winter at temperatures of 3°C, both species, whether together or separate, preferred pools and overhead cover.

Changes in water temperatures resulting from land and water use may affect fish indirectly as well as directly. In a small Vancouver Island stream, coho salmon emerged earlier when winter water temperatures became higher after logging, and detrimental downstream movement of the newly emerged fish occurred when freshets took place soon after emergence (Scrivener and Andersen 1984). Growth rate of coho salmon juveniles was inversely related to density in the stream, and the fish were larger in autumn after logging than before because of the earlier

FIGURE 4.23.—Specific growth rate (percent of body weight per day ± SE) of fingerling coho salmon (5–10 g) in relation to oxygen concentration at 15°C. (From Brett and Blackburn 1981.) Dotted lines are 95% confidence limits for values with dissolved oxygen above 6 mg/L. Sloped line (fitted by eye) defines the zone of dependence of growth on dissolved oxygen.
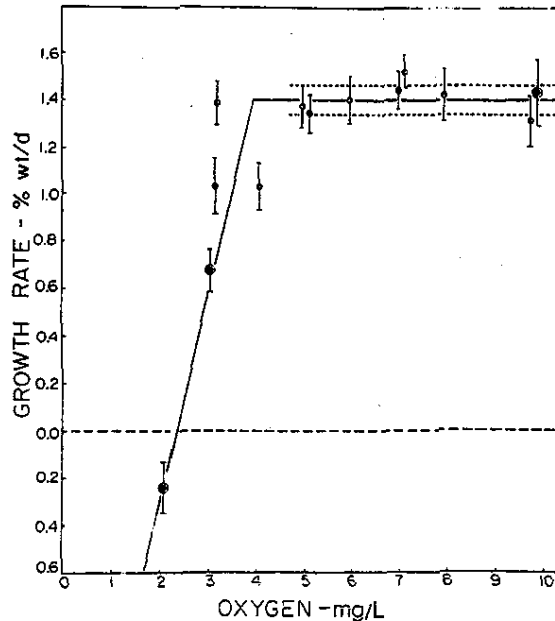
gence and longer period of growth. A dam on the Rogue River, Oregon, ·d flows and temperatures in both summer and winter, and changed the ·g of salmon and steelhead fry emergence, adult migration, fish distribution in iver, and adult mortality (Cramer et al. 1985).

Dissolved Oxygen

The waters of most natural salmonid streams have enough DO for juveniles, although concentrations in small streams may be reduced by large amounts of organic debris when temperatures are high and flows low (Hall and Lantz 1969). Streams downstream from deep, productive reservoirs may have marginally low DO concentrations at times if the discharge comes from the hypolimnion. The DO must be above a critical level for salmonids to exist in streams. Rainbow trout have survived laboratory tests at DO concentrations of less than 2 mg/L (Alabaster et al. 1957), and the survival threshold concentration for Atlantic salmon smolts is about 3.3 mg/L (Alabaster et al. 1979), but growth rate (Figure 4.23) and food conversion efficiency (Figure 4.24) are probably limited by concentrations less than 5 mg/L. Davis (1975), who reviewed information on incipient DO response thresholds and developed oxygen criteria related to concentration, water temperature, and percent saturation (Table 4.9), concluded that salmonids would not be impaired at concentrations near 8 mg/L (76–93% saturation), and that initial symptoms of DO deprivation would occur at about 6 mg/L (57–72% saturation). Davis et al. (1963) and Dahlberg et al. (1968) found the maximum sustained swimming performances of coho and chinook salmon decreased when DO concentrations were much below air-saturation levels (about 8–9 mg/L at 20°C).

In summary, salmonids may be able to survive when DO concentrations are relatively low (<5 mg/L), but growth, food conversion efficiency, and swimming
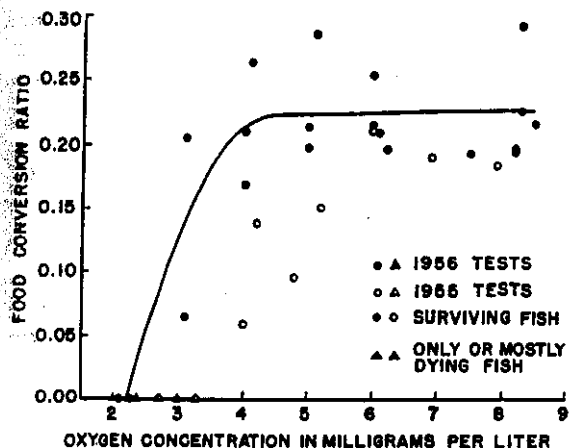
FIGURE 4.24.—Food conversion ratio (weight gained by fish/weight of food consumed) for frequently fed age-0 coho salmon in relation to dissolved oxygen concentration. A food conversion ratio of zero (not a negative ratio) has been assigned to each group of fish that lost weight. The curve has been fitted only to the 1956 data. (From Herrmann et al. 1962.)

performance will be adversely affected. High water temperature, which reduces oxygen solubility, can compound the stress on fish caused by marginal DO concentrations.

Most data on the oxygen requirements of salmonids come from laboratory studies. Brett and Blackburn (1981) appropriately urged caution when such data are extrapolated to fish in natural streams. Water qualities and the biological activities necessary for survival may differ between laboratory and field environments.

Turbidity

In most streams, there are periods when the water is relatively turbid and contains variable amounts of suspended sediments. Larger juvenile and adult salmon and trout appear to be little affected by ephemerally high concentrations of suspended sediments that occur during most storms and episodes of snowmelt (Cordone and Kelley 1961; Sorenson et al. 1977). Bisson and Bilby (1982) reported, however, that juvenile coho salmon avoided water with turbidities that exceeded 70 NTU (nephelometric turbidity units), which may occur in certain types of watersheds and with severe erosion. Berg and Northcote (1985) reported that feeding and territorial behavior of juvenile coho salmon were disrupted by short-term exposures (2.5–4.5 d) to turbid water (up to 60 NTU).

Newly emerged fry appear to be more susceptible to even moderate turbidities than are older fish. Turbidities in the 25–50-NTU range (equivalent to 125–275 mg/L of bentonite clay) reduced growth and caused more young coho salmon and steelhead to emigrate from laboratory streams than did clear water (Sigler et al.

TABLE 4.9.—Response of freshwater salmonid populations to three concentrations of dissolved oxygen. (Modified from Davis 1975.)

Response	Dissolved oxygen (mg/L)	Percent saturation at temperature (°C)					
		0	5	10	15	20	25
Function without impairment	7.75	76	76	76	76	85	93
Initial distress symptoms	6.00	57	57	57	59	65	72
Most fish affected by lack of oxygen	4.25	38	38	38	42	46	51

1984). Juvenile salmonids tend to avoid streams that are chronically turbid, such as glacial streams or those disturbed by human activities (Lloyd et al. 1987), except when the fish have to traverse them along migration routes.

Productivity of Streams

Streams vary in productivity due largely to the nutrients and energy available. The rates of primary and secondary production largely determine the amount of food available to fish. A detailed discussion of energy sources and processes is presented by Murphy and Meehan (1991, this volume).

The amount of food available to fish is one of the factors that set the salmonid carrying capacity of streams. In many infertile streams, summer fish production appears to be food-limited. A change in fish production, density, or growth when food availability increases or decreases is proof of food limitation. More coho salmon could be produced in a small Vancouver Island stream during summer when Mason (1976) increased the amount of food available. In another Vancouver Island stream, Slaney et al. (1986) added inorganic fertilizers (phosphorus and nitrogen) to a 29-km section and found large increases in primary production, no significant changes in invertebrate abundance and fish density, and significant increases in trout growth. The increased growth allowed steelhead to become smolts at a younger age; because this period of juvenile mortality was reduced, the stream produced more smolts.

