Chapter 1

Westslope Cutthroat Trout

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Introduction

The westslope cutthroat trout inhabits streams on both sides of the Continental Divide. On the east side of the divide, they are distributed mostly in Montana but also occur in some headwaters in Wyoming and southern Alberta (Behnke 1992). They are in the Missouri Basin downstream to about 60 km below Great Falls and in the headwaters of the Judith, Milk, and Marias rivers. On the west side of the Continental Divide the subspecies occurs in the upper Kootenai River; the Clark Fork drainage in Montana and Idaho downstream to the falls on the Pend Oreille River; the Spokane River above Spokane Falls; the Coeur d'Alene and St. Joe drainages; and the Clearwater and the Salmon river basins. Several disjunct populations of westslope cutthroat trout persist in the mid-Columbia River basin (Behnke 1992) in the Methow, Entiat, and Wenatchee river basins in Washington and in the John Day River in Oregon. Behnke (1992) considered all cutthroat trout native to the upper and middle Columbia, South Saskatchewan, and upper Missouri basins to be this subspecies.

Life History Characteristics

Westslope cutthroat trout are adfluvial, fluvial, or resident (with the exception of a single lake-spawning population; Carl and Stelfox 1989) (table 1). Adfluvial fish live in the large lakes in the upper Columbia drainage and spawn in lake tributaries. Fluvial fish live and grow in rivers instead of lakes, but they too immigrate to tributaries for spawning. Most adults return to the river or lake after spawning (Rieman and Apperson 1989; Behnke 1992). Resident fish complete their entire life in tributaries and seldom exceed 300 mm in length (Miller 1957; Averett 1962; Bjornn 1975; Thurow and Bjornn 1978). All three life-history forms may occur in a single basin (Averett and MacPhee 1971; Rieman and Apperson 1989).

Westslope cutthroat trout begin to mature at age 3 but usually spawn first at age 4 or 5 (table 2). Sexually maturing adfluvial fish move into the vicinity of tributaries in fall and winter where they remain until they begin to migrate upstream in the spring (Liknes 1984). They spawn from March to July at water temperatures near 10°C (Roscoe 1974; Liknes 1984; Shepard et al. 1984). A population of adult fish in the St. Joe River, Idaho, included 1.6 females for each male (Thurow and Bjornn 1978). Average length was 334 mm for females and 366 mm for males. A similar population in Big Creek, Montana, included 4.1 females for each male (Huston et al. 1984), and the average length was 381 mm for females and 386 mm for males. Ratios of females to males in other locations in Montana ranged from 1:1 to 6.2:1 (Huston et al. 1984).

Alternate-year spawning has been reported in the Flathead River basin in Montana (Shepard et al. 1984) and other populations. Repeat spawners composed from 0.7 to 24% of the adult populations (Shepard et al. 1984), although Block (1955) concluded that few fish spawn more than twice. Mortality of fish in the spawning run from Lake Koocanusa to Young Creek ranged from 27 to 60%, the rates being somewhat higher for males than for females (Huston et al. 1984).

Westslope cutthroat trout are thought to spawn predominantly in small tributaries. Migratory forms may spawn in the lower reaches of the same streams used by resident fish (Johnson 1963). Body size (migrants are larger) might influence the suitability or selection of sites related to stream size. Not all of the same tributaries used for spawning in one year may be used in the following year (Block 1955). Headwaters and upper reaches of large river basins like the Coeur d'Alene and St. Joe are typically dominated by resident and fluvial forms, but tributaries to lakes primarily support adfluvial fish (Averett and MacPhee 1971; Thurow and Bjornn 1978; Rieman and Apperson 1989).

Table 1.—Summary of life history, habitat use, population, and community information for westslope cutthroat trout. Data were summarized from Bjornn (1957), Averett (1962), Averett and MacPhee (1971), Rankel (1971), Mauser (1972), Athearn (1973), Pratt (1984b), Shepard et al. (1984), Lewynsky (1986), Hoelscher and Bjornn (1989), and Rieman and Apperson (1989).

	Stream order				
Life history	**Winter (D-J-F)**	**Spring (M-A-M)**	**Summer (J-J-A)**	**Fall (S-O-N)**	**Habitat type**
Total	Highest densities in 2nd and 3rd order streams				pools
Fluvial					
spawners	>3	1–4	1–4	>3	pools with overhead cover
fry	1–4	1–4	1–4	1–4	stream margins, low velocity areas, backwaters, side channels
juvenile	2–4	2–4	2–4	2–4	main channel pools
subadult	>3	>3	>3	>3	pools with overhead cover
Adfluvial					
spawners	lake	1–4	1–4	lake	same as fluvial
fry	1–4	1–4	1–4	1–4	same as fluvial
juvenile	2–4	2–4	2–4	2–4	same as fluvial
subadult	lake	lake	lake	lake	top of thermocline
Resident					
spawners	1–3	1–3	1–3	1–3	same as fluvial
fry	1–3	1–3	1–3	1–3	same as fluvial
juvenile	1–3	1–3	1–3	1–3	same as fluvial
subadult	1–3	1–3	1–3	1–3	same as fluvial

