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EFFECTS OF DENSITY-DEPENDENCE, ENVIRONMENT AND SPECIES INTERACTION DURING SPAWNING AND INCUBATION ON POPULATION DYNAMICS OF PINK AND SOCKEYE SALMON IN THE AUKE LAKE SYSTEM, SOUTHEAST ALASKA

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

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Juneau, Alaska

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ABSTRACT

Mechanisms that regulate or influence fry and smolt production of pink and sockeye salmon in the Auke Lake system, southeast Alaska, were studied with special emphases on effects of: 1) density-dependence; 2) environmental effects; and 3) species interaction. There has been an increasing trend in the residuals of spawner-recruit models for pink and sockeye salmon since the late 1970's. A strong positive influence of precipitation was found in sockeye smolt production. Estimated spawner capacity of pink salmon was 15 times greater than sockeye salmon in the system.

Pink salmon spawners varied in stream life (5-11 days), spawning efficiency (30-70% of daily cohorts of females retained less than 500 eggs at death), and habitat selection (30-70% spawned in Auke Creek rather than Lake Creek, the inlet stream). Variation of these attributes in female pink salmon was explained by various environmental variables using generalized linear models.

Repeated use of limited spawning grounds by Pacific salmon, i.e., redd superimposition, can cause density-dependent mortality. Pink salmon egg loss from part of Auke Creek, estimated by a series of mark and recapture experiments, was roughly proportional to spawner abundance and not related to discharge. The maximum daily egg loss was estimated to be 3-400,000 eggs. Eggs in samples were more advanced in development later in the season. Eggs were washed out from the streambed due to redd superimposition; eggs spawned by early pink salmon spawners suffered higher mortality than eggs spawned by later spawners.

The peak sockeye spawning preceded the peak pink spawning by approximately one week in Lake Creek, and the major spawning areas of sockeye salmon occurred approximately 250-350 m upstream from those of pink salmon. Microhabitat selection measured by four variables differed significantly between the species, but discrimination between the species was impossible because of large overlaps. Habitat variation was greater among different runs of sockeye salmon than between the two species. Sockeye salmon shifted spawning sites from riffles to pools as the season progressed.

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CHAPTER 1. INTRODUCTION

This dissertation explores mechanisms that regulate or influence the fry and smolt production of pink salmon (*Oncorhynchus gorbuscha*) and sockeye salmon (*O. nerka*) in the Auke Lake system, southeast Alaska. It focuses on three components of mortality source: 1) density-dependence; 2) environmental effects; and 3) species interaction. Based on findings in historical data analysis, several field experiments were conducted in the Auke Lake system to understand biological and environmental events occurring between spawning migration and fry (smolt) outmigration and to determine relative importance of each mortality component for the population dynamics of pink and sockeye salmon in this system.

Density-dependence in the smolt production of Pacific salmon has been pointed out theoretically as early as the 1950's (Neave 1953; McNeil 1964a; Chapman 1973). Subsequently, it was described by biometrical or experimental approaches (McNeil 1969; Heard 1978; West and Mason 1987; Ignell 1988; Parenskiy 1990; Chebanov 1991; Bonnell 1991). A number of studies were also conducted for Atlantic salmon (*Salmo salar*) to demonstrate density-dependent, especially compensatory, mortality in smolt production from natural streams (Elliott 1993; Kennedy and Crozier 1993; Ward and Slaney 1993). Despite the numerous studies on this subject, there is little agreement on the underlying mortality mechanisms of density-dependence in the smolt production of salmonids.

Repeated use of limited spawning grounds by an excessive number of Pacific salmon spawners can cause redd superimposition and thus density-dependent mortality (Buklis and Barton 1984; Chebanov 1986; McNeil 1964a; Heard 1978; Ignell 1988; Semenchenko 1988; Parenskiy 1990; Chebanov 1991). Redd superimposition can be a major mortality factor at high spawning densities (Smironov 1947, McNeil 1964a). Salmonids including pink and sockeye salmon construct redds by digging a certain area of streambed to deposit their eggs into more than a few spots called egg pockets (Crisp and Carling 1989). Since available areas for spawning are limited, later spawners may superimpose their redds on previously constructed redds, displacing eggs deposited by earlier spawners. The rate of redd superimposition could be an increasing function of the egg density in the gravel, such that the total number of eggs successfully deposited in a stream approaches an asymptote (i.e., carrying capacity) as the number of spawners increases (McNeil 1964a). Unlike sockeye salmon that normally spend at least one year in the freshwater after emergence, pink salmon utilize the freshwater environment only for spawning and egg incubation. Thus, if any density-dependence is detected in the fry production of pink salmon, an exact stage at which the density-dependent mortality occurred may be pointed out by conducting a field experiment. In this study I hypothesize that such density-dependence would occur if redd superimposition is a major mortality source for the pink salmon fry production. This hypothesis is in part based on previous work in which an asymptotic production curve of pink salmon fry was observed (Ignell 1988).

It is always possible to add environmental variables into any spawner-recruit model. Indeed adding environmental variables to explain residuals from a predicted spawner-recruit model is a frequent approach (e.g., Anderson and Wilen 1985; Stocker et al. 1985; Lorda and Crecco 1987; Holtby and Scrivener 1989; Clark 1992; Quinn and Niebauer 1995). However, when several different sets of environmental data are available for given spawner-recruit data, some environmental variables may both correlate significantly with the residuals of a predicted model and give some potentially understandable mechanism to explain the interaction, even if such interaction really does not exist (Hilborn and Walters 1992). The same caution must be taken into account when incorporating a species interaction term into a spawner-recruit model.

Pink and sockeye salmon, the two most dominant species in the Auke Lake system, enter Lake Creek with similar run timings (at the same time of year) and are known to occupy relatively similar spawning habitats. In a broad sense, all five species of Pacific salmon require quite similar spawning habitat and perform similar spawning behavior. In terms of hydrology and geomorphology, measurements of habitat variables obtained from streams in North America largely overlap among species of Pacific salmon (Burner 1951; Smith 1973). Furthermore, spawning behaviors such as digging, mating and redd defense are almost indistinguishable among species (Briggs 1953; Mathisen 1962; McCart 1969; Heard 1972; Tautz and Groot 1975; Chebanov 1980; Schroder 1981). For sympatric populations of salmon, it is thus likely that some kind of species interaction exists during spawning, which may influence fry or smolt production of competing species. If later spawners of pink salmon in Auke Creek cause any mortality of previously deposited eggs by earlier pink salmon spawners through redd superimposition, the same mechanism may also apply among different sympatric species which displace eggs of one species with their own eggs. Instead, some species may force others to spawn at less suitable habitat for egg incubation through competition for limited spawning areas.

In the absence of competitive interaction, niche breadth of a species would increase with increasing abundance of the species as a result of intraspecific interaction or density-dependence, since they can no longer specialize on their preferred resources but must exploit other resources as well. Under the presence of competitive interaction, on the other hand, species may reduce their niche breadth and niche overlap among the competing species through displacement or exclusion (Diamond 1970; Colwell and Futuyma 1971; MacArthur 1972). Available literature on the species interaction of salmonids is scarce and limited to study of interaction during rearing stages in the freshwater (Nyman 1970; Fausch and White 1981) or during the first feeding stage in the saltwater (Gallagher 1979; Smoker 1984; Beacham 1993). A few exceptions include Maruyama (1981) and Witzel and MacCrimmon (1983) who investigated the selection of spawning habitat by two sympatric species of salmonids.

Although some researchers (e.g., Peterman 1987) consider that many density-dependent and density-independent mechanisms of variability in freshwater survival of Pacific salmon have been widely understood, the existing studies on smolt production have been subject to great uncertainty in part due to lack of adequate data, which has been neither sufficiently accurate or of sufficiently long duration. These studies often provided unreliable parameter estimates for production curves. Recently reliable weir count data of salmonids have become available to fisheries researchers from several streams in North America. The Auke Lake system is one system where populations of Pacific salmon have been monitored since the late 1970s with a substantial accuracy. A weir at Auke Creek is capable of counting both immigrants into and emigrants from the system; it has provided separate estimates of freshwater and oceanic survival rates for different species of Pacific salmon in each brood year. Data collected at this weir are precise because both adults and smolts (fry) are completely enumerated. Study of these multiple data sets obtained from different sympatric Pacific salmon during the same period (i.e., under the same environment) allow better understanding of density-dependence and independence than the study of a spawner-recruit relationship of single species.