Positive correlations between stream productivity and production, standing crops, and growth of brown trout were observed by McFadden and Cooper (1962). In Idaho streams that differed in conductivity by a factor of 10 (40 to 400 $\mu S/cm^3$), the production and standing crop of age-0 chinook salmon differed by a similar factor (T. C. Bjornn, unpublished data). Konopacky (1984) found juvenile chinook salmon and steelhead lost weight and eventually left laboratory streams when no food was supplied; he also found proportionate increases in production, but not in density, in response to two levels of daily ration. Wilzbach (1985) reported that most cutthroat trout left laboratory channels when they were given a daily ration of frozen brine shrimp equal to only 5% of their body weight, whether cover was provided or not, but they stayed when given a 15% ration.

Brett et al. (1969) defined the daily rations needed for maximum growth of sockeye salmon at various temperatures. If this relation is similar for other species of salmon and trout, a yearling salmonid in a stream with daily mean temperature of 10°C would need a daily food supply equivalent to 6–7% of its body weight to attain maximum growth. In streams that are food-limited, maximum growth rates may not be achieved by the fish because that may not be the most efficient use of resources. The social interactions that fish use to regulate densities and respond to food abundance may result in more fish growing at less-than-maximum rates, rather than fewer fish growing at maximum rates.

Juvenile salmonids can consume a large fraction of the invertebrates drifting during daylight in the streams they occupy (Allan 1982; Wilzbach et al. 1986), but fish do not appear to regulate the abundance of benthic or drifting invertebrates in streams except in very limited situations of time and space (Allan 1983). Production of aquatic invertebrates that juvenile salmonids eat depends on the amount of organic material available in streams. Bilby and Likens (1980) showed the importance of debris dams in small streams for the accumulation of coarse

particulate organic matter. Nearly 75% of the organic matter deposited in first-order streams was associated with the dams, versus 58% in second-order streams and 20% in third-order streams. Fish also eat terrestrial invertebrates that are associated with vegetation surrounding streams.

Space

Space suitable for occupancy by salmonids in streams is a function of streamflow, channel morphometry, gradient, and (in many instances) various forms of instream or riparian cover. Suitable space for each salmonid life stage has water of sufficient depth and quality flowing at appropriate velocities. The addition of cover (extra depth, preferred substrates, woody debris, etc.) increases the complexity of the space and usually the carrying capacity. The addition of certain types of cover (overhead, for example) may make some areas in streams suitable for fish that would not otherwise be used.

The space an individual fish needs and uses—in some instances a territory—is a part of the total suitable space available. Food abundance (Chapman 1966), the competitors (Fausch and White 1981, 1986) and predators present, and the complexity of the habitat determine what part of the available suitable space an individual fish uses.

Fish densities in streams provide a measure of the spatial requirements of juvenile salmonids, but the wide variation in observed densities illustrates the diversity of habitat quantity and quality and other factors that regulate fish abundance. In a productive Idaho stream, end-of-summer densities of age-0 chinook salmon (9.6 g mean weight) have been as high as 1.35 fish/m^2 and 12.9 g/m^2 (Bjornn 1978). With the age-0 steelhead (4.5 g) also produced in the stream, the combined densities were 2.05 fish/m^2 and 16.1 g/m^2. These salmonids were not uniformly distributed throughout the length of the stream and densities in some sections were as high as 3.4 fish/m^2 (21.8 g/m^2). Total salmonid density, including the age-1 and older fish, has been as high as 3.5 fish/m^2 and 27.0 g/m^2. Spring-to-fall production (tissue elaborated) by age-0 chinook salmon and steelhead has been measured at rates as high as 20.3 g/m^2.

In less productive third- and fourth-order streams in Idaho, age-0 chinook salmon were less dense (usually <0.8 fish/m^2), the fish grew slower (end-of-summer weight, about 5 g), biomass standing crops were only 1–3 g/m^2, and few fish of other species were produced. Summer production was 1–2 g/m^2 (T. C. Bjornn, unpublished data). In coastal and inland British Columbia streams, Shepherd et al. (1986b) reported overall maximum densities of 0.14 age-0 chinook salmon/m^2 (five streams) and 0.41 age-0 and age-1 coho salmon/m^2 (nine streams).

Salmonids, especially the juveniles, also use the space available in side channels for rearing. Mundie and Traber (1983) found higher densities of steelhead (0.66 smolts/m^2 and 9.94 g/m^2) and coho salmon (0.85 smolts/m^2 and 12.8 g/m^2) in side-channel pools than are commonly found in the main channels of Pacific coastal streams. Peterson (1982a, 1982b) reported coho salmon moving into side-channel pools for the winter.

The amount of space needed by fish increases with age and size. Allen (1969) assembled data on densities for a variety of salmonids and found a positive relation between area per fish in streams and age (Figure 4.25) or length. For the streams he evaluated, 7–10-cm fish (which had completed the first year of life)

FIGURE 4.25.—Average area per fish (on a logarithmic scale) versus age for several salmonids in streams. (Redrawn from Allen 1969.)
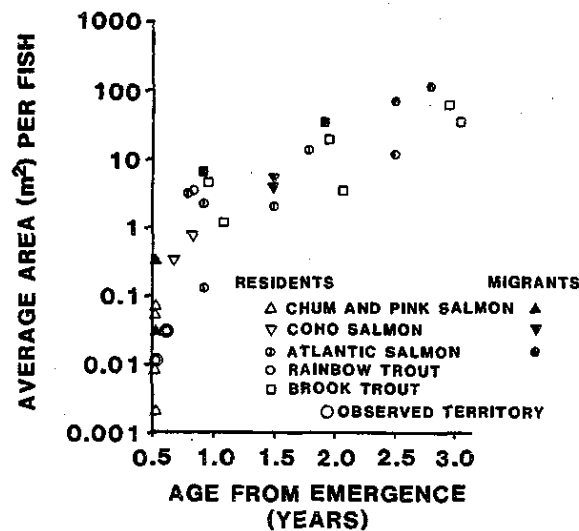
were found at densities of 0.1 to 1.0 fish/m^2 (10-cm fish averaged 0.17 fish/m^2 and 1.7 g/m^2). Densities of larger and older fish were usually less than 0.1 fish/m^2.

Based on the foregoing, the summer space requirements of juvenile salmonids during their first year in streams probably range from 0.25 to 10 m^2 of stream per fish, depending on such things as the species and age composition of fish present, stream productivity, and quality of the space. The space required in winter has not been as well defined.

The presence of abundant space does not necessarily mean there will be large numbers of fish. The space must be in the right context with other needs of the fish. For example, the abundance of age-0 chinook salmon in some infertile Idaho nursery streams appeared to be asymptotically related to the size of pools (Figure 4.26). In pools up to about 200 m^2 in area (volume, 150 m^3), the number (or biomass) of fish observed was directly related to size of the pools. In larger pools, however, much of the space in the downstream portions was unused, despite the presence of suitable depths and velocities. Fish abundance was probably food-limited in these streams and thus the fish were concentrated in the upper portions of each pool, close to the incoming food supply.

The effect of reducing space available to fish in small pools of third-order streams was illustrated by Bjornn et al. (1977) in a stream sedimentation experiment. When sand was added to a natural pool, reducing pool volume by half and surface area of water deeper than 0.3 m by two-thirds, fish numbers declined by two-thirds.