Life history	**Temperature (°C)**	**Age (y)**	**Biomass (g/m^2)**	**Abundance (#/100m^2)**
Total	< 16	all	5–18	0.3–500
Fluvial				
spawners		3–6		
fry		0		
juvenile	7–16	1–3		0.3–122
subadult		3+		0.2–7
Adfluvial				
spawners		3–6		
fry		0		
juvenile	7–16	1–3		
subadult		3+		
Resident				
spawners		3–5		
fry		0		
juvenile		1–3		
subadult		3+		

Fry emerge after yolk absorption, and at a length of about 20 mm (Shepard et al. 1984). After emergence, many fry disperse downstream. Hoelscher and Bjornn (1989) captured 1,512 trout (cutthroat trout and rainbow trout) fry between 9 June and 5 August in North Fork Grouse Creek, a tributary of Lake Pend Oreille, Idaho. Fry emerged from gravel between 20 June and 14 July. Peaks in the number of fry moving downstream coincided with peaks in stream discharge.

After an initial exodus of fry, offspring of migratory forms that remain may spend 1–4 years in their natal stream (Block 1955; Johnson 1963; Averett and MacPhee 1971; Rankel 1971; Thurow and Bjornn 1978; Huston et al. 1984; Liknes and Graham 1988). Most emigrants from tributaries of the St. Joe River in Idaho

Table 1.—Continued

Life history	Other fishes in community
Fluvial	
spawners	sculpin, mountain whitefish, bull trout, brook trout, steelhead, hatchery rainbow trout, chinook salmon
fry	sculpin, mountain whitefish, bull trout, brook trout, steelhead, hatchery rainbow trout, chinook salmon
juvenile	northern squawfish, mountain whitefish, brook trout, steelhead, rainbow trout, chinook salmon, cyprinids
subadult	northern squawfish, mountain whitefish, brook trout, steelhead, rainbow trout, chinook salmon, cyprinids
Adfluvial	
spawners	for all life stages, same as fluvial, plus lake species: kokanee, lake trout, brown trout, cyprinids, northern pike, bass, yellow perch
fry	
juvenile	
subadult	
Resident	
spawners	for all life stages: sculpin, bull trout, brook trout, steelhead, hatchery rainbow trout
fry	
juvenile	
subadult	

Table 2.—Maturity rates (proportion mature at age) of westslope cutthroat trout. Data for Hungry Horse Creek, St. Joe River, and Wolf Lodge Creek were summarized by Lukens (1978) and are predicted rates from age composition of spawners. Data for the Coeur d'Alene River (Lewynsky 1986; Apperson et al. 1988) and Middle Fork Salmon River (Mallet 1963) are actual proportions of maturing fish in population samples. Table was adapted from Rieman and Apperson (1989).

Population	Age 3	Age 4	Age 5	Age 6
Hungry Horse Creek	0.10	0.73	0.98	—
St. Joe River	0.18	0.88	0.98	—
Wolf Lodge Creek	0.00	0.03	0.65	0.90
Middle Fork Salmon River	—	0.75	1.00	0.00
Coeur d'Alene River[a]	0.13	0.14	0.60	1.00
Coeur d'Alene River[b]	0.20	0.55	1.00	—

[a] Lewynsky (1986).

[b] Apperson et al. (1988).

Table 3.—Age distribution of migrant westslope cutthroat trout from tributaries of the St. Joe River, Idaho (Thurow and Bjornn 1978), Hungry Horse Creek, Montana (Huston 1973), and Young Creek, Montana (Huston et al. 1984).

		Age		
Location	Number	1	2	3
St. Joe River	141	25%	74%	1%
Hungry Horse Creek	563	37%	53%	10%
Young Creek	7168	13%	54%	33%

and from Hungry Horse Creek in Montana were age 1 (table 3). As many as 49% of these migrants from Young Creek to Lake Koocanusa, Montana, survived to return as spawners (Huston et al. 1984). Only 28% of adult fish examined in the St. Joe River, however, had immigrated at age 1 (Averett 1962), suggesting that older migrants may have better survival to maturity than do younger ones. Most juvenile migrants leave tributaries in spring or early summer, and most movement is at night (Huston et al. 1984). Some systems may have a fall migration (Liknes 1984). Size of migrants may depend on environment (table 4). Juvenile migrants obtained in sporadic sampling in tributaries of Hayden Lake, Idaho, from April to June were from 94 to 158 mm long (Gamblin 1988). Migrants from a St. Joe River tributary in Idaho captured from 5 to 29 June were mostly from 100 to 170 mm long (Thurow and Bjornn 1978).

Subadult and adult fluvial westslope cutthroat trout (greater than 150 mm) often make long seasonal migrations, e.g., as much as 100 km or more (Bjornn and Mallet 1964; Thurow and Bjornn 1978; Liknes 1984). Tagged fish in the St. Joe River, Idaho, moved downstream in the fall and back upstream in the spring with little movement in the summer (Thurow and Bjornn 1978). Most downstream migrants moved at night and after the water temperature had declined below about 15°C. Such migrations presumably are to find areas of suitable winter habitat (Lewynsky 1986; Peters 1988). Little or no movement was observed in systems with an abundance of high quality pools that could be used for winter habitat (Mauser 1972; Peters 1988).