This dissertation consists of seven chapters, the first is this introduction. Chapter 2 describes some background of Auke Creek pink and sockeye salmon biology including a brief summary of weir operation, historical escapement pattern, spawning habitats, spawning efficiency in different habitats, and fry and smolt outmigration timing in the system. In Chapter 3, I examine the historical fry and smolt production of pink and sockeye salmon collected at the Auke Creek weir since 1980. According to predicted production models, spawner capacity that maximizes fry and smolt production in the system can be proposed for pink and sockeye salmon. The analyses in this chapter are a basis for the designs and analyses of subsequent field experiments conducted in the Auke Lake system.

The field experiments conducted at Auke and Lake Creeks are described in Chapters 4, 5 and 6, which attempt to explain mechanisms of density-dependent mortality in pink salmon fry production and investigate a species interaction within and between pink and sockeye salmon and its effect on fry and smolt production. Chapter 4 analyses three attributes of pink salmon reproduction: i.e., stream life, spawning efficiency, and selection of spawning streams. The analyses are based on the results of a tagging study which simultaneously studied a relationship between these attributes and environmental variables measured during the spawning season. Analysis in Chapter 5 estimates the amount of eggs lost from the spawning ground at different levels of spawner abundance and egg density. The study uses a mark and recapture technique and tests the hypothesis that redd superimposition is a significant source of density-dependent mortality in pink salmon fry production. Analysis in Chapter 6 compares spatiotemporal spawner distributions and microhabitat selections between pink and sockeye salmon. The microhabitat analysis examines hydrological and geomorphological characteristics of redds using multivariate statistical techniques.

The final chapter summarizes the findings in this dissertation and discusses the relative importance of each mortality component during spawning and incubation of pink and sockeye salmon to their population dynamics in the Auke Lake system.

CHAPTER 2. BACKGROUND

Auke Creek is a short and steep lake-fed outlet stream that flows approximately 350 m from Auke Lake. Auke Lake is located 17.7 km north of Juneau, Alaska, with an area of 92 hectares. Lake Creek is the primary tributary inlet of the lake (Figure 2.1). The National Marine Fisheries Service Auke Bay Laboratory (NMFS ABL) operates a salmon hatchery and a weir near the mouth of the creek at the head of the tidewater and obtains precise counts of both adult spawners and downstream migrants. The lake system supports populations of pink salmon (*Oncorhynchus gorbuscha*), sockeye salmon (*O. nerka*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), cutthroat trout (*O. clarki*) and Dolly Varden (*Salvelinus malma*). Nonsalmonid fish such as stickleback and freshwater sculpin also occur.

Auke Creek weir operation

The weir is operated during mid March through mid June to count all immigrant salmonids and during mid June through October to count all emigrant salmonids. For smolt aging of sockeye and coho salmon, outmigrating smolts are periodically sampled at the weir. The age compositions are estimated based on 300 to 500 scale samples obtained several times throughout an emigration period (Taylor and Munk 1988; Taylor 1990-1994; Taylor and Carney 1995, 1996). There have been several weirs on Auke Creek. Between 1961 and 1965, temporary weirs were used to count immigrant fish into Auke Creek. In 1965, a wooden weir was constructed at the head of the tide water. In 1979, the present more permanent weir was constructed. Complete data sets of fish counts, the number of hatchery releases, and smolt aging are available in the Auke Creek Data file (NMFS ABL, Juneau, Alaska 99801).

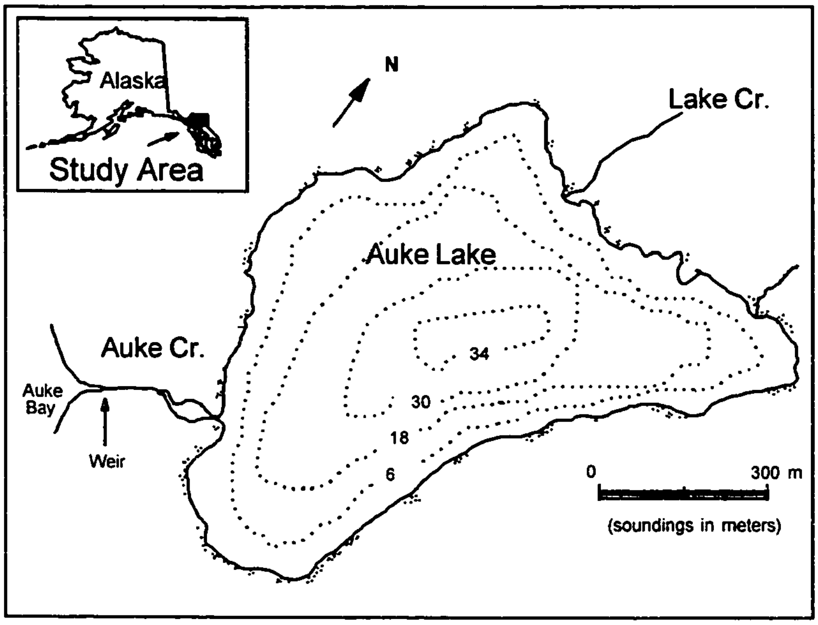

Figure 2.1. Study area, the Auke Lake system, showing Auke and Lake Creeks, Auke Lake, and the Auke Creek weir.

Four species of Pacific salmon in the Auke Lake system

The most abundant species of Pacific salmon in the Auke Lake system is pink salmon, followed by sockeye, chum and coho salmon in a decreasing order.

Pink salmon escapement in Auke Creek has greatly increased from the estimated 2,500 fish that returned annually before the 1960's (Taylor et al. 1981). More than 20,000 pink salmon on average returned to Auke Creek annually in recent years. However, the odd-year stock of pink salmon has seriously dwindled for some unknown reason since the late 1980's (Table 2.1).

Sockeye salmon escapement was fairly constant during the 1960's and 70's with an approximate average annual return of 6,000 to 8,000 fish to the system. The escapement diminished in the 1980's with the lowest record of 240 fish observed in 1985 (Table 2.1). Potential causes of the decline could include alteration of water flows caused by new residential construction and domestic water demands around Auke Lake, domestic waste water effluent, successive years of naturally occurring low egg-to-fry survival in Lake Creek, superimposition of pink salmon eggs in Lake Creek, or mortality through diseases (S.G. Taylor, pers. comm.). Subsequent recovery of sockeye escapement observed in the 1990's may be largely due to a restoration program developed by the Alaska Department of Fish & Game (ADF&G) and the NMFS Auke Creek Hatchery (Taylor et al. 1992).

Chum salmon in the Auke Lake system are considered to be mostly strays from other systems. Annual escapement of this species was below 100 fish until hatchery released fish started to return to Auke Creek in 1980. Natural production of chum salmon fry from the system was not observed until 1985. Coho salmon escapement has been relatively constant at around 1,000 fish annually at Auke Creek. Recently, it was revealed that historical scale readings for coho salmon smolts in the Auke Lake system are inaccurate and are actually younger than previously thought. The scales are currently being reassessed by ADF&G (C.W. Farrington, ADF&G pers. comm.). Chum and coho salmon are, thus, excluded from any analyses in this dissertation because of the small number of spawner-recruit observations for the former and because of an inaccurate spawner-recruit relationship for the latter.

During 1971-78, some attempts were made to estimate pink salmon fry production (Taylor, S.G., NMFS unpublished data) using an egg pumping technique (McNeil 1964b). However, precise counts of emigrant fish were not obtained until the spring of 1980, the first spring after the installation of the present weir.