Streamflow.—Streamflow, one of the basic determinants of the amount of space available for fish, varies seasonally in ways that depend on geography and climate. In coastal streams, flows are often high in winter because of heavy rain and snowfall. In inland areas, flows are most often high in spring as a result of snowmelt, but rain-on-snow events occasionally cause high flows in winter. In most unregulated salmonid streams of North America, flows are usually lowest in late summer, fall, or winter (Stalnaker and Arnette 1976a). Diversion of water
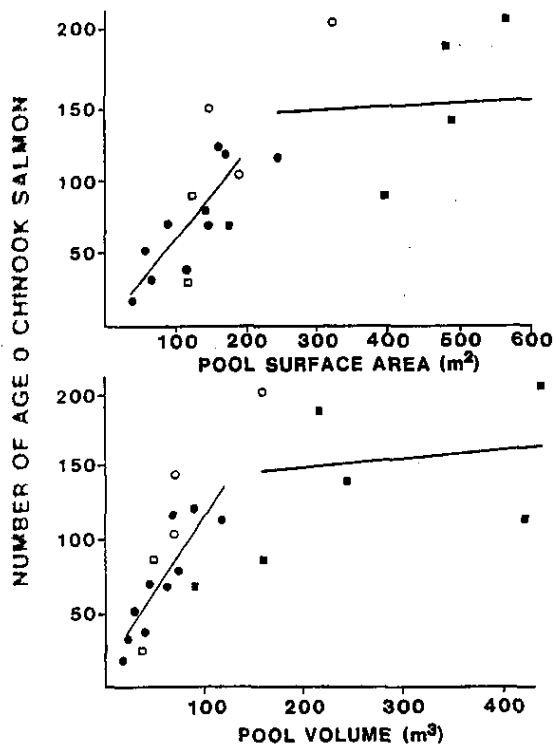
FIGURE 4.26.—Relation between pool surface area or volume in several Idaho streams (denoted by different symbols) and number of juvenile chinook salmon per pool. (Redrawn from Konopacky 1984.)

from streams and storage of water for municipal, agricultural, flood control, and hydropower uses usually lead to altered streamflows and potential changes in the carrying capacity of streams for salmonid fishes. The relation between streamflow and carrying capacity could vary with channel geometry and surrounding land forms: it probably differs, for example, between streams consisting mostly of riffles in a V-shaped canyon and streams with alternating pools and riffles in a broad valley. In general, the relation must start at the origin (no flow, no fish), increase (perhaps not uniformly) with increases in flow up to a point, and then level off or decline if flows become excessive. The relation between flow and carrying capacity is difficult to assess directly in natural streams, however, and there are few studies for reference. The roles of flow magnitude and seasonality in setting the carrying capacity of a stream have not been well defined.

Kraft (1972) diverted water from a 520-m section of natural stream channel in Montana for 3 months in summer and found that both physical stream characteristics and resident brook trout were more affected in runs than in pools. After a 90% reduction from normal summer flows (about 1.0 m³/s), depth in runs decreased 38%, average water velocity decreased 73%, and cover decreased 50%; decreases were smaller in pools. The response of brook trout to the 90% flow reduction was variable, but many fish in the dewatered section moved from runs into pools; the number of fish decreased an average 62% in dewatered runs compared with 20% in runs that were not dewatered (Figure 4.27).

In an Oregon flume studied by White et al. (1981), water velocities, depths, wetted perimeters, and surface areas in runs declined with decreases in flow, as

FIGURE 4.27.—Relations of fish number and cover to reductions in summer base flow in three runs in Blacktail Creek, Montana. (Data from Kraft 1968, as plotted by White 1976.)
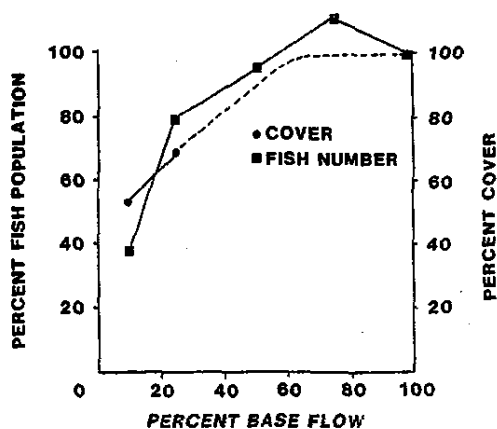
did the abundance of wild steelhead juveniles, but the researchers were unable to determine the relative influences of the physical features on fish abundance. The authors also calculated an index (weighted usable area, WUA) of the amount of suitable habitat in the flumes for juvenile steelhead, based on IFIM. Their estimates of WUA from suitability curves for velocity and depth did not correspond closely with the number of fish remaining at each flow.

The IFIM, although controversial and incompletely validated, is a modeling procedure designed to help evaluate the importance of differing streamflows to the production of fish. The procedure generates a relation between WUA and flow. Typically, WUA increases asymptotically with flow (Figure 4.28), but the estimates can vary widely depending on the velocity and depth suitability indexes used. In an Idaho stream, WUA estimates for age-0 chinook salmon were highest at flows that occurred near the end of summer, and decreased when flows were higher or lower. The WUA values based on velocity and depth were highest for pools, followed by runs, and then riffles.

For IFIM models to be useful, there must be a definable relation between WUA index values and the standing crop or production of fish in a stream. Such relations can exist only if the physical variables included in the model (velocity, depth, substrate, cover, etc.) are the factors that regulate abundance. Stalnaker (1979) found that standing crop of brown trout was strongly correlated with WUA in 19 sections of 8 Wyoming streams. Orth and Maughan (1982) and Conder and Annear (1987) had less success in relating WUA index values to standing crops of fish or to another habitat quality index. Conder and Annear (1987) discussed the use of the IFIM to estimate changes in fish production in streams as related to streamflow. Nickelson et al. (1979) reported on studies of models that could be used to evaluate streamflow requirements of salmonids in Oregon streams. After several years of study, they recommended use of the IFIM with the addition of variables for pool volume and cover.

Smoker (1955) found a correlation between the commercial catch of coho salmon and annual runoff, summer flow, and lowest monthly flow in 21 western Washington drainages 2 years previously; the data covered the years 1935–1954. In the last two decades, hatchery production of coho salmon smolts has increased markedly and made such comparisons more difficult, but Mathews and Olson (1980) analyzed data
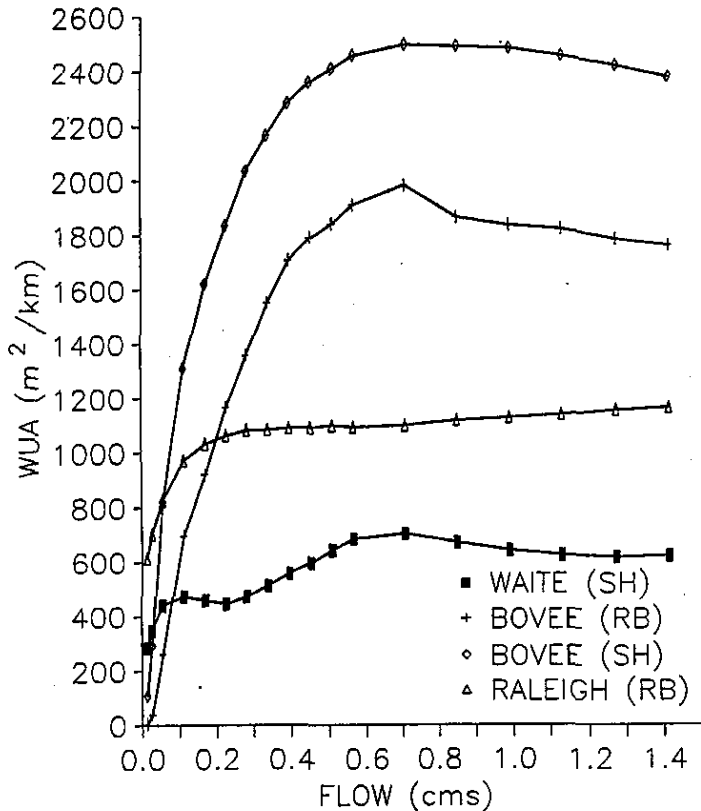
FIGURE 4.28.—Indices of suitable area (weighted usable area, WUA) versus flow (cubic meters per second) for juvenile steelhead (SH) and rainbow trout (RB) in a California stream based on different probability-of-use curves devised by Waite, Bovee, and Raleigh. (Ian Waite, unpublished data.)

from Washington for the years 1952–1977 and found that summer streamflow still had an important influence on total coho salmon production in Puget Sound area streams. Scarnecchia (1981) found that the coho salmon catch off the Oregon coast for the years 1942–1962 was correlated with total flow in five coastal rivers during the salmon's freshwater existence; however, the catch was poorly correlated with the 60-d period of lowest flow in these rivers. Nickelson (1986), in an analysis of coho salmon survival from smolt to adult off the Oregon–California coast, concluded that survival at sea was variable (related to upwelling), but density independent. The implication of the above studies is that the abundance of adult coho salmon is a function of the number of smolts produced, which is in turn related to streamflow and the other factors that regulate the production of smolts.