Habitat Relations

Waters inhabited by westslope cutthroat trout generally are cold and nutrient poor (Liknes and Gra-

Table 4.—Estimated mean length-at-age (in mm) for fluvial and adfluvial westslope cutthroat trout. Table was adapted from Rieman and Apperson (1989). Data were summarized by Lukens (1978) and Pratt (1985).

Life history Water	Age						
	1	2	3	4	5	6	7
Fluvial (river) Middle Fork Salmon River	60	100	174	254	322	371	
Flathead River	55	103	157	242	305	336	381
Coeur d'Alene River	74	115	175	270	350	420	
St. Joe River	52	91	143	192	243	291	
Marble Creek	50	133	178	235	254		
Kelly Creek	66	101	153	212	251	306	
Adfluvial (lake)							
Wolf Lodge Creek[a]	74	125	214	287	328	365	
Wolf Lodge Creek[b]	69	107	149	236	299	343	
St. Joe River	72	143	266	338	386		
Flathead River	64	120	189	261	311	350	382
Lake Pend Oreille	80	148	261	358			
Priest Lake[a]	89	147	271	326	366		

[a] 2-year migrants.

[b] 3-year migrants.

ham 1988; Rieman and Apperson 1989). Growth varies widely but is probably strongly influenced by habitat productivity. Growth is generally higher for migrant forms that spend some period in the larger rivers or lakes (Rieman and Apperson 1989).

Although westslope cutthroat trout may be found throughout large river basins, spawning and early rearing occurs mostly in headwater streams (Platts 1979; Rieman and Apperson 1989; Mullan et al. 1992). Spawning habitat has been characterized as gravel substrates with particle sizes ranging from 2 to 75 mm, mean depths ranging from 17 to 20 cm, and mean velocities between 0.3 and 0.4 m/s (Liknes 1984; Shepard et al. 1984). Redds are 0.6 to 1.0 m long and 0.32 to 0.45 m wide (Liknes 1984).

Substrate composition is believed to strongly influence survival. Weaver and Fraley (1991) demonstrated a negative relation between emergence success and the percentage of fine sediment in artificial substrate. Others report that sediment reduces embryo survival (Irving and Bjornn 1984) and food and space for rearing juveniles (Bjornn et al. 1977). Highly embedded substrates may be particularly harmful for juvenile cutthroat trout that typically enter the substrate for cover in winter. Accurately predicting the effects of fine sediment on wild populations remains difficult (Everest et al. 1987; Chapman 1988), and some populations persist despite abundant sediment (Magee 1993). Evidence for a negative influence of fine sediment concentrations is widespread, however, and in general increased sediment in substrates must be viewed as an increased risk for any population.

Often westslope cutthroat trout are widely distributed in occupied basins (Miller 1957; Platts 1979; Shepard et al. 1984) and may occur in virtually every stream with suitable habitat. Densities may vary widely, however, among streams (Rieman and Apperson 1989; Ireland 1993). Cutthroat trout microhabitats are associated with water velocities ranging from 0.1 to 0.3 m/s (Griffith 1970; Pratt 1984a). Westslope cutthroat trout less than 100 mm long are found predominantly in pools and runs. The distribution and abundance of larger westslope cutthroat trout has been strongly associated with pools (Shepard 1983; Pratt 1984a; Peters 1988; Ireland 1993) and in general stream reaches with numerous pools support the highest densities of fish (Shepard 1983; Peters 1988; Hoelscher and Bjornn 1989; Ireland 1993). Habitats that provide some form of cover also seem to be preferred over those that do not (Griffith 1970; Pratt 1984a; Lider 1985). Fraley and Graham (1981) found the best models for predicting the distribution of trout in the Flathead Basin included cover as an independent variable. In winter, small fish tend to use areas where cover is provided by the interstitial space in the substrate (Wilson et al. 1987; Peters 1988) hence the concern about sediment and embedded substrates. Larger fish congregate in pools during winter (Peters 1988), often in very large numbers (Lewynsky 1986).

It is not clear how strongly variability among local habitats influences the characteristics and dynamics of westslope cutthroat trout populations. A tendency to home to natal streams for reproduction must result in some isolation among groups or subpopulations. A logical consequence of this behavior is that natural selection should tend to produce adaptations to local environments (Leary et al. 1985). No systematic study of the character of site-specific adaptations has been completed for westslope cutthroat trout, but they are thought to be adapted to the presence of a parasite that is indigenous to waters of Glacier National Park (Marnell 1988). Other indirect evidence of local adaptation is the observation that other subspecies of cutthroat trout sometimes do not grow and survive as well as westslope cutthroat trout when they are planted in its habitats (Heimer 1970; Beach 1971; Goodnight and Mauser 1974; Rieman and Apperson 1989).

The relations between salmonid fishes and their habitats have been considered predominantly at the reach, channel unit, and microhabitat scales. Very little is known about habitat relations at larger scales. The potential for separate breeding groups among tributaries suggests that populations exist as part of a larger regional population. The collection of subpopulations within a population is consistent with the concept of a metapopulation (Hanski and Gilpin 1991). Emerging metapopulation theory suggests that the spatial distribution of local populations within a heterogenous environment may have an important influence on long-term persistence. If populations are not exposed to the same risks, their extinction at the same time is unlikely. The connection of local populations through dispersal is critical to metapopulation dynamics (Hanski and Gilpin 1991; Shaffer 1991; Sjögren 1991). The complexity in such structure provides a species with a mechanism for spreading the risk of extinction (den Boer 1968).