Table 2.1. Adult and outmigrant counts and the production of fry and smolts for pink and sockeye salmon at Auke Creek during 1978-95. For sockeye salmon, proportions of smolt ages are also shown, from which smolt production for each brood was estimated.

	Pink salmon			Sockeye salmon					
	Fry count	Adult count[a]	Fry produc.[b]	Smolt count[c]	Smolt age (proportion)			Adult count[a]	Smolt produc.[d]
Year					Age 1	Age 2	Age 3		
1978	-	18,410	-	-	-	-	-	3,177	11,229
1979	-	19,003	74,047	-	-	-	-	6,022	1,487
1980	74,047	20,187	111,416	25,299	.09	.78	.13	4,564	3,026
1981	111,416	14,450	118,399	9,183	.07	.90	.03	4,089	16,719
1982	118,399	10,653	164,784	1,719	.33	.27	.40	1,334	17,696
1983	164,784	24,827	169,552	3,170	.36	.52	.12	1,805	8,098
1984	169,552	5,271	110,001	20,251	.33	.63	.04	964	17,709
1985	110,001	26,317	123,887	11,747	.02	.74	.24	240	5,674
1986	123,887	2,305	43,502	14,503	.31	.53	.16	952	21,547
1987	43,502	7,901	113,061	17,598	.24	.75	.01	2,767	18,559
1988	113,061	7,060	116,870	14,808	.91	.09	.00	1,215	9,590
1989	116,870	4,294	98,355	10,303	.22	.77	.01	2,333	21,883
1990	98,355	19,595	243,037	16,796	.02	.97	.01	3,383	16,844
1991	243,037	6,289	100,613	25,705	.64	.36	.00	5,168	51,013
1992	100,613	22,101	240,209	13,248	.59	.41	.00	4,628	-
1993	240,209	1,696	11,600	33,615	.76	.24	.00	8,476	-
1994	11,600	21,312	88,237	32,009	.18	.79	.03	5,336	-
1995	88,237	1,548	-	17,857	.01	.98	.01	4,948	-

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[a] Adult counts are the numbers of spawners that actually passed the weir, and any pre-spawn mortalities including coded wire tag recovery are deducted from a total escapement.

[b] Fry production of pink salmon is simply the count of fry outmigrants in the next springs.

[c] Smolt counts during 1988-90 were obtained by subtracting hatchery origin smolts from total smolt outmigrants (Taylor et al. 1992).

[d] Sockeye smolt production is the sum of annual smolt counts multiplied by the proportion of a corresponding age group outmigrating two to four years after the adult migration.

Spawning habitat of Auke Creek salmon

Habitat selection

All native species of Pacific salmon use both Auke and Lake Creeks as spawning ground. In addition to these creeks, sockeye salmon spawn along the beaches of Auke Lake (Bucaria 1968). Potential sockeye spawning grounds in the lake have been found near the outlet and inlet areas of Auke Lake and along the west side of the lake where shore gradient is less steep compared to the east side (H.R. Carlson, NMFS ABL pers. comm.). Pink salmon are also known to spawn at an intertidal zone of Auke Creek, but historical counts of intertidal spawners are unavailable because the weir is located at the head of the tidewater.

Auke Creek and Lake Creek offer quite different spawning and incubation habitats to Pacific salmon in terms of variables such as stream temperatures and discharges (Table 2.2).

Maximum stream temperatures normally occur during July, when average temperatures in Auke and Lake Creeks exceed 15 °C and 10 °C, respectively. Lake Creek temperatures are uniformly colder than those of Auke Creek, and the difference is greatest during summer. During winter, Lake Creek temperatures drop to near 0 °C, while the Auke Creek temperatures remain above 1 °C. The temperature variation measured by standard deviation (SD) is almost equal between the creeks except in July (Table 2.2).

Stream discharge reaches its peak in September in both creeks. On average, Lake Creek discharge is always smaller than that of Auke Creek as a natural consequence of geographical situations. However, Lake Creek discharge which is not regulated by the buffer effect of Auke Lake shows greater SD caused by more frequent freshets and droughts than in Auke Creek.

Salmon eggs deposited in Auke Creek may be subject to lethal high temperature during summer, whereas eggs deposited in Lake Creek may be subject to lethal low temperature during winter (Combs 1965). Due to relatively frequent and severe freshets, eggs in Lake Creek may also be subject to mechanical shock and wash out from gravel, which can be a significant mortality source especially before the eyed stage (Smirnov 1954).

Table 2.2. Stream temperatures and discharge of Auke and Lake Creeks from July to December during 1965-72. Monthly means and standard deviations (in parentheses) are given.

Month	Auke Cr.		Lake Cr.	
Stream temperature (°C)[a]				
Jul.	15.5	(2.4)	10.8	(1.8)
Aug.	14.4	(1.9)	10.4	(1.7)
Sep.	11.4	(1.6)	7.8	(1.7)
Oct.	7.4	(1.7)	4.8	(1.8)
Nov.	4.0	(1.5)	1.5	(1.4)
Dec.	1.5	(.7)	.5	(.5)
Stream discharge (m^3/s)[b]				
Jul.	.36	(.43)	.32	(.62)
Aug.	.65	(.62)	.62	(1.13)
Sep.	.81	(.71)	.67	(.81)
Oct.	.67	(.53)	.46	(.62)
Nov.	.44	(.48)	.29	(.59)
Dec.	.19	(.18)	.09	(.14)

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[a] Auke Creek temperatures were measured by NMFS ABL.

[b] Auke Creek discharges were measured by U.S. Geological Survey.

Spawning efficiencies of pink and sockeye salmon in different habitats

Throughout the spawning seasons of pink and sockeye salmon during 1992, 1993 and 1994 female carcasses were periodically examined for egg retention both in Auke and Lake Creeks. Although egg retention alone cannot represent the efficiency of spawning, it serves as an index of how successful spawners were in depositing their eggs into the gravel. Other aspects contributing to "spawning efficiency" are examined and discussed in subsequent chapters. Samples of pink salmon carcasses were taken at Auke Creek in 1994 and at Lake Creek in 1992. Sockeye salmon carcasses were taken at Auke Creek in 1993 and at Lake Creek in 1992 and 1993. Only those carcasses that had undergone any digging activity before death were sampled, and any carcasses that died accidentally during upmigration were not sampled. Whether fish dug up the gravel or not was determined by observing the degree of deterioration in its caudal fin. The data were arbitrarily divided into early and late components such that the number of samples are roughly equal between the components. The absolute numbers of egg retention for pink salmon would be expected to be much smaller than those for sockeye salmon simply because the former have lesser fecundity (1,141-2,205 eggs for pink salmon vs. 2,800-4,400 eggs for sockeye salmon; Heard 1991; Burgner 1991). Observed egg retentions (E, number of retained eggs in a spawned-out female carcass) were categorized into six ranks R1 through R6 such that: (R1) $E \leq 10$; (R2) $10 < E \leq 100$; (R3) $100 < E \leq 500$; (R4) $500 < E \leq 1{,}000$; (R5) $1{,}000 < E \leq 2{,}000$; and (R6) $E > 2{,}000$.

A remarkable pattern in egg retention of pink and sockeye salmon is the apparently greater egg retention for both species at Auke Creek than at Lake Creek (Figure 2.2). For both species the most frequent rank of egg retention was rank 5 at Auke Creek, whereas rank 1 was most frequent at Lake Creek. At Auke Creek, a temporal difference in egg retention was observed in pink salmon spawners and, to a lesser extent, in sockeye spawners, such that early fish had greater egg retention than late fish. It appears that the spawning efficiency of the Pacific salmon is lower in Auke Creek than in Lake Creek, especially during an early migration period.