Velocity.—Given flow in a stream, velocity is probably the next most important factor in determining the amount of suitable space for rearing salmonids (Chapman 1966; deGraaf and Bain 1986); if the velocities are unsuitable, no fish will be present. Natural streams contain a diversity of velocities (Figure 4.29) and depths,

FIGURE 4.29.—Frequency of velocities at sites (focal points) occupied by trout in three sections of Uvas Creek, California, and frequency of velocities measured along transects in the stream. (From Smith and Li 1983.)
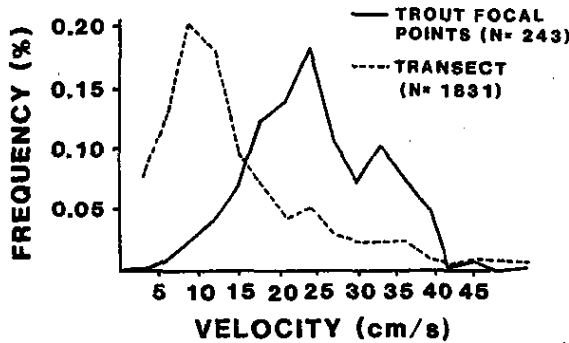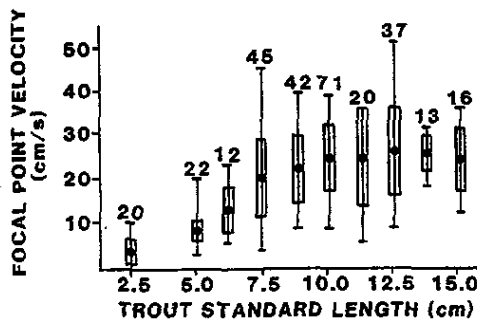
some of which are suitable for most salmonids. The velocities required and used by juvenile salmonids vary with size of fish, and sometimes with species. Some juvenile salmonids, as they grow, select sites in streams with increasingly faster velocities (Chapman and Bjornn 1969; Everest and Chapman 1972; Rimmer et al. 1984; Moyle and Baltz 1985), presumably to gain access to more abundant food (Chapman and Bjornn 1969; Fausch 1984). Sites used for feeding over long periods and the size of food items eaten may be selected largely to maximize net energy gain (Bachman 1984).

Water velocities required by fish of various sizes have been estimated from studies of the sites fish occupy in streams and of the swimming performance of fish in laboratories. Use of data from so-called field microhabitat studies to establish velocity and depth requirements has limitations because the sites selected by fish in natural streams are influenced by factors other than their velocity and depth preferences. Interactions with other fishes and the presence and location of cover alter sites selected by fish (Fausch and White 1981, 1986). Wild brown trout placed in a flume shifted position to stay within a suitable velocity range when flows were increased (Baldes and Vincent 1969). In a study by Shirvell and Dungey (1983), velocity was the most important factor determining the preferred sites of large brown trout (42 cm), but the fish often chose compromise positions to be close to food or cover.

Velocity and depth preferences may change seasonally. Chisholm et al. (1987) noted that brook trout selected areas of lower velocity (<15 cm/s) and deeper water (>30 cm) in winter than in summer, but showed no preference for substrate. Tschaplinski and Hartman (1983) noted similar shifts by coho salmon in winter to

FIGURE 4.30.—Water velocities at focal points (means, ranges, and 95% confidence intervals) for trout of different standard lengths in a California stream. Numbers above data points are sample sizes. (From Smith and Li 1983.)

STEELHEAD

r = 0.75

r = 0.60

CHINOOK SALMON

r = 0.92

r = 0.65

0   10   20   30   40   0 20 40 60 80 100 120
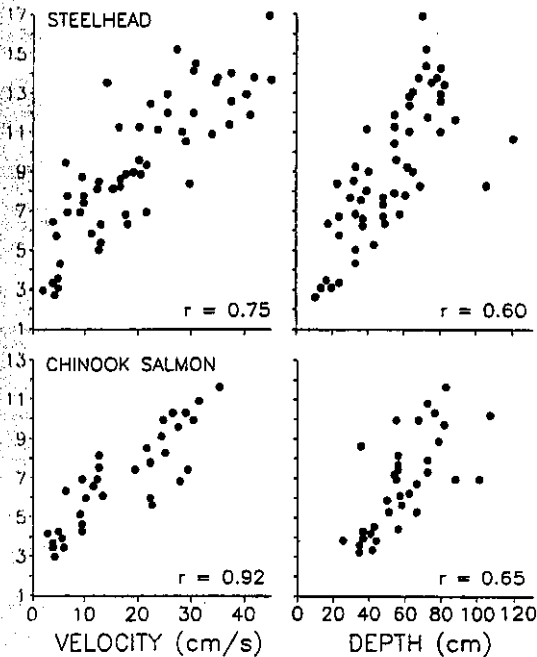   VELOCITY (cm/s)   DEPTH (cm)

FIGURE 4.31.—Correlations between length of juvenile steelhead and chinook salmon and velocity and depth of water at sites (focal points) used by the fish in two Idaho streams. (Redrawn from Everest and Chapman 1972.)

sites (deep pools, undercuts, debris jams, side sloughs) with low velocity (<30 cm/s) but good cover.

Newly emerged fry (20–35 mm long) of salmon, trout, and char require velocities of less than 10 cm/s, based on studies of sites selected by the fish in streams (Chapman and Bjornn 1969; Everest and Chapman 1972; Griffith 1972; Hanson 1977; Smith and Li 1983; Konopacky 1984; Pratt 1984; Bugert 1985; Moyle and Baltz 1985; Sheppard and Johnson 1985). Larger fish (4–18 cm long) usually occupy sites with velocities up to about 40 cm/s (Figures 4.30, 4.31, 4.32; Table 4.10). Velocities at the sites occupied (focal points) by juvenile steelhead in a California stream were higher than the modal velocities in the stream (Figure 4.29), increased asymptotically with fish length (Figure 4.30), increased with temperature, and were less than the velocities at their usual feeding sites (Smith and Li 1983). Because invertebrate drift abundance increased with velocity across a stream section, there was a potential energetic benefit from feeding in the fastest water possible. In Idaho streams, young chinook salmon and steelhead occupied deeper and faster water as they increased in size (Figure 4.31), presumably to gain better access to food. By the end of summer, young chinook salmon (4–10 cm long) were found in the full range of available depths, but in velocities that were on the low end of those available (Figure 4.32).

Swimming performance as measured in the laboratory provides a measure of the ability of a fish to swim under specified conditions, but may not reveal velocities preferred by the fish. Brett et al. (1958) reported cruising speeds (speeds a fish could maintain for at least 1 h under stimulation) of juvenile coho salmon increased with fish size and temperature (Figure 4.33). At 10°C, cruising speeds
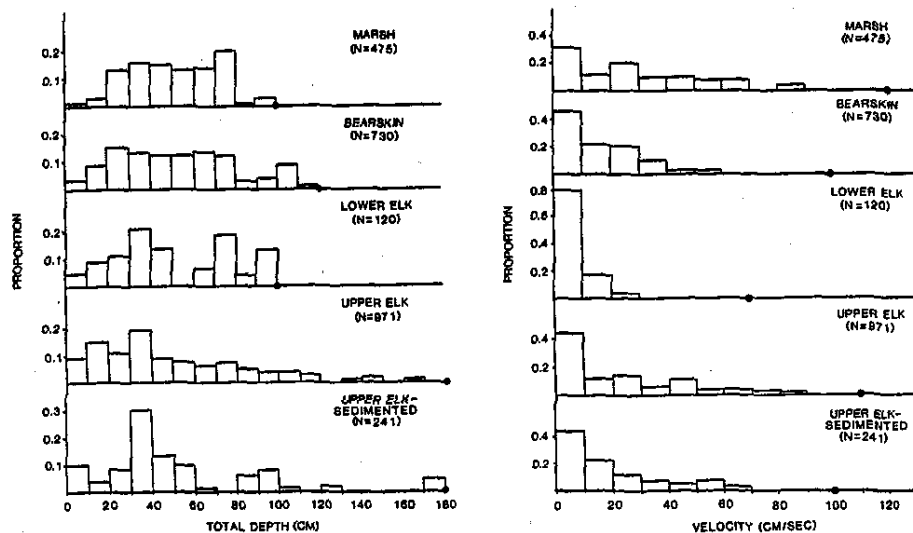
FIGURE 4.32.—Distribution of age-0 chinook salmon (77–89 mm mean total length) relative to water depth and velocity in pools of Idaho streams in August 1979. Dots indicate maximum water depth or velocity observed in the pools surveyed. (From Konopacky 1984.)