Biotic Interactions

Westslope cutthroat trout coevolved with mountain and pygmy whitefish, several sculpins, cyprinids, and catostomids. In Columbia River tributaries, the subspecies is most commonly associated with bull trout, resident and anadromous rainbow trout or steelhead, and chinook salmon.

Although closely related, cutthroat trout and rainbow trout have remained reproductively distinct where they evolved in sympatry (Behnke 1992). Where nonnative rainbow trout have been introduced, the species may segregate with rainbow trout in downstream reaches and cutthroat trout in upstream reaches (Hoelscher and Bjornn 1989). Segregation from introduced rainbow trout has been incomplete, however, and hybridization is widespread (Behnke and Zarn 1976; Rieman and Apperson 1989). Hybrids have been identified in the zone of overlap in their distributions (Hoelscher and Bjornn 1989) but are also found throughout much of the range of westslope cutthroat trout where introduced rainbow trout populations are not necessarily strong (Liknes 1984; Rieman and Apperson 1989).

Yellowstone cutthroat trout have also been introduced widely into the range of westslope cutthroat trout (Liknes 1984; Rieman and Apperson 1989). Yellowstone cutthroat trout were often cultured for routine stocking and were particularly popular for use in high mountain lakes (Rieman and Apperson 1989). Hybridization between these subspecies is common and again appears to be a problem throughout most of the range of westslope cutthroat trout.

Westslope cutthroat trout do not seem to be as piscivorous as other cutthroat trout or rainbow trout. Behnke (1992) speculated that adoption of a feeding strategy aimed at invertebrates was a cost of coevolving with the highly piscivorous bull trout and northern squawfish. Sympatric populations of bull trout and westslope cutthroat trout appear to selectively segregate in use of habitat and prey (Pratt 1984a; Nakano et al. 1992). Small rainbow trout and cutthroat trout in Lake Koocanusa, Montana, derived approximately 50% of their caloric intake from *Daphnia* spp. (McMullin 1979). In summer the diets of both species were supplemented with terrestrial insects, fish, and aquatic Diptera. As individuals grew, their diets included increasing amounts of fish, but the rainbow trout ate greater amounts than did cutthroat trout.

Brook trout are thought to have replaced many westslope cutthroat trout populations in headwater streams (Behnke 1992), but the mechanism of interaction is not clear (Fausch 1988; Rieman and Apperson 1989). In the laboratory, Griffith (1972) was unable to show that brook trout displaced equal-sized cutthroat trout. Brook trout may have replaced cutthroat trout through some form of competitive displacement or simply filled empty habitat when cutthroat trout declined from some other cause (Griffith 1970,1988). Cutthroat trout fry did survive better when planted in tributaries of Priest Lake, Idaho, where brook trout were absent (Cowley 1987; Irving 1987). When the two species coexist, cutthroat trout seem to predominate in the higher gradient reaches (Griffith 1988), whereas brook trout may prevail in lower gradients. Existing data for Idaho and Montana watersheds suggest that westslope cutthroat trout are most abundant in reaches with 6 to 14% gradient and occur in gradients up to 27% (Fausch 1989). Fausch (1989) indicated that brook trout attained greatest abundance at less than 3% gradient and were not found at greater than 15% gradient. Fausch (1989) speculated that brook trout either do not enter or do not survive and reproduce in reaches that exceed 7% gradient. As a result, high-gradient reaches provide refuges for cutthroat trout. He concluded that brook trout probably are not well adapted to life in steep gradients whether or not cutthroat trout are present, and cutthroat trout would be more abundant than has been observed in lower gradient reaches if brook trout were absent.

Feldmuth and Eriksen (1978) conducted experiments to estimate the "critical thermal maximum" (CTM) for westslope cutthroat trout. The CTM was 27.1°C for cutthroat trout, a value lower than those estimated for brook trout (29.8°C), brown trout (29.6°C), and rainbow trout (31.6°C). Native cutthroat trout are apparently less tolerant of warm water than are nonnative salmonids. Native cutthroat trout might therefore fare better in interactions with nonnative salmonids in colder waters, but less well in warmer waters (cf. DeStaso and Rahel 1994). Mullan et al. (1992) speculated that water temperature may play an important role in the displacement of native cutthroat trout and bull trout by rainbow trout in tributaries of the Methow River, Washington.

Reasons for Concern

The current distribution and abundance of westslope cutthroat trout appear to be severely restricted compared with historical conditions (Bjornn and Liknes 1986; Liknes and Graham 1988; Rieman and Apperson 1989; Behnke 1992). Declines are probably continuing in much of the remaining range. Westslope cutthroat trout are now believed to persist in only 27% of their historical range in Montana, and are genetically unaltered in only 2.5% of the native range (Liknes 1984; Liknes and Graham 1988). Rieman and Apperson (1989) estimated that populations considered as "strong" (greater than or equal to 50% of historical potential) by Idaho Department of Fish and Game biologists remained in only 11% of the historical range. Idaho biologists also believed that less than 4% of the historical range supported strong populations not threatened by hybridization (Rieman and Apperson 1989).