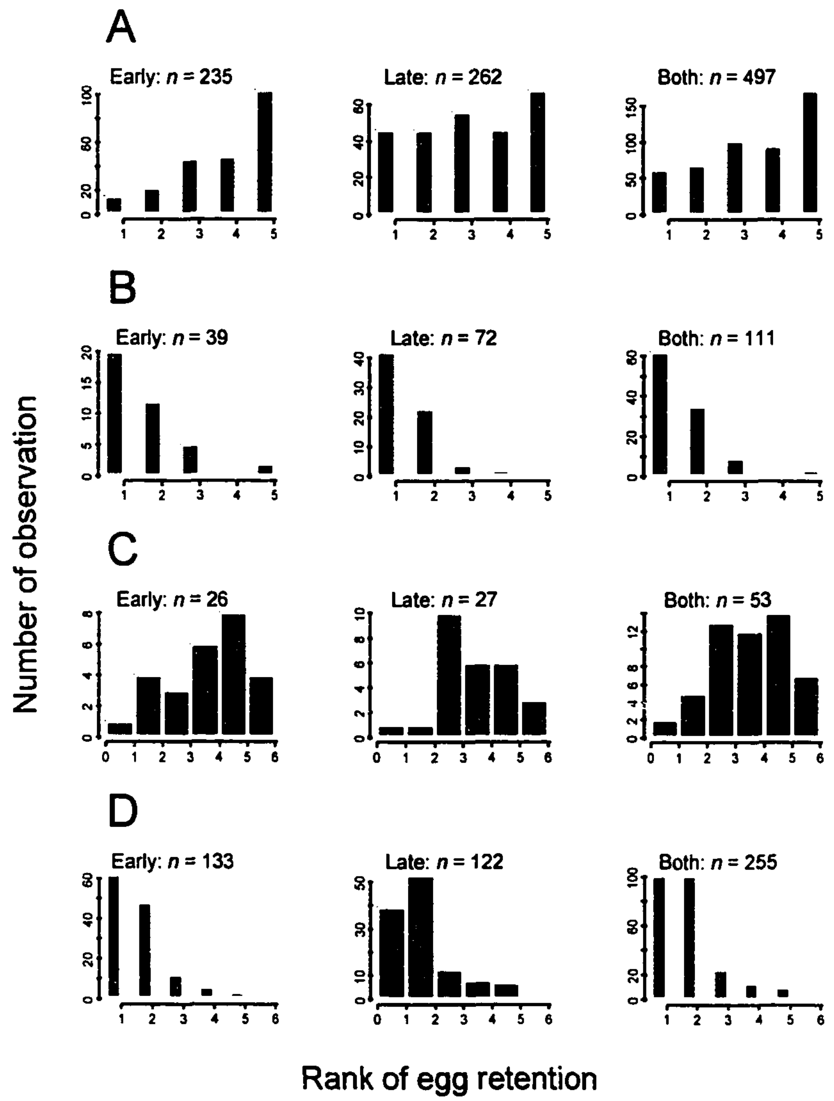

Figure 2.2. Histograms of egg retention of early, late and combined components of pink and sockeye salmon. Observations are from pink salmon in Auke Creek (A), pink salmon in Lake Creek (B), sockeye salmon in Auke Creek (C) and sockeye salmon in Lake Creek (D). See text for the notation of ranks for egg retention.

Effect of stream temperature on fry outmigration timing in pink salmon

Laboratory experiments where temperature regimes and other variables such as water flow and light intensities were accurately controlled or held constant have shown a strong relationship between water temperatures and development rates of Pacific salmon (Alderdice and Velsen 1978; Tang et al. 1987). It is, however, largely unknown whether the predicted relationship in laboratory experiments also holds for embryos spawned in a natural stream like Auke Creek by wild populations of Pacific salmon and whether interannual variation of stream temperature is great enough to cause variation of timing of fry and smolt outmigration.

From the daily count data of pink salmon adults and fry at the Auke Creek weir (Taylor and Munk 1988; Taylor 1990-1994; Taylor and Carney 1995, 1996), percent cumulative migration can be calculated for both upstream and downstream migrants of pink salmon. Then incubation periods (*IP* days) may be represented by a time period from 50 % adult upstream migration to 50 % fry outmigration in the following spring. Each *IP* estimate was calculated based on thousands of adults and more than 100 thousand fry, although the number of data points for *IP* is relatively small. Note that the *IP* actually includes not only the incubation period but the entire time between adult upmigration and fry outmigration of pink salmon. Mean incubation temperatures (T °C) can be represented by the mean Auke Creek temperatures during the period between 50 % upstream migration and 50 % outmigration for each brood. Then the relationship between *IP* and T was examined using data from 1980-92 broods except the 1982 brood for which the observations of stream temperature was not complete enough to obtain reliable incubation temperature.

Adult and fry migration pattern of pink salmon

Upstream adult immigration usually started in early August, reached 50 % in late August, and ended in mid September. Downstream fry emigration started in mid March to early April, reached 50 % in late April, and ended by early May (Table 2.3). Note that the immigration timings of pink salmon adults were fairly constant from year to year compared to the timings of fry downstream migration.

Table 2.3. Dates of 2.5%, 50%, and 97.5% cumulative migration of pink salmon adults (Upmigration) and of fry (Outmigration) for brood years 1980-94 and span of the migrations. Dates are abbreviated numerically with the number of the month (3 = March, 4 = April, 5 = May, 7 = July, 8 = August, 9 = September) separated from the day of the month by a (/).

Brood	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94
Upmigration															
2.5 %	8/17	7/28	8/17	8/ 3	8/10	7/31	8/ 6	8/ 3	8/ 3	8/ 3	8/ 3	8/ 3	7/28	8/16	8/22
50 %	9/ 4	9/ 6	8/27	8/17	8/25	8/23	8/27	8/26	8/26	9/ 3	8/30	8/22	8/17	9/ 1	8/29
97.5 %	9/17	9/15	9/17	9/19	9/17	9/16	9/15	9/10	9/12	9/18	9/18	9/10	9/11	9/12	9/15
Span	31	49	31	47	38	47	40	38	40	46	46	38	45	27	24
Outmigration															
2.5 %	3/23	4/11	3/19	3/12	4/ 2	3/21	3/25	3/13	4/ 2	4/ 1	4/ 1	3/17	3/29	3/28	4/ 8
50 %	4/19	5/ 6	4/15	4/11	4/24	4/26	4/ 9	4/16	4/24	4/19	4/25	4/ 7	4/25	4/16	4/29
97.5 %	5/ 1	5/19	5/ 2	4/29	5/ 8	5/10	4/24	4/27	5/ 5	5/ 2	5/11	4/24	5/ 7	4/27	5/ 7
Span	39	38	44	48	36	50	30	45	33	31	40	38	39	30	29

Relationship between mean incubation temperature and incubation periods

Linear regression analysis between mean stream temperatures T and incubation periods IP resulted in the following equation:

$$IP = 295.5 - 13.52\,T.$$

The slope of this model was significantly negative ($p < .05$, $R^2 = .405$, $n = 14$). Despite such a small range of observed variation (1.2 °C) in incubation temperature at Auke Creek, a decrease in mean incubation temperature by one degree causes nearly two weeks of delay in fry emigration timings (Figure 2.3). The incubation period would be expected to be a nonlinear function of mean temperature for an extended temperature range (Brannon 1987; Tang et al. 1987).