were 20–25 cm/s for 5-cm coho salmon and 35–40 cm/s for 9-cm fish; at 20°C, the speeds were 5–6 cm/s faster. Cruising speeds of fish are lower than speeds at which fish can swim for short bursts, but may be higher than water velocities observed at focal points selected by fish in streams. In a southeast Alaska stream, the mean velocity at focal points selected by age-0 (<7 cm long) and yearling (up to 12 cm long) coho salmon averaged 13–14 cm/s (T. C. Bjornn, unpublished data). Brett (1967) reported that juvenile sockeye salmon (136 mm mean length) could swim for 300 min in velocities up to about 37 cm/s (at 15°C) without becoming fatigued; at increasingly higher velocities, all fish eventually became fatigued (Figure 4.34). Velocities that did not produce fatigue in 300 min (<37 cm/s) were about half the cruising speed for fish of a given size.

Depth.—The depth of water juvenile salmonids use depends on what is available, the amounts and type of cover present, and the perceived threat from predators and competitors. Young trout and salmon have been seen in water barely deep enough to cover them and in water more than a meter deep. Densities (fish/m²) of some salmonids are often higher in pools than in other habitat types (runs, riffles, pocket waters; Figure 4.35), but that may reflect the space available (there is more volume in pools per unit of surface) rather than a preference for deep water, especially for smaller fish (<15 cm long).

Fish usually are not uniformly distributed at all depths in a stream. Raleigh et al. (1986) presented index curves for chinook salmon in which suitabilities for newly emerged fry and juveniles were highest at depths of 25–60 cm. The curves were constructed from observations of fish distributions in streams. Everest and Chapman (1972) found significant correlations between size of fish and total water

TABLE 4.10.—Depths and velocities at sites used by salmonids in streams.

| Species and source	Age[a] or size	Depth (cm)	Velocity (cm/s)
Steelhead			
Bugert (1985)	31–44 mm	24	40
Everest and Chapman (1972)	0	<15	<15
	1	60–75	15–30
Hanson (1977)	1	51 mean	10 mean
	2	58 mean	15 mean
	3	60 mean	15 mean
Moyle and Baltz (1985)	0	35	7.3
	Juvenile	63	19.4
	Adult	82	28.6
Sheppard and Johnson (1985)	37 mm	<30	<25
Smith and Li (1983)	25 mm		4
	50 mm		8
	75 mm		18
	100 mm		24
	150 mm		24
Stuehrenberg (1975)	0	<30	14 (range, 3–26)
	1	>15	16 (range, 5–37)
Thompson (1972)	0	18–67	6–49
Chinook salmon			
Everest and Chapman (1972)	0	15–30	<15
Konopacky (1984)	77–89 mm	55–60	12–30
			18 (dawn)
			12 (midday)
			25 (dusk)
Stuehrenberg (1975)	0	<61	9 (range, 0–21)
	1	<61	17 (range, 5–38)
Thompson (1972)	0	30–122	6–24
Steward and Bjornn (1987)	78–81 mm	40–58	8–10
Coho salmon			
Bugert (1985)	40–50 mm	24	39 (flume)
	0		15
	1		18
Nickelson and Reisenbichler (1977)	0	>30	<30
Pearson et al. (1970)	0		9–21
Sheppard and Johnson (1985)	62 mm	30–70	<30
Thompson (1972)	0	30–122	5–24
Cutthroat trout			
Hanson (1977)	1	51 mean	10 mean
	2	56 mean	14 mean
	3	57 mean	20 mean
	4	54 mean	14 mean
Pratt (1984)	<100 mm	32	10
	>100 mm	62	22
Thompson (1972)	0, 1	40–122	6–49
Atlantic salmon			
Rimmer et al. (1984)	40–100 mm		30
	100–150 mm		38
Bull trout			
Pratt (1984)	<100 mm	33	9
	>100 mm	45	12

[a] Ages are in years or life stages, without units.
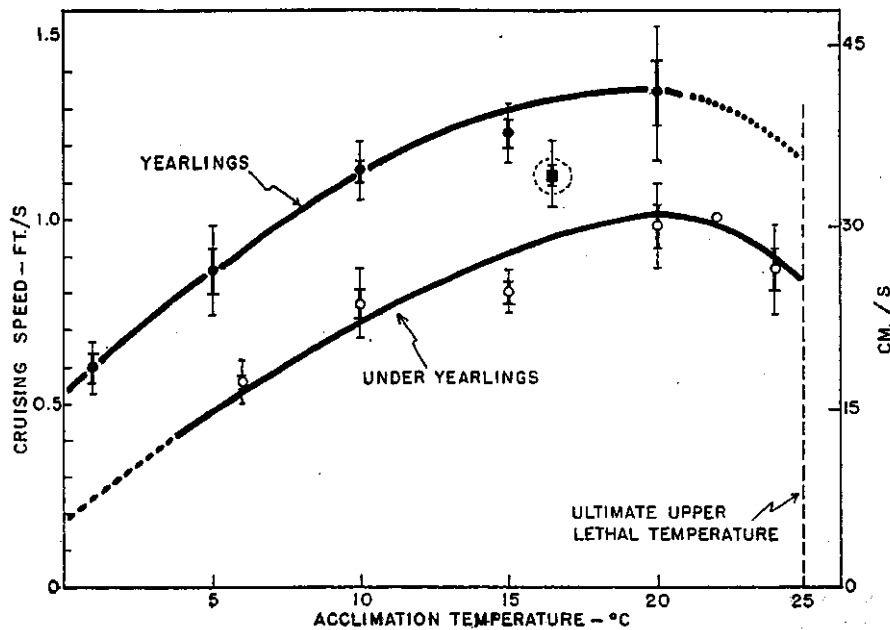
FIGURE 4.33.—Variation in cruising speed for temperature-acclimated underyearling and yearling coho salmon, adjusted in each age group to common mean lengths of 5.4 cm and 8.9 cm, respectively. The circled point between two curves is for exercised underyearling coho salmon acclimated to 16.5°C. Standard deviation (thin vertical bar) and standard error (heavy bar) are indicated for each sample. (From Brett et al. 1958.)

depth at sites (focal points) occupied by juvenile chinook salmon and steelhead (Figure 4.31). Correlations were poor between fish size and distance of focal point from the bottom; most fish, regardless of size, were near the bottom. In two Newfoundland Rivers, water depth was an unimportant factor in site selection by juvenile Atlantic salmon (deGraaf and Bain 1986). ·

If fish have a preferred depth of water, we believe it is readily subjugated to the needs for suitable velocities, access to food, and security from predators. Sites that fish select in streams must satisfy all the basic needs to enable the fish to survive. In laboratory streams, chinook salmon fry 30–40 mm long occupied a wide variety of