Construction of dams, irrigation diversions, or other migration barriers such as culverts (Rieman and Apperson 1989) have isolated or eliminated areas of westslope cutthroat trout habitat that were once available to migratory populations. There has been no effort to quantify the amount of habitat lost, but whole river basins have been blocked (e.g., Pend Oreille River, South Fork Flathead River). Resident forms may persist in isolated segments of streams, but the loss of the migratory life history and the connection with other populations potentially important to gene flow or metapopulation dynamics may seriously compromise the potential for long-term persistence.

Climate change may play an important role in the further restriction of westslope cutthroat trout populations in the future. Westslope cutthroat trout appear to prefer colder water than do other salmonids. The primary distribution of rearing populations is often in the upper, cooler reaches of drainage basins. Mullan et al. (1992) speculated that warmer temperatures associated with climate change would result in further restriction of cutthroat trout in the Methow River basin. Neitzel et al. (1991) summarized available models of climate change, suggested that mean air temperatures in the Pacific Northwest may increase by 2°C to 5°C in the next 50 to 100 years, and inferred catastrophic effects for many salmon stocks. Kelehar and Rahel (1992) used a similar approach to predict that the current range of cutthroat trout in Wyoming would decline by 65% with a 3°C warming in summer air temperature. An equally severe restriction in distribution might also be expected in the range of westslope cutthroat trout in Idaho and Montana.

Fragmentation of habitats and the consequent isolation of local populations may threaten the persistence of many species (Gilpin and Soulé 1986; Hanski and Gilpin 1991; Sjögren 1991; Rieman et al. 1993). Isolation of cutthroat trout populations has resulted from human-caused habitat and environmental changes. Overfishing and competition also restrict their distribution to a smaller portion of the original range. Populations have been reduced in abundance and an increasing number are being isolated from other populations (Rieman and Apperson 1989).

The probability that a local population will persist depends on the quality of its habitat, but perhaps also on chance events and the connections to other populations. In general, managing cutthroat trout has focused on preserving good habitat wherever it remains. Although biologists generally have some sense of what good habitat is and how to protect it, relatively little is known about the appropriate amount or distribution of habitat necessary to ensure long-term persistence. A growing body of both theoretical and empirical work indicates that the persistence of many species will be strongly dependent on both the amount and spatial geometry (or isolation) of available habitat (see Rieman et al. 1993). Viability analyses have been conducted for many species both to quantify extinction risks and to evaluate the design of conservation reserves. Such analyses generally require extensive data that are unavailable for most westslope cutthroat trout populations. It is still useful, however, to consider the processes of extinction and the nature of the risks relevant for many cutthroat trout populations.

Extinction risks for a species might be characterized as deterministic, genetic, or stochastic (Leigh 1981; Gilpin and Soulé 1986). Deterministic risks include cumulative effects that result in mortality that cannot be compensated by increased survival at another stage. For example, increased fishing and cumulative habitat degradation have led to increased mortality in westslope cutthroat trout populations (Bjornn et al. 1977; Weaver and Fraley 1991) and may be responsible for the disappearance of many populations (Rieman and Apperson 1989). The regional declines in abundance and continuing loss of populations indicate that deterministic risks are high for westslope cutthroat trout through much of its range.

Genetic risks include loss of genetic variation through reduction in population size and loss of genetic integrity through hybridization with introduced species (Allendorf and Phelps 1980; Leary et al. 1984; Allendorf and Leary 1988). Hybridization has been widely recognized, and the loss of variation is becoming better known (Liknes 1984; Liknes and Graham 1988). Loss of variation and fitness through small population size has been demonstrated in hatchery stocks of westslope cutthroat trout (Allendorf and Phelps 1980) and in hybridized populations of other salmonids (Leary et al. 1985). The effects of small population size have not been demonstrated in situ (R. Leary, University of Montana, pers. commun.). Nevertheless, loss of genetic variation must be considered a long-term risk in isolated or severely restricted populations of any species (Soulé 1980; Gilpin and Soulé 1986). In the short term, however, many populations likely face greater risks from deterministic and stochastic effects than from loss of genetic variation associated with restricted population size (Shaffer 1987; Stacey and Taper 1992).

Stochastic risks are associated with chance events. They have been characterized as demographic and environmental (Leigh 1981; Shaffer 1987,1991; Ginzburg et al. 1990). Demographic stochasticity includes the random variation in individual birth, death, reproduction, or other characteristics even though the underlying rates may be stable. In general, demographic effects for most species will be felt only at very small (i.e., fewer than 20 to 50 adults) population sizes (Leigh 1981; Shaffer and Sampson 1985; Gilpin and Soulé 1986; Quinn and Hastings 1987; Shaffer 1987). Environmental stochasticity includes random variation in mortality and birth rates driven by environmental variation and is potentially more important than is demographic stochasticity (Shaffer 1987). Risks related to random variation may be high for many species (Leigh 1981; Gilpin and Soulé 1986; Shaffer 1987; Dennis et al. 1991) but generally have not been considered for salmonids.