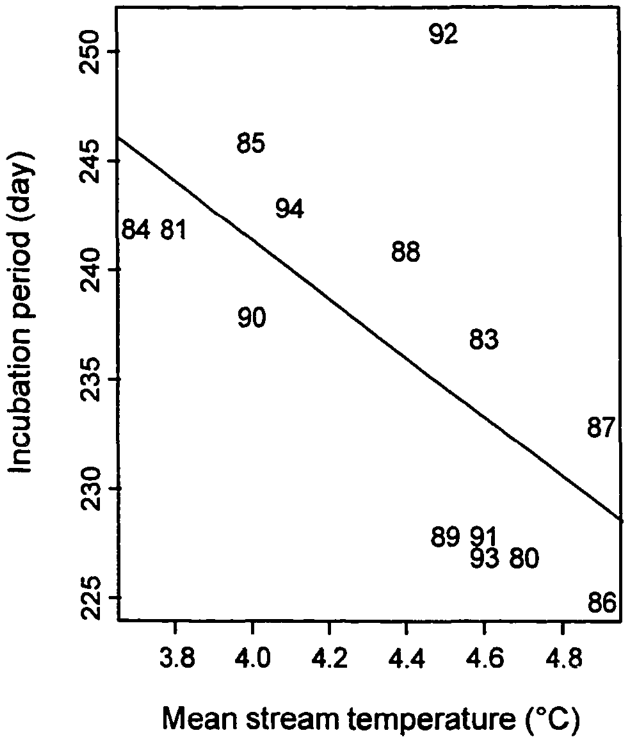

Figure 2.3. Incubation periods (*IP*) of Auke Creek pink salmon plotted against mean stream temperature for 1980-94 broods which are denoted with the last two digits in the plot. See the definition of *IP* in the text. The regression is $IP = 295.5-13.52\ T$.

Stream life of sockeye salmon

In the summer of 1993, I conducted a tagging study to examine stream life of sockeye salmon in the Auke Lake system. Pink salmon could not be tagged because of a concern that tagging might adversely affect natural reproduction of 1993 brood pink salmon that was extremely small in escapement size (1,696 fish). However, pink salmon were studied by tagging for stream life and other reproduction attributes in the following year (1994), which is described in Chapter 4.

The upstream migration of the 1993 sockeye salmon into Auke Creek showed roughly two distinct waves: the first wave occurred in late July and the second in mid August (Figure 2.4A). During the early part of spawning season, a lack of rainfall severely reduced Auke Creek discharge, delaying upstream migration of sockeye spawners from the ocean (Figure 2.4A, B).

Individually numbered dart tags (FT-1 Dart tags, Floy Tag Inc.) were applied to a total of 711 adult sockeye salmon (both males and females) of both waves at the Auke Creek weir (Table 2.4). Colors of the dart tags applied were different during nine dates of tagging, so that I could identify when the fishes were tagged without capturing them at spawning. In addition to dart tags, numbered disk tags (1¼" disk, Floy Tag Inc.) were applied to 30 female sockeye salmon on July 27 (20 fish) and July 29 (10 fish).

Table 2.4. Numbers of dart tags and disk tags (in parentheses) applied to sockeye salmon at the Auke Creek weir during 1993.

Date	No. of fish	
	Female	Male
Jul. 27	56 (20)	36
Jul. 29	61 (10)	17
Jul. 30	42	16
Aug. 16	45	28
Aug. 17	50	22
Aug. 18	50	44
Aug. 22	71	30
Aug. 23	46	25
Aug. 23	32	40
Total	453 (30)	258

The numbers of sockeye spawners both with tags and without tags were separately counted in Lake Creek, the tagged fish were recorded for the color of dart tags or the number of disk tags, and the tags were recovered from sockeye carcasses during daily foot surveys on the entire spawning areas of Lake Creek (1,250 m) which was divided into 25 sections with equal distance (50 m). Two kinds of stream life were examined based on the tag recovery data. The first stream life (Life A) was a total period between tagging and death in Lake Creek, i.e., total residence time in the Auke Lake system. The second stream life (Life B) was a period between Lake Creek entry from Auke Lake and death. The disk tags probably provided more accurate estimates of stream entry timings into Lake Creek and thus more accurate Life B estimates than the dart tags. However, it was usually possible to know the exact dates of the stream entry even from dart tagged fish, since only a few fish with specific tag color were usually seen in a specific stream section. During the daily foot surveys, 66 and 85 tags were recovered in Auke and Lake Creeks, respectively. Among the 85 tags found in Lake Creek, 62 tags were recovered from fresh carcasses which had died since a previous survey on the day before. Of the 62 tagged fish, 37 fish could be identified for the exact dates of Lake Creek entry.

Sockeye spawners from the first wave (i.e., fish tagged on July 27, 29 and 30) had Life A of approximately one month, whereas spawners from the second wave (i.e., fish tagged on August 16, 17, 18, 22 and 23) had Life A of only about ten days (Figure 2.5A). The regression line of Life A against tagging dates had a significantly negative slope ($\beta = -.809, p < .0001, n = 62, R^2 = .842$). On the contrary, Life B was almost constant and independent of tagging dates (Figure 2.5B). The slope of the regression line was not significant ($\beta = -.002, p > .5, n = 37$). The mean and standard error of Life B were 5.2 ± .4 days. Obviously, the first-wave spawners spent most of the time during freshwater residence in the lake, waiting for the timing of further upstream migration into Lake Creek. This migration pattern was also inferred by comparing sockeye daily escapements at Auke Creek and daily spawner counts at Lake Creek (Figure 2.4A). The sockeye salmon that entered Auke Creek in late July did not appear in Lake Creek until mid August. Gard et al. (1987) observed a similar phenomenon for sockeye salmon in the Karluk Lake system, Kodiak Island, and speculated that early spawning sockeye were not sexually mature upon arrival at the lake and required more time to ripen.

The stream discharge in Lake Creek was not high enough until mid August for sockeye spawners to ascend the creek to reach the spawning ground (Figure 2.4C). When spawners from the second wave arrived at the lake, however, Lake Creek was providing constantly high streamflow, so that the spawning by the second wave fish was not delayed. Stream temperature in Lake Creek was probably low enough (lower than Auke Creek temperature by 5 °C) for the first-wave spawners to perform normal spawning at any time and should not have caused the delay in the Lake Creek entry (Figure 2.4D). It is not known whether the early spawning sockeye were sexually mature or not upon arrival at Auke Lake.

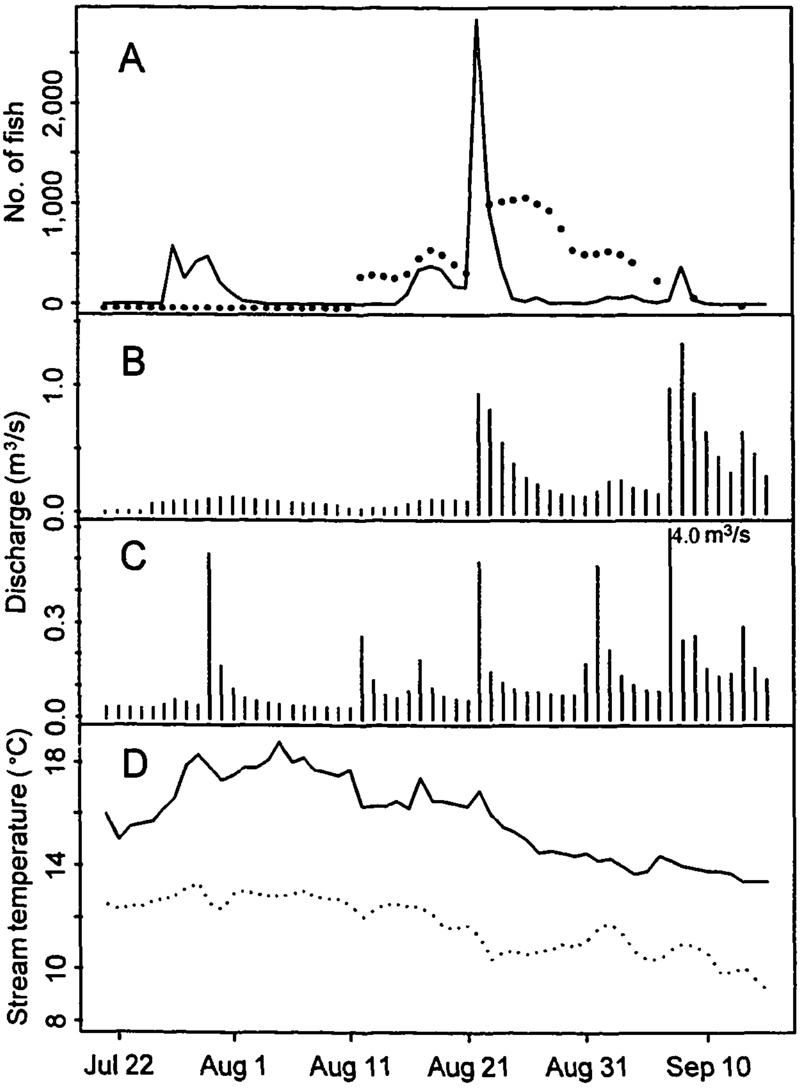

Figure 2.4. Sockeye salmon daily escapement at Auke Creek (solid line) and daily spawner counts in Lake Creek (closed circle) (A); Auke Creek discharge (B); Lake Creek discharge (C); and Auke Creek (solid line) and Lake Creek (dotted line) temperatures (D) during the 1993 spawning season.