FIGURE 4.34.—Percentage of young sockeye salmon that became fatigued within 300 min at 15°C when forced to swim at the velocity indicated. The mean total length of the 104 fish in the sample was 13.6 cm. (Redrawn from Brett 1967.)
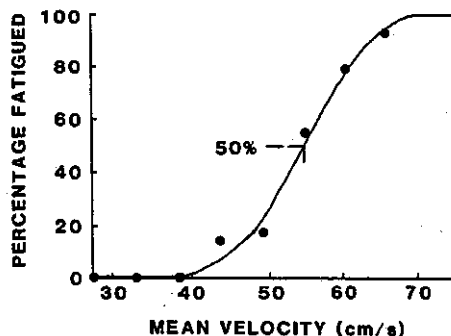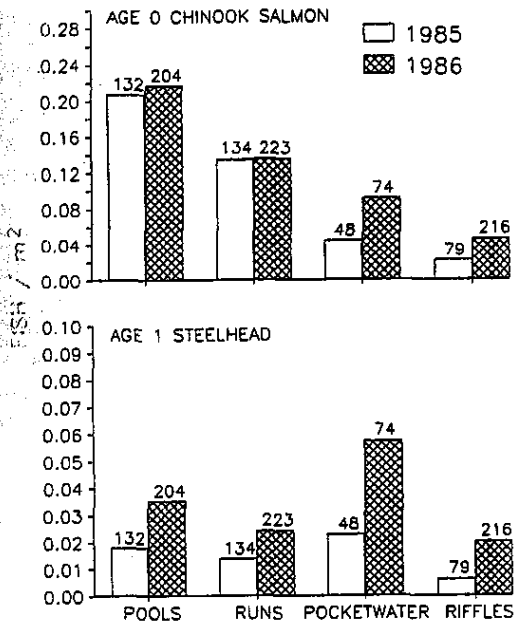
FIGURE 4.35.—Densities of age-0 chinook salmon and age-1 steelhead in various types of habitat in 22 Idaho streams. Numbers above bars represent the number of units of each type of habitat surveyed. (Authors' original data.)

sites (including the deepest water) when they were the only fish present, but only restricted areas when they shared the streams with yearling steelhead 70–120 mm long (T. C. Bjornn, unpublished data). The newly emerged fry were distributed throughout the water in both small pools (0.6 m wide, 1.2 m long, 0.32 m deep) and larger pools (1.5 m wide, 2.5 m long, 1.1 m deep) when no other fish were present and there was no threat of bird predation. The presence of only two yearling steelhead in a 4.8-m section of the smaller stream (two pools, two riffles, one run) changed the behavior of and site selection by the chinook salmon fry: some left the stream and those that remained stayed close to the bottom in the pools or moved into the interstitial spaces of the gravel substrate. When larger numbers of yearling steelhead were present, all chinook salmon fry left the stream or were eaten. In the larger stream, the fry moved to shallow water (<6 cm deep) above a sand bar, left the stream, moved into the substrate, or were eaten when yearling steelhead were present. A simulated kingfisher flight over the sand bar frightened the fry into the pool where they were vulnerable to predation by steelhead.

The relation between water depth in streams and fish numbers has not been empirically defined, but depends on the mixture of fish species and sizes, types and amounts of other cover present, and size of stream. In second- to fourth-order salmon streams, we suspect the relation is asymptotic, fish abundance increasing with increases in depth (more space) up to a point. We see no reason why fish that form schools in pools should become less abundant in extra deep water, but territorial fishes and those that select sites close to the substrate may not be as abundant in deep pools as in shallower types of habitat (runs and pocket water; Figure 4.35).

Substrate.—The substrates of salmonid streams are important habitats for incubating embryos and aquatic invertebrates that provide much of the food of
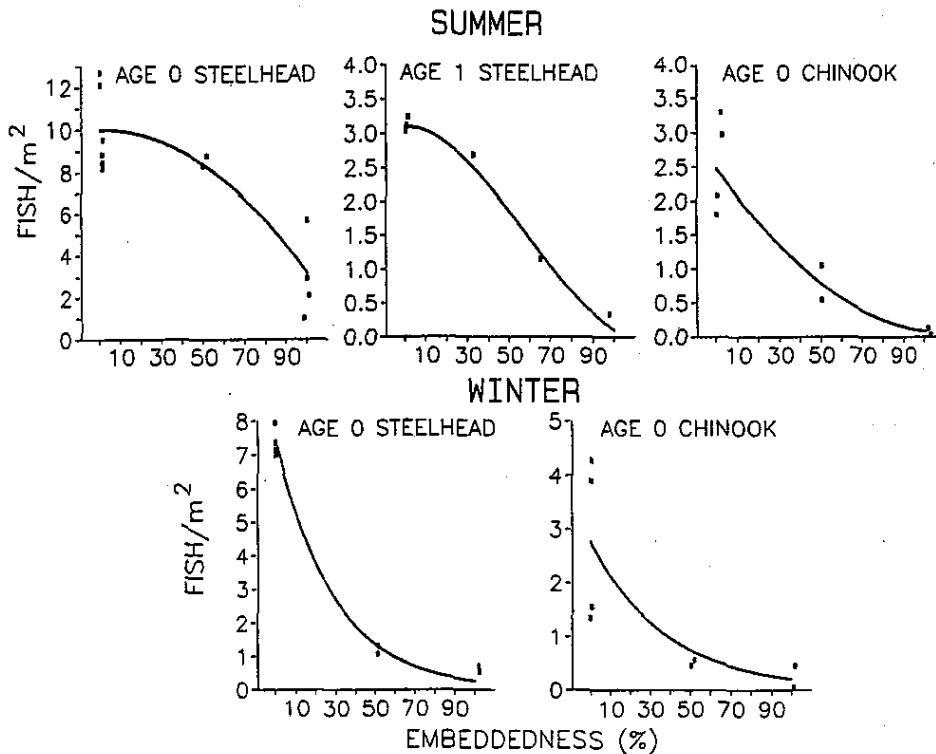
FIGURE 4.36.—Densities of chinook salmon and steelhead juveniles remaining in laboratory stream channels after 5 d during winter and summer tests to evaluate the effects of sedimentation. The channels had alternating pool–riffle configurations; fine sediments (<6 mm) were added to pools and riffles to embed the cobbles and boulders from 0 to 100%. (From Bjornn et al. 1977.)

salmonids, and they provide cover for fish in summer and winter. Silt and sand substrates have little or no value as cover for fish. Larger substrate materials (up to 40 cm in diameter) provide visual isolation and their interstitial spaces are often the primary cover, along with depth and water turbulence, in some streams.

Salmonids will hide in the interstitial spaces in stream substrates, particularly in winter, when the voids are accessible (Chapman and Bjornn 1969; Bjornn and Morrill 1972; Gibson 1978; Rimmer et al. 1984; Hillman et al. 1987). Newly emerged fry can occupy the voids of substrate made up of 2–5-cm diameter rocks, but larger fish need cobble and boulder-size (>7.5-cm diameter) substrates. The summer or winter carrying capacity of the stream for fish declines when fine sediments fill the interstitial spaces of the substrate (Figure 4.36). In a laboratory stream experiment, Crouse et al. (1981) found that production (tissue elaboration) of juvenile coho salmon was related to the amount of fine sediments in the substrate. When large substrate particles (>12 mm in diameter) were covered (embedded) with various amounts of fine sediments (<2 mm in diameter), fish production was reduced in direct proportion to the degree of embeddedness (expressed as a substrate score or geometric mean size of particles). In another laboratory stream study, Bjornn et al. (1977) found that the density of juvenile

steelhead and chinook salmon in summer and winter was reduced by more than
half when enough sand was added to fully embed the large cobble substrate
(Figure 4.36).

Much of the food eaten by salmonid fishes in streams is produced in the
substrate. Particles that make up stream substrates, and thus the habitat of aquatic
invertebrates, vary widely from silts and sands to boulders and barely fractured
bedrock. Invertebrates differ in their ability to thrive in various types of
substrates. Chironomids of various species do well in silts and sands, but the
larger ephemeropterans, trichopterans, and plecopterans prefer a mixture of
coarse sands and gravels. The addition of fine sediments to stream substrates as
a result of watershed disturbances and erosion is worrisome because sedimenta-
tion may reduce the abundance of invertebrates. In streams where food is limiting
for fish, a reduction in aquatic invertebrate abundance would lead to reduced fish
production.