Dennis et al. (1991) developed an analytic estimation method for extinction parameters based on time series data of population sizes. In essence the probability of a population dropping below some critical number within some period of time can be estimated from information on the variability in number, the initial size of the population, and any trend in population growth. We used the methods of Dennis et al. (1991) to approximate such risks for small populations of westslope cutthroat trout.

We used sequential population density estimates from several streams to estimate variance in the rate of population growth (table 5) as described by Dennis et al. (1991). An extended time series (more than 5 years) was not available for cutthroat trout populations in the Bitterroot River system so we replicated observations through space rather than time. In substituting space for time we assumed that all populations are representative of a single population and that the annual transitions are independent among populations. Those assumptions may be inappropriate in the strictest interpretation, but we believe they are still useful for a first approximation of variation possible in these populations. Violation of our assumptions will most likely lead to an underestimate of the true variances, because of the limited time scale (Pimm and Redfearn 1988) and the potential for spa-

Table 5.—Estimated variance in the infinitesimal rate of growth for westslope cutthroat trout populations monitored in Idaho and Montana. The 95% confidence interval is shown in parentheses. Estimates are calculated after Dennis et al. (1991).

Stream State	Years	Variance	Source
Bitterroot River,[a] Montana	22	0.29 (0.19–0.52)	C. Clancy, Montana Dept. Fish, Wildlife and Parks, pers. commun.
Young Creek, Montana	11	0.3 (0.16–0.78)	Huston et al. (1984)
North Coal Creek, Montana	10	0.11 (0.06–0.29)	Weaver (1992)
South Coal Creek, Montana	6	0.2 (0.09–0.88)	Weaver (1992)
Middle Fork Salmon River, Idaho	7	1.02 (0.49–3.78)	Liter and Lukens (1992)
Lochsa River, Idaho	7	0.69 (0.31–3.01)	Lindland (1982)
St. Joe River, Idaho	10	0.07 (0.04–0.21)	T.C. Bjornn, University of Idaho, pers. commun.

[a] Transitions from 12 streams monitored over 2 to 3 years were pooled as a single population.

tial autocorrelation among populations within years. We considered the annual transitions observed over 3 years within 12 headwater streams to be suitable, although probably conservative estimates of the transitions expected in one system over a longer time.

We estimated the probability of persistence above a threshold of 100 individuals in a population for 100 years. From existing work it appears that adult fish probably represent 20% or fewer of total individuals in most populations (Johnson and Bjornn 1978; Liter and Lukens 1992). We assumed then that 100 total individuals represented an adult population size of fewer than 20, a point short of complete extinction, but certainly low enough to result in serious risk from other factors, i.e., genetic and demographic (Dennis et al. 1991). We did not estimate the mean annual growth rate for populations (Dennis et al. 1991), but rather assumed that all populations varied around some equilibrium with no long-term trend of growth or decline. Our results therefore represent the risks associated with random and not deterministic effects.

The estimated variances for the annual growth rates ranged from 0.07 to about 1.0 (table 5). Estimates were relatively imprecise because of small sample sizes, but provide some indication of the relative stability expected in westslope cutthroat trout populations over a range of sites. The data suggest that variances less than 0.05 are unlikely but substantially higher values are possible, considering our conservative estimates. General predictions of persistence above the threshold were strongly influenced by both the variance and initial population size (figure 1).

If the estimated variances are representative, the results indicate that stochastic risks will increase quickly for many populations that drop to fewer than 2,000 individuals. Any habitat condition or environmental variation that resulted in population variances comparable to the higher estimates used here would also result in high risks. Hunt and Bjornn (1992) estimated that only 800 cutthroat trout remained in the North Fork Coeur d'Alene River. Extrapolations of population density estimates to available habitat suggest that some populations in tribu-

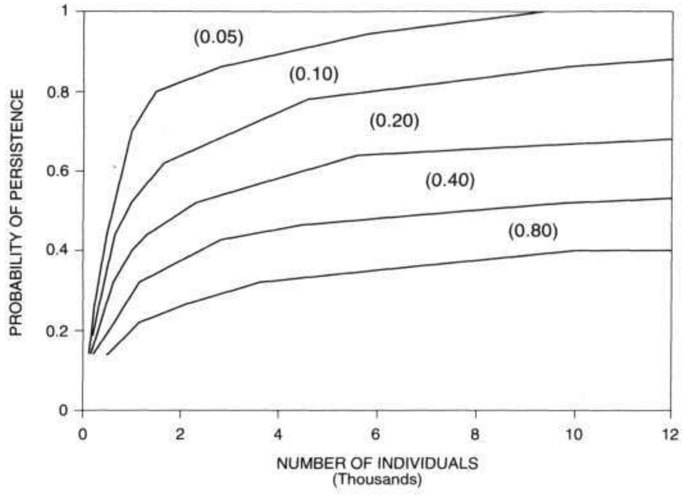

Figure 1.—Estimated probabilities of persistence for 100 years for populations of different initial size and temporal variance in instantaneous rate of growth. Variances are shown in parentheses. Calculations are after Dennis et al. (1991). The threshold of persistence was assumed to be 100 individuals.

taries to the Bitterroot River number from 1,000 to 2,000 individuals (C. Clancy, Montana Department of Fish, Wildlife and Parks, pers. commun.). Elsewhere, some isolated populations are even smaller (B. Shepard, Montana Department of Fish, Wildlife and Parks, pers. commun.).