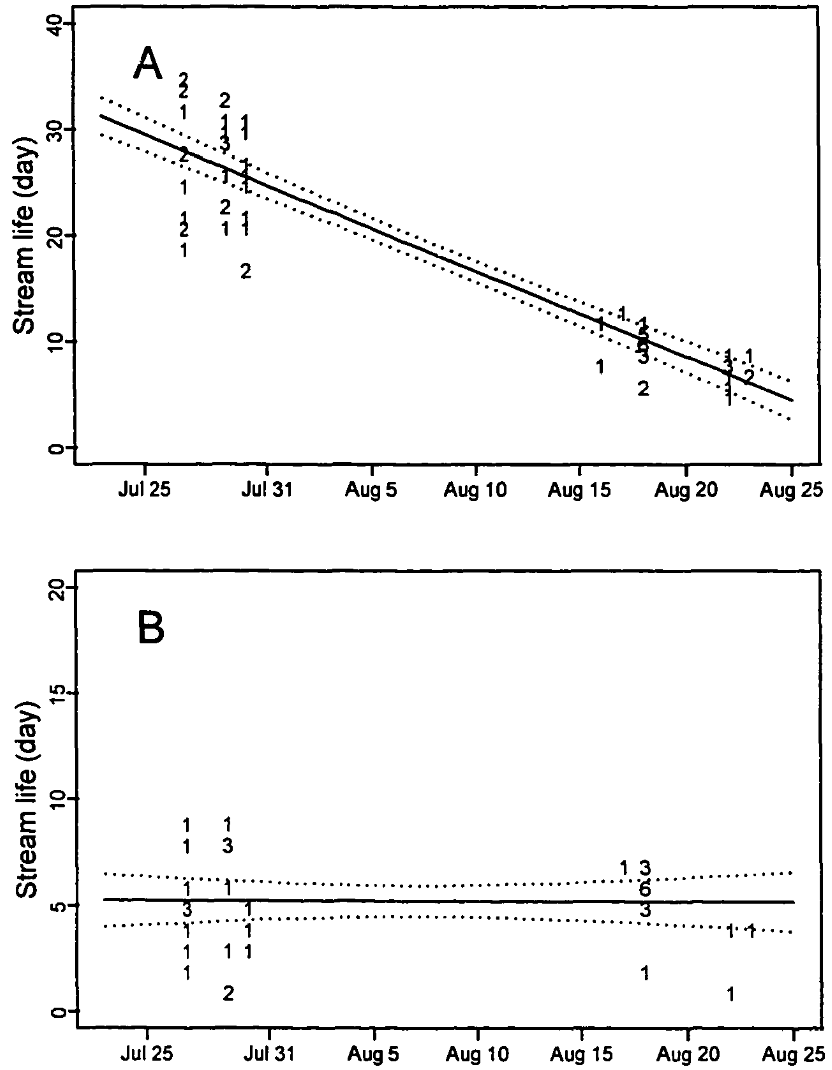

Figure 2.5. Stream life of sockeye salmon in the Auke Lake system during the 1993 spawning season. Life A (A) and Life B (B) were plotted against tagging dates with a linear regression line (solid line) and its 2 x SE confidence intervals (dotted lines). Numbers inside the plots indicate the numbers of observation (i.e., tagged carcasses).

CHAPTER 3. FRY AND SMOLT PRODUCTION OF PINK AND SOCKEYE SALMON

Precise counts of both immigrants into and emigrants from the Auke Lake system during the last 15 years are available for pink and sockeye salmon and other salmonids. In addition, records of environmental variables such as air and stream temperatures and precipitation have been collected for this system since the 1960's. Reliable data with little error are essential for understanding of biological and environmental mechanisms in the process of fry and smolt production of Pacific salmon.

Methods

Spawner-recruit data

Smolts of Pacific salmon have been counted at the Auke Creek weir as early as 1972. The counts prior to 1980 were, however, made with a different fish weir that was less efficient than the current weir, so that only the data collected after 1980 were used in this analysis. Spawner-recruit data were prepared from the Auke Creek Weir Annual Report (Taylor and Munk 1988; Taylor 1990-1994; Taylor and Carney 1995, 1996). Brood years included in this analysis were 1979-93 (15 broods) for pink salmon and 1978-91 (14 broods) for sockeye salmon. The first brood years for the analysis correspond to years when offspring of the brood initiated emigration in 1980, while the last brood years for the analysis correspond to years when offspring of the brood completed emigration by the spring of 1994. Prespawning adult mortality, such as adult samples for coded wire tags and genetic markers and unspawned adults recovered at the weir, was subtracted from the recorded counts in the Auke Creek Weir Annual Report.

Unlike pink salmon, recruitment of sockeye salmon occurs over multiple years after spawning as different age groups. Thus, smolt production of sockeye salmon was estimated by a cohort analysis, such that the recruitment equals to the sum of subsequent total smolt counts multiplied by a proportion of the corresponding age group (see Table 2.1).

Smolt counts of sockeye salmon during 1988-91 did not entirely consist of wild production but included hatchery production from fry releases into Auke Lake (Taylor et al. 1992). Since all the hatchery fry had been previously marked, Taylor et al. (1992) accurately estimated the proportions of hatchery and thus wild production of sockeye smolts. The estimated hatchery production was subtracted from the weir counts in this analysis.

Spawner-recruit models

Biological processes underlying the fry and smolt production of pink and sockeye salmon were examined by fitting the spawner-recruit data to three different models with different underlying mechanisms. The models include the Ricker model (Ricker 1954), the Beverton-Holt model (Beverton and Holt 1957), and the McNeil-Chapman model (McNeil 1964a; Chapman 1973). The Ricker and Beverton-Holt models are probably most frequently used in fisheries science. McNeil (1964a) applied a mathematical model specifically to the fry production of pink salmon, assuming that redd superimposition (i.e., physical displacement of eggs by excessive spawners due to limited spawning ground) is the major mortality source during a freshwater phase. Later, a similar but somewhat more general model was proposed by Chapman (1973). A preliminary analysis applied a more complicated three-parameter model (e.g., Deriso 1980; Schnute 1985) to the present data, but no significant parameter estimates were obtained because of a small number of degrees of freedom and a large variability of spawner-recruit data. The forms of the Ricker, Beverton-Holt, and McNeil-Chapman models are shown in (3.1), (3.2), and (3.3), respectively:

$$R_t = \alpha S_{t-1}\, e^{-\beta \cdot S_{t-1} + w_t} \tag{3.1}$$

$$R_t = \frac{\alpha S_{t-1}}{\beta + S_{t-1}} e^{w_t} \tag{3.2}$$

$$R_t = \alpha\left(1 - e^{-\beta \cdot S_{t-1}}\right) e^{w_t} \tag{3.3}$$

where w_t is a normally distributed random variable with mean 0 and variance σ^2. Lognormal error structure is used because of its wide acceptance in spawner-recruit analyses (e.g., Peterman 1981; Quinn et al. 1990; Quinn and Collie 1990; Hilborn and Walters 1992) and more importantly because of the variation pattern of Auke Creek smolt production shown later. In order for the different models to be comparable with one another, the logarithm of recruitment was used as a response variable. Thus, (3.1), (3.2), and (3.3) become

$$\ln R_t = a + \ln S_{t-1} - \beta \cdot S_{t-1} + w_t \tag{3.4}$$

$$\ln R_t = a + \ln S_{t-1} - \ln(\beta + S_{t-1}) + w_t \tag{3.5}$$

$$\ln R_t = a + \ln(1 - e^{-\beta \cdot S_{t-1}}) + w_t \tag{3.6}$$

where $a = \ln \alpha$. Model selection for each species was based on the significance of the parameters and overall fit in terms of the coefficient of determination.