The influence of fine sediments on aquatic invertebrates and ultimately on fish
has been investigated, but has not been clearly defined. Cordone and Kelley
(1961) reported that fine sediments were detrimental to aquatic organisms.
Bjornn and Prather (1974) found that invertebrate abundance was reduced when
larger streambed particles were fully embedded in fine sediments. Bjornn et al.
(1977) found that many ephemeropterans, trichopterans, and simuliids were less
abundant in riffles fully embedded with fine granitic sediments than in less-
embedded riffle substrates. Hawkins et al. (1983) found decreasing numbers of
invertebrates in shaded riffles as the percentage of fine sediments increased, but
no such correlation existed in unshaded riffles. In seminatural laboratory streams,
benthic and drifting invertebrates (mostly chironomids and ephemeropterans)
were more abundant in sections with sand–pebble substrate than in sections with
large gravel (Konopacky 1984).

Summer and winter carrying capacities of streams for salmonids may differ
markedly because of the substrate present. For example, more than half the
steelhead and chinook salmon that reared in two Idaho streams in summer left
during fall and winter, but ceased migrating downstream when they encountered
areas with larger substrate (Bjornn 1978). In laboratory experiments, fall and
winter migrants stopped migrating downstream when placed in channels with
large rocks, but continued migrating when put in channels with small gravel
(Bjornn and Morrill 1972). After piles of large rock were added to provide cover
in sections of a stream with small gravel, more juvenile steelhead stayed there in
winter than previously (Chapman and Bjornn 1969). In summer, substrates
contribute to a stream's carrying capacity by providing habitat for invertebrates
that fish eat and, perhaps less importantly, by providing cover. In winter, the
substrate is more important as a source of cover than as a source of food.

Cover

Cover is an important, but difficult to define, aspect of salmonid habitats in
streams. Some of the features that may provide cover and increase the carrying
capacity of streams for fish are water depth, water turbulence, large-particle
substrates, overhanging or undercut banks, overhanging riparian vegetation,
woody debris (brush, logs), and aquatic vegetation. Cover provides security from
predation for fish and allows them to occupy portions of streams that they might

5352

not use otherwise. The needs of fish for cover may vary diurnally, seasonally, by species, and by size of fish (Kalleberg 1958; Hartman 1963, 1965; Chapman 1966; Ruggles 1966; Butler and Hawthorne 1968; Edmundson et al. 1968; Allen 1969; Chapman and Bjornn 1969; Everest 1969; Lewis 1969; Wesche 1973; Hanson 1977; Cunjak and Power 1986). Cover is usually an important variable in models developed to estimate the standing crop of salmonids that could be expected in streams (Binns and Eiserman 1979; Conder and Annear 1987).

Fish abundance in streams has been correlated with the abundance and quality of cover. Standing crops of cutthroat trout in summer were correlated with the indices of cover (Figure 4.37) and surface area used by Wesche (1974). Juvenile steelhead and chinook salmon responded to various types (Figure 4.38) and amounts (Figure 4.39) of cover in winter by either staying in or leaving outdoor laboratory streams (T. C. Bjornn and C. R. Steward, unpublished data). More fish remained in channel pools with a combination of deep water, undercut bank, large rocks, and a bundle of brush than in pools with less cover. The number of chinook salmon remaining in pools increased with increasing amounts of cover (Figure 4.39).

The addition of structures or large boulders to streams to create pools and cover can increase the abundance of salmonids if the amount of suitable habitat is limiting the fish population. When gabions were added to an Oregon stream after logging, debris removal, and floods, the number, depth, and total volume of pools increased, as did the biomass of salmonids (House and Boehne 1985).

Large woody debris originating from riparian timber is a form of cover in many streams and its importance has become more widely known in recent years (Bisson et al. 1987; Holtby 1988a). For example, coho salmon production declined when woody debris was removed from second-order streams in southeast Alaska (Dolloff 1983). More large woody debris and juvenile coho salmon were found in
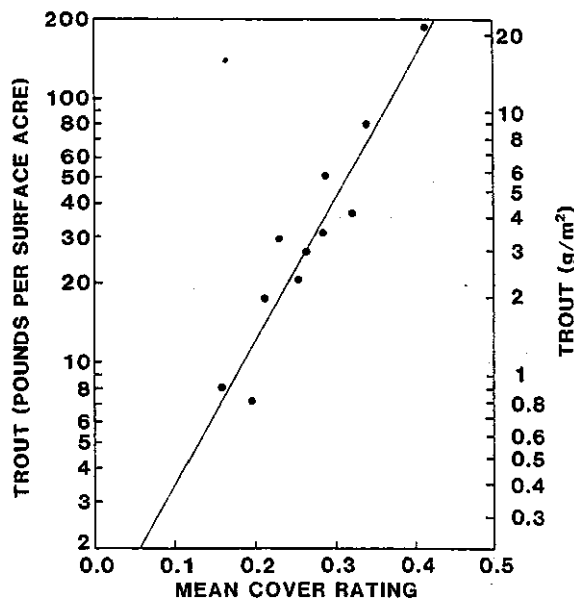

FIGURE 4.37.—Relation between mean trout cover rating and standing crop estimate of trout for 11 study areas. (From Wesche 1974.)
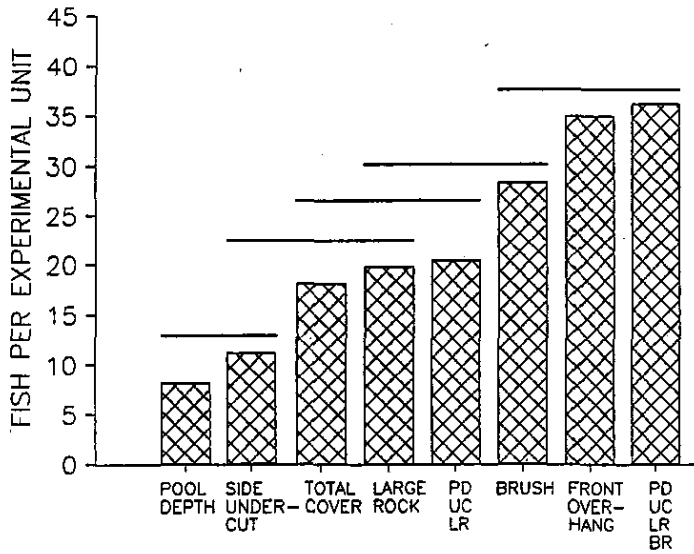
FIGURE 4.38.—Number of yearling steelhead that remained in sections of an outdoor laboratory stream in winter in pools that contained various types of cover. (T. C. Bjornn and C. R. Steward, unpublished data.) Bars not covered by the same horizontal lines were statistically different ($P < 0.05$).

streams surrounded by mature, mixed-conifer forest than in streams lined by red alder that had grown in a 20-year-old clear-cut (House and Boehne 1986). When wood debris was removed from a stream, the surface area, number, and size of pools decreased, water velocity increased, and the biomass of Dolly Varden decreased from 12.5 to 3.9 g/m^2 (Elliott 1986). In another stream, young steelhead were more abundant in clear-cut than in wooded areas in summer but moved to areas with pools and forest canopy in winter (Johnson et al. 1986). Bryant (1983, 1985)
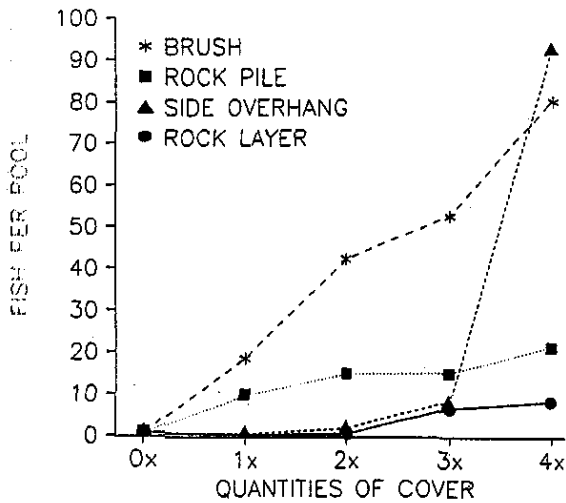

FIGURE 4.39.—Response (number remaining in pools) of yearling chinook salmon to various amounts of different types of cover in an outdoor laboratory stream during winter. (C. R. Steward and T. C. Bjornn, unpublished data.)

proposed guidelines for woody debris management in streams after he found a gradual loss of large debris from streams where riparian timber had been removed.