Extinction risks related to random variation of populations appear to be an important cause for concern. Extinction for many isolated populations may simply be a matter of time. Although our estimates are the result of crude approximations, they are consistent with a growing body of evidence for similar risks for many species (see Rieman et al. 1993). Our estimates do not include the potential for catastrophic loss and might therefore be overly optimistic (see Mangel and Tier 1994). If chance events represent an important risk for many populations, further loss of cutthroat trout populations will likely continue even with no further loss of habitat. Effective conservation of the subspecies will probably require the maintenance or restoration of well-connected mosaics of habitat (see Frissell et al. 1993; Rieman et al. 1993; Rieman and McIntyre 1993).

Causes of the Decline

Causes of the decline of westslope cutthroat trout include competition with and predation by non-native species, genetic introgression, overfishing, habitat loss and fragmentation, and habitat degradation (Liknes 1984; Liknes and Graham 1988; Rieman and Apperson 1989). Habitat loss was identified as the primary cause of decline in 87% of the stream reaches supporting depressed populations in Idaho (Rieman and Apperson 1989). Fishing contributed to the decline in 47% of the reaches. Competition and genetic introgression were considered to be important causes for decline in 12% and 15%. Genetic introgression was believed to be the most important cause for decline of westslope cutthroat trout populations in Montana (Liknes and Graham 1988).

Nonnative salmonids have been planted throughout the range of westslope cutthroat trout including Glacier National Park (Marnell 1988). Behnke (1992) speculated that nonnative species such as kokanee, lake trout, and lake whitefish caused declines of westslope cutthroat trout in lakes. Predation and competition are both thought to be important. Opossum shrimp (*Mysis relicta*) have also been introduced in several lakes in Idaho and Montana and might influence cutthroat trout populations as well. As westslope cutthroat trout declined in several locations, planted kokanee populations increased, but it is not clear whether the trends are circumstantial or reflect an important interaction. Some westslope cutthroat trout populations have persisted despite the presence of large kokanee populations (Rieman and Apperson 1989).

Fausch (1988,1989) concluded that the persistence of westslope cutthroat trout is jeopardized in streams also supporting brook trout or brown trout. Behnke (1992) concluded that brown trout, brook trout, and rainbow trout, along with changes in flow and water quality, were responsible for the demise of westslope cutthroat trout in the Spokane and Clark Fork drainages.

Westslope cutthroat trout have been identified in stomachs of bull trout, lake trout, and sculpins (Beach 1971; Athearn 1973; Mauser 1986). Predation clearly happens, but the relative importance of such predation in the decline of westslope cutthroat trout has not been identified. Jeppson and Platts (1959) and MacPhee and Reid (1971) reported increased survival of cutthroat trout following intensive removal of northern squawfish, but others have found little evidence that such predation was important (Bjornn 1957; Jeppson 1960; Falter 1969; Apperson et al. 1988). Rieman and Apperson (1989) argued that predation, especially in combination with fishing, can act as a depensatory source of mortality and maintain a population in a low equilibrium region compared with historical levels (see Peterman 1977). The importance of such a predator trap for westslope cutthroat trout, however, is yet to be demonstrated.

Westslope cutthroat trout are highly susceptible to angling (MacPhee 1966; Lewynsky 1986; Behnke 1992). Population abundance and average body size have increased in several populations following angling restrictions (Johnson and Bjornn 1978; Thurow and Bjornn 1978; Peters 1988; Rieman and Apperson 1989). Rieman and Apperson (1989) found evidence of a depensatory effect in fishing (mortality increases with decline in population size) and speculated that harvest could lead to the elimination of some small populations. Others believe that angling pressure led to the virtual elimination of fluvial fish in some river systems (T.C. Bjornn, University of Idaho, pers. commun.). Special harvest restrictions may be necessary to maintain most westslope cutthroat trout populations (Rieman and Apperson 1989).

Despite the obvious influence of fishing, its importance relative to other causes of decline is not clear.

The westslope cutthroat trout in the Coeur d'Alene River, for example, did not respond to special regulations, perhaps because of noncompliance with angling regulations, harvest during other portions of the life history, or stress caused by catch-and-release angling (Rieman and Apperson 1989). Fishery managers speculated that degraded habitat prevented any population response (N. Horner, Idaho Department of Fish and Game, pers. commun.). Fishing has clearly caused the decline of the older and larger members of some populations and may ultimately limit recruitment. Thurow and Bjornn (1978) reported greater densities of cutthroat trout fry in stream reaches closed to fishing and concluded that fishing may have limited fry recruitment in other unregulated reaches.