If there is correlation between the residuals of a fry or smolt production curve and later spawning stock, the estimated model parameters are biased especially when the number of observations is small (Walters 1985). The production model of pink salmon may be subject to such bias, since they exclusively mature at a two year cycle. Thus a large positive (or negative) residual of fry production for the t th brood is likely to cause large (or small) spawning stock for the (t+2) th brood. If the ocean survival, including commercial harvest, is sufficiently variable from year to year, the correlation is lessened, and so is the bias. The magnitude of bias was estimated for pink salmon by performing Monte Carlo simulations.

Environmental variables

Auke Creek stream temperatures have been measured every morning since the 1960s by personnel at the National Marine Fisheries Service, Auke Bay Laboratory. Monthly average temperatures were calculated for the period of the present analysis (i.e., 1978-94). In addition to Auke Creek temperatures, air temperatures measured at the Juneau Airport (National Climatic Data Center 1978-94) were also used in order to approximate stream temperatures of Lake Creek, since continuous records of Lake Creek temperature are not available. Monthly averages of air temperature were calculated from daily mean temperatures.

Monthly averages of precipitation were obtained from daily precipitation data measured at the Juneau Airport (National Climatic Data Center 1978-94). A record of stream discharge is available only during 1962-75 (U. S. Geological Survey). Thus, there is virtually no discharge record for Auke Creek during the study period. However, it was found that the Auke Creek discharges can be reconstructed based on the old discharge and the precipitation data using a multiple linear regression (Appendix I).

Upstream migration timing was quantified for each species and each brood by calculating days after July 1 to the date of 50 % completion of escapement at the weir. The run timing is known to be a significant explanatory variable for the freshwater survival of pink salmon in Sashin Creek, southeast Alaska (McNeil 1969).

Correlations between residuals from the best spawner-recruit models and the environmental variables above were examined. Only the variables that are significantly correlated with the residuals at .05 level and also provide a biologically explainable mechanism for the recruitment variability are included in the spawner-recruit models (Hayman and Tyler 1980).

Maximum fry and smolt production

If the spawner-recruit relationship is best explained by a dome-shaped Ricker model, maximum smolt production R_{max} and corresponding spawner abundance, hereafter referred to as spawner capacity, S_{max} can be obtained, such that

$$S_{max} = \frac{1}{\beta} \tag{3.7}$$

and

$$R_{max} = \frac{1}{\beta} e^{\alpha - 1} . \tag{3.8}$$

The 95 % confidence intervals for S_{max} and R_{max} were obtained by generating 1,000 bootstrap samples of residuals from the Ricker curve, adding them to predicted recruitment values, and estimating model parameters and pairs of S_{max} and R_{max} (Wu 1986). Then the bias-corrected percentile method was used to compute confidence intervals for observed S_{max} and R_{max} (Efron 1982).

Results

Spawner-recruit relationships

Pink salmon data were fitted to the three models with similar and relatively high coefficients of determination (Table 3.1). However, only the Ricker and McNeil-Chapman models provided parameter estimates which were both significantly different from zero ($p <$ .05). Observed data points showed a typical multiplicative error pattern around the predicted curves with an asymptotic increase over the range of observed spawning levels but with little indication of overcompensation (Figure 3.1). Observed ocean survival rates $h_t = S_{t+2} / R_t$ were quite variable with a mean of .100 and a standard deviation of .066. Based on the observed ocean survival rates, estimated Ricker parameters, a residual standard error, and first two observations of odd and even spawner abundance, 15 consecutive broods of spawner-recruit data were simulated for 500 times, providing 500 sets of simulated Ricker parameters. The mean values of the simulated parameters were slightly biases upward at 1 % for α and 7 % for β, so that the density-dependence of pink salmon fry production may have been overestimated to some extent.

Sockeye salmon data, on the other hand, provided three models with considerably different coefficients of determination (Table 3.1). The Ricker model exhibited strong overcompensation, whereas both the Beverton-Holt and McNeil-Chapman models provided almost constant predicted recruitment over a wide range of spawning levels because of the limitation of these models that production curves are always asymptotic (Figure 3.1). Only the Ricker model provided significant parameter estimates at the .05 level. It should be recalled that, unlike pink salmon, sockeye smolts in the Auke Lake system must have experienced density-dependent mortality not only during spawning and incubation but also during freshwater rearing of juvenile fish because they spend at least one year in Auke Lake before outmigration. The poor model fit for this species may be partly attributable to a longer time span between spawning and recruitment events and to an error in the calculation of recruitment sizes from cohort analysis.

Apparently, the strong overcompensation in the sockeye spawner-recruit relationship was caused by the two data points of 1979 and 1980 broods (Figure 3.1). For these two broods, smolt production was only .25 and .66 smolt per spawner, respectively. Note that the spawner-recruit relationship of pink salmon also indicated a large negative residual for 1979 brood (Figure 3.1). Thus, the overcompensation of sockeye salmon may have resulted not only from density-dependence but also from a combined density effect of both pink and sockeye spawners (i.e., species interaction) and/or from an environmental anomaly that affected freshwater survival of multiple species simultaneously. In contrast, a remarkably positive residual occurred for the 1991 brood of sockeye salmon at a spawning stock size similar to those of the 1979 and 1980 broods.

Table 3.1. Parameter estimates, standard errors (±1 SE), residual degrees of freedom d.f., residual sum of squares *RSS*, and coefficients of determination R^2 for the spawner-recruit models of pink and sockeye salmon in the Auke Lake system. Abbreviations are "R" for Ricker model, "BH" for Beverton-Holt model, and "MC" for McNeil-Chapman model. Significance levels of parameter estimates are: * $p < .05$ and ** $p < .01$.

	Parameter estimate ± 1 SE				
Model	a (= ln α)	β	d.f.	*RSS*	R^2
Pink salmon					
R	2.966E+00** ± 2.05E-01	4.663E-05** ± 1.36E-05	13	2.397	.685
BH	1.245E+01** ± 3.70E-01	1.232E+04 ± 7.89E+03	13	2.615	.656
MC	1.205E+01** ± 2.45E-01	1.169E-04* ± 5.19E-05	13	2.487	.673
Sockeye salmon					
R	3.306E+00** ± 4.12E-01	5.801E-04** ± 1.29E-04	12	8.004	.239
BH	9.446E+00** ± 3.44E-01	1.178E+02 ± 3.80E+02	12	10.359	.016
MC	9.413E+00** ± 2.68E-01	3.453E-03 ± 5.20E-03	12	10.074	.043