Overhead cover (including undercut banks, overhanging vegetation, logs, and debris jams) is often an important component of fish habitat in streams. Boussu (1954) reported increases in trout standing crop after the addition of overhanging brush as cover, and decreases when brush and overhanging banks were removed. Overhead bank cover, in association with water depths of at least 15 cm, was the single most important type of cover for brown trout in Wyoming streams (Wesche et al. 1985, 1987). In a small Lake Erie tributary, the distribution of subyearling rainbow trout, brown trout, and coho salmon was related to bank and instream cover (Gordon and MacCrimmon 1982). Brusven et al. (1986) found that 82% of age-0 chinook salmon preferred sections of a small stream channel with one-third overhead cover to sections without such cover. With the same stream channel, Meehan et al. (1987) showed that the fish preferred shade from artificial canopies to open areas, especially in the shallow reaches. Juvenile Atlantic salmon and brook trout were attracted to shaded areas of a shallow flume, but moved to deeper water when given the opportunity (Gibson 1978). Wilzbach et al. (1986), however, found that cutthroat trout foraged more effective on experimentally introduced invertebrate prey in pools within a recently logged area than in forested pools, presumably because light levels were higher in the logged area. Growth of trout was higher in pools of the logged section, but the investigators thought differences in foraging efficiency alone did not fully account for the slower growth in the forested pools.

Use of stream habitat and cover by juvenile salmonids may depend on the presence of other fish. Glova (1986) reported evidence of interactive segregation between juvenile coho salmon and cutthroat trout in summer. When tested separately, most fish of both species were found in pools, but when tested together, most coho salmon were in pools and cutthroat trout were in riffles. In winter, Glova (1986) found that both species, whether together or separate, preferred pools and overhead cover. Similar interactive segregation in summer has been demonstrated for coho salmon and steelhead: salmon used the pools and steelhead the riffles when the species were together in the same streams (Hartman 1965). In southeast Alaska streams, cover affected habitat use by coho salmon, steelhead, and Dolly Varden with respect to depth, position in the water column, and water velocity. Coho salmon and steelhead selected lower positions in the water column in pools without cover than in pools with overhead bank cover or instream cover (Bugert 1985). The presence or absence of Dolly Varden 10–20 cm long in pools caused shifts in habitat use by age-0 steelhead and coho salmon, even when some forms of cover were provided.

Seaward or Lakeward Migration

In some populations of salmonids, the fish spend their entire lives in a limited reach of stream (Miller 1954, 1957; Hunt 1974; Bachman 1984). In many other populations, however, juveniles may live in their natal streams for a few days to more than 3 years and then move to other areas to complete their maturation. Nonanadromous salmon, trout, and char may move downstream into lakes (upstream in some cases) or larger rivers. The anadromous salmonids eventually

migrate to the sea, but in some cases spend extended periods rearing or overwintering in streams (or lakes) other than their natal sites (Bjornn 1978; Leider et al. 1986). Regardless of the destination of the juvenile migrants, flows and water quality must be suitable for the migration to be successful.

The timing of most lakeward or seaward migrations of salmonids that rear for an extended period in steams appears to be regulated primarily by photoperiod, but streamflow, water temperatures, and growth may play a role in some areas. Chinook salmon and steelhead smolts migrated seaward from an Idaho stream at slightly different times, but the timing for each species was similar each year, and was modified only slightly by flow and moon phase (Bjornn 1971); water temperatures were similar each year. In a Norwegian river, water temperature (increase and general temperature in spring) accounted for most of the variation in timing of the seaward migrations of Atlantic salmon (Jonsson and Ruud-Hansen 1985); streamflow, cloudiness, and lunar cycle were not correlated with the migration.

Streamflows are usually adequate in unaltered streams because seaward migration commonly occurs in the spring. Seaward migration has been altered in streams and rivers from which large amounts of water are diverted or along which large reservoirs have been created. Streamflows that were sufficient before construction of dams become inadequate in large reservoirs. There is evidence that smolts depend on river currents during their downstream migration (Fried et al. 1978), and they have difficulty finding their way through large reservoirs with barely perceptible currents. The time required for a smolt to travel the 517 km from the Salmon River in Idaho to The Dalles Dam in the lower Columbia River increased by about 30 d during years with low flows after completion of six intervening dams. The poor success of smolts moving down through large reservoirs with low flows may be due in part to the suppression of some parr-to-smolt physiological processes; Adams et al. (1973) observed this condition when fish were held in relatively high water temperatures (15–20°C). The parr-to-smolt transition is often incomplete when fish begin to migrate and may fail to develop fully if the fish encounter high temperatures and reservoirs without perceptible currents.   •

Another hazard created at some dams is supersaturation of dissolved gases, particularly nitrogen, which can cause gas bubble disease in both upstream- and downstream-migrating salmonids (Ebel 1970; Ebel and Raymond 1976). Salmon may be more successful than steelhead in sensing and avoiding highly supersaturated waters (Stevens et al. 1980), but most salmonids migrating in the rivers are susceptible to gas bubble disease.

The magnitude of the effect dams and associated reservoirs can have on anadromous fishes is evident in data from the Columbia River drainage. Salmon and steelhead must pass up to nine dams in the Columbia and Snake rivers during their migrations to and from the sea. Smolt-to-adult survival rates declined from more than 4% before 1968 to less than 1.5% in the mid-1970s when all the dams were completed (Raymond 1988). In years with low flows (such as 1973 and 1977), smolt mortality averaged 45% at each dam and reservoir, compared to 15% in years with higher flows. In recent years, smolt-to-adult survival rates of steelhead and chinook salmon from the Snake River have increased to 2–5% with the help of spillway deflectors to reduce gas supersaturation, fish bypasses around

turbines, transportation around dams, and supplemental spills at dams without bypasses (Raymond 1988).

Summary

In the foregoing discussion of habitat variables, each factor was addressed separately, but the reader should keep in mind that fish usually respond to the combined effect of two or more of the physical, chemical, and biological variables in their environment. The fish may respond physiologically (altered growth and health) and behaviorally (site selection and interactions) to the array of environmental features they encounter. In streams where fish live and reproduce, all the important factors are in a suitable (but usually not optimum) range throughout the life of the fish. The mix of environmental factors in any stream sets the carrying capacity of that stream for fish, and the capacity can be changed if one or more of the factors are altered. The importance of specific factors in setting carrying capacity may change with life stage of the fish and season of the year.

Low streamflows, high water temperatures, and excessive turbidities impede adult salmon, trout, and char on their migration to spawning areas. These impediments occur even in pristine environments on occasion, but more often in drainages with irrigation, extensive agriculture, hydropower, surface mining, forest harvesting, and flood control projects. Once in the spawning areas, the amount and suitability of stream substrate and flows in the spawning areas are key factors. During incubation of the embryos and alevins, conditions within the redd dictate the number of young fish that will emerge into the stream. Adequate flows of well-oxygenated water and relatively small amounts of fine sediments (organic and inorganic) will allow a high percentage of the young fish to survive and emerge from the redd.

As soon as the young fish begin rearing in the stream, they become subject to predation by other fish, birds, and mammals, and they interact with the other fish present for choice feeding sites and cover. Given adequate numbers of young fish to use all the available habitat, the number and size of fish that can be produced in a stream is governed by the quantity and quality of space available, productivity of the stream, and the presence of competitors and predators. In summer, juvenile fish are primarily concerned with feeding and they select sites in streams that optimize the opportunity to obtain food, yet provide acceptable security from predation. In winter where water temperatures are low, the fish appear to be primarily concerned with security; they hide in cover or adopt behavior patterns that may have security benefits (such as gathering in large schools) and they are less interested in feeding. Because the requirements of salmonids and their use of habitat in winter are different from those in summer, the carrying capacity of streams or stream reaches may not be the same during both seasons. The changes in carrying capacity that result from alteration of stream features depend on the roles those features play in establishing the carrying capacity—roles that can change with time.