Habitat loss and degradation are primary concerns of many biologists working with westslope cutthroat trout (Liknes 1984; Liknes and Graham 1988; Rieman and Apperson 1989). Forest management has probably played an important role in habitat disruption but its effects are not always consistent or easily predictable. Increased fine sediment has generally been a primary concern of biologists dealing with fish habitat relations (e.g., Stowell et al. 1983; Rieman and Apperson 1989). The number of salmonids, including westslope cutthroat trout, observed in snorkeling surveys in the South Fork Salmon River, Idaho, was negatively correlated with measures of substrate embeddedness (Thurow 1987); other work predicted a substantial reduction in incubation or emergence survival with increased fine sediment (Irving and Bjornn 1984; Weaver and Fraley 1991). Westslope cutthroat trout abundance, however, could not be clearly associated with intragravel fine sediment in Idaho's Coeur d'Alene River (Gamblin 1988) or in tributaries to the Bitterroot River, Montana (Clancy 1993). Much of the area where westslope cutthroat trout are located is in belt geologies where roads and timber harvest seem to aggravate problems associated with coarse (50–150 mm) rather than with fine substrates (Gamblin 1988; Rieman and Apperson 1989; G. Kappesser, Idaho Panhandle National Forests, pers. commun.). In many watersheds excessive bedload transport and scour are obvious problems during peak flows (G. Kappesser, Idaho Panhandle National Forests, pers. commun.). In low-gradient reaches bed aggradation may result in the loss of pools, reduced pool volume, and channel dewatering during low flows. The relatively simple and unstable channels that result from intensive management of these basins were overlooked as problems in earlier concerns focused on fine sediment (Gamblin 1988; Rieman and Apperson 1989). It is evident now, however, that intensive management may lead to habitat disruption through a variety of mechanisms.

Disturbance of stream banks and riparian areas, construction of roads, and removal of upland vegetation have been associated with alteration of stream flows, increased erosion and sediment loading, and increased temperatures. There is a large body of information documenting the effects of such disturbance on habitat for stream salmonids (e.g., Brown and Krygier 1970; Salo and Cundy 1987; Meehan 1991). The nature and magnitude of channel and habitat changes may vary with the type, extent, and intensity of disturbance, with the species involved, and with physiographic characteristics of the watershed. Often it has proven difficult to quantify or predict effects precisely. The results of existing studies do not permit clear conclusions regarding causes or the magnitude of population declines. It is clear, however, that habitat disruption can result from intensive forest management, and that such changes can directly influence populations in negative ways.

The causes for decline of westslope cutthroat trout are no doubt varied. That most strong populations remain largely in roadless and wilderness areas or national parks (Liknes 1984; Liknes and Graham 1988; Marnell 1988; Rieman and Apperson 1989), however, is clear evidence that human intervention has been important.

Current Management

Westslope cutthroat trout are considered sensitive by Regions 1 and 4 of the USDA Forest Service and by the USDI Bureau of Land Management, and considered a species of special concern by the Idaho Department of Fish and Game (Moseley and Groves 1990). The Idaho Department of Fish and Game has made extensive use of restrictive fishing regulations (e.g., size limits, reduced bag limits, catch and release, closures) in most systems supporting westslope cutthroat trout populations (Rieman and Apperson 1989). The Montana Department of Fish, Wildlife, and Parks has undertaken extensive habitat restoration (Rieman and Apperson 1989) and instituted a system of protective harvest regulations (Liknes 1984). Both states have established captive broodstocks free of introgression from rainbow trout or Yellowstone cutthroat trout. In Montana, stocking has been used to restore westslope cutthroat trout populations in waters where they once occurred but have been either eliminated or introgressed with nonnative trout. Westslope cutthroat trout are now stocked in place of other trout in Idaho mountain lakes within the subspecies' range. Net pen and hatchery rearing are also used to supplement or support fisheries for westslope cutthroat trout in Idaho where wild populations are believed to be nonviable, where they have been displaced by other species, or where hybridization with other subspecies of cutthroat trout or rainbow trout has been extensive (Rieman and Apperson 1989). The range of westslope cutthroat trout in Idaho has been reduced to such an extent that the remaining populations are considered extremely important (Rieman and Apperson 1989).

Research Needs

Interactions with nonnative species through predation, competition, or hybridization are believed to be an important threat. The risks and magnitude of displacement are poorly understood. It is not clear whether displacement by nonnative species is inevitable throughout the range or whether some populations are at much greater risk than others. It is not clear how habitat disruption or other human effects may aggravate the risks.

Westslope cutthroat trout populations are becoming increasingly fragmented and isolated. New work should describe risks associated with small population size and isolation. Emerging metapopulation theories may apply to trout populations, but there is little information to validate this. New work considering larger scale spatial patterns in habitat and fish distribution, dispersal rates and mechanisms, and disturbance regimes is needed.

The spatial and temporal distribution of each lifestage of westslope cutthroat trout is not well documented. Habitat preferences or requirements are suspected, but not well defined. More effective measures of habitat quality or suitability are needed to improve recognition of important habitat disruption. Such measures would also help identify the most productive or highest potential areas for long-term conservation.

Life history diversity is suspected to be an important mechanism for stabilizing populations in highly variable environments and may play an important role in the long-term persistence of cutthroat trout populations. The relation between resident and migratory forms and the differences in habitat requirements or sensitivity to habitat disruption should be better defined.

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