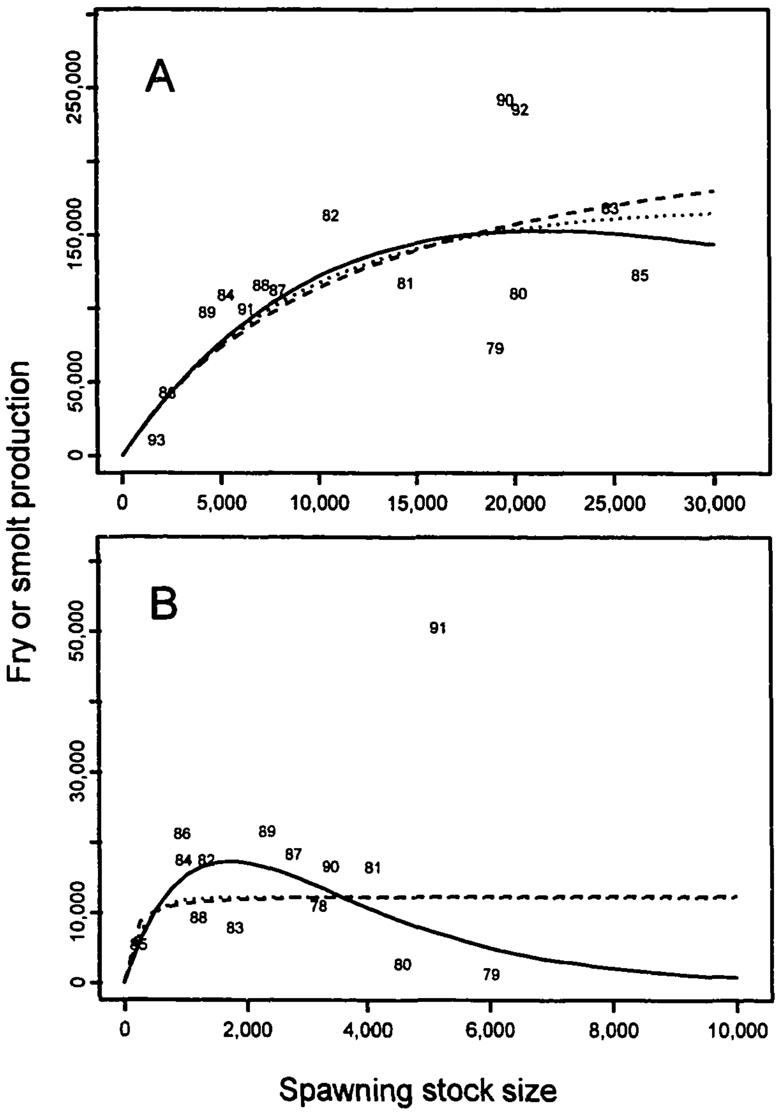

Figure 3.1. Fry and smolt production of pink salmon (A) and sockeye salmon (B) in the Auke Lake system. Numbers inside plots indicate brood years. Predicted spawner-recruit curves are from Ricker model (solid line), Beverton-Holt model (dotted line), and McNeil-Chapman model (broken line).

Recruits-per-spawner and residuals from Ricker models

Despite longer freshwater residence and thus possibly higher mortality of sockeye salmon, their recruits-per-spawner (mean = 9.27; range = .25-23.64; $n = 14$) was almost comparable with that of pink salmon (mean = 12.33; range = 3.90-22.91; $n = 15$). Note that the estimated α parameters of the Ricker models, which measure fry or smolt production at very small spawning levels, were also similar between the species (Table 3.1). Not only were values of recruits-per-spawner comparable, but also the time series of recruits-per-spawner were positively correlated between pink and sockeye salmon ($r = .650$, $p < .05$).

The residuals of production curves of pink and sockeye salmon showed an increasing time trend, indicating that egg-to-fry and egg-to-smolt survival improved since 1978 after the density-dependent effect was taken into account (Figure 3.2; pink salmon; $r = .728$, $p < .01$, and sockeye salmon; $r = .628$, $p < .05$). The 1993 brood of pink salmon was excluded from the correlation analysis, because it is questionable whether the Ricker model could correctly predict smolt production for such small spawning stock as the 1993 brood (1,695 adults).

Some environmental variables, such as July creek temperature and September and winter precipitation, indicated a linearly increasing or decreasing trend since 1978, which may explain the time trend of fry and smolt production. However, the correlations between these variables and the residuals from production curves were not significant ($p > .05$).

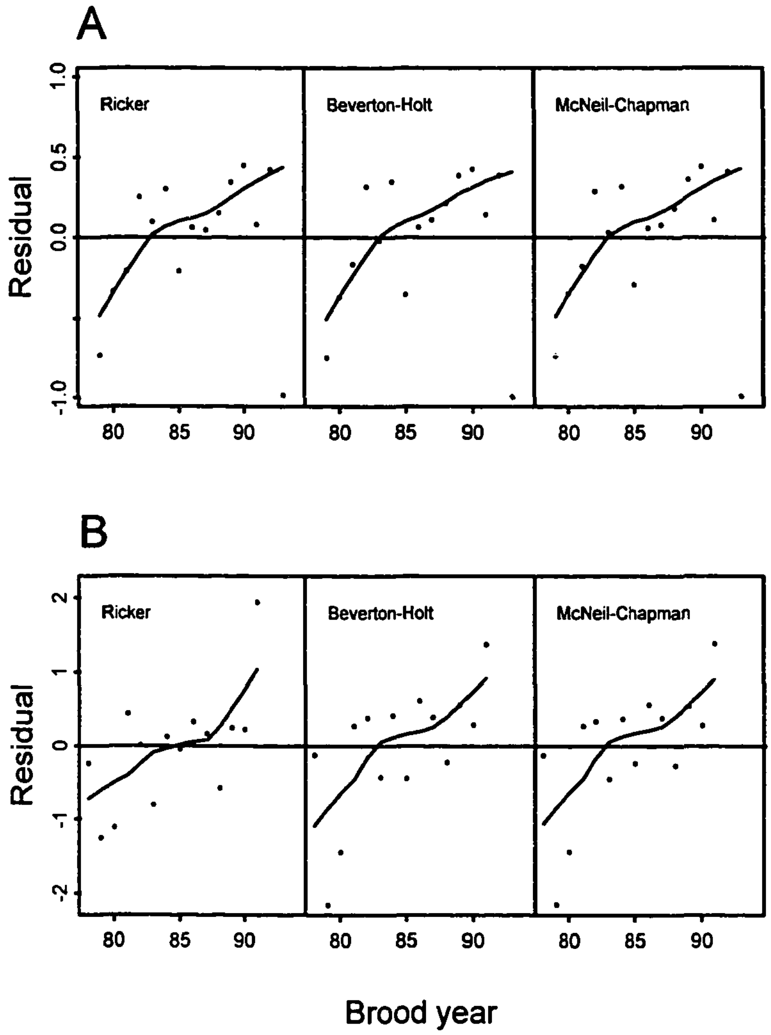

Figure 3.2. Residuals of of production models for pink salmon fry (A) and sockeye salmon smolt (B) plotted against brood years. The residuals were obtained from Ricker, Beverton-Holt and McNeil-Chapman models. Superimposed are LOWESS (robust locally weighted regression) lines with $F = 2/3$ (Cleveland 1979).

Effects of environmental variables

Among all environmental variables examined, nine variables were significantly correlated with the residuals of the Ricker models of either pink or sockeye salmon (Table 3.2 and Figure 3.3). For pink salmon, the most significant variable correlating with the residuals was November stream discharge ($r = -.708, p < .01$); the higher the discharge, the lower the residuals were. Stream temperatures in most months were negatively correlated with pink salmon residuals (Figure 3.3), indicating that the cooler stream temperatures were after spawning until outmigration, the higher fry production was. The pink salmon residuals were also negatively correlated with sockeye spawning stock ($r = -.639, p < .05$). Furthermore, when 50 % migration was later, the residuals tended to be smaller ($r = -.541, p < .05$).

For sockeye salmon, the most significant environmental variable was May precipitation in the following springs after spawning ($r = .741, p < .01$). The higher May precipitation, the higher the residuals were. This correlation was probably related to negative correlation with May air temperatures ($p < .05$, Figure 3.3). Monthly averages of precipitation between August and May, except October, were consistently positively correlated (not all of them were significant) with sockeye residuals unlike pink salmon.

Table 3.2. Environmental variables significantly correlated with the residuals of Ricker models ($p < .05$). "P" and "N" denote positive and negative correlation, respectively. Correlation between pink salmon residuals and brood years is significant only after the 1993 brood is excluded.

	Correlation	
	Pink	Sockeye
Variables	$n = 15$	$n = 14$
October air temperature	N	-
December air temperature	-	P
May air temperature[a]	-	N
September precipitation	-	P
May precipitation[a]	-	P
September discharge	-	P
November discharge	N	-
50 % migration timing	N	-
Brood year	(P)	P

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[a] May air temperature and May precipitation are from the following springs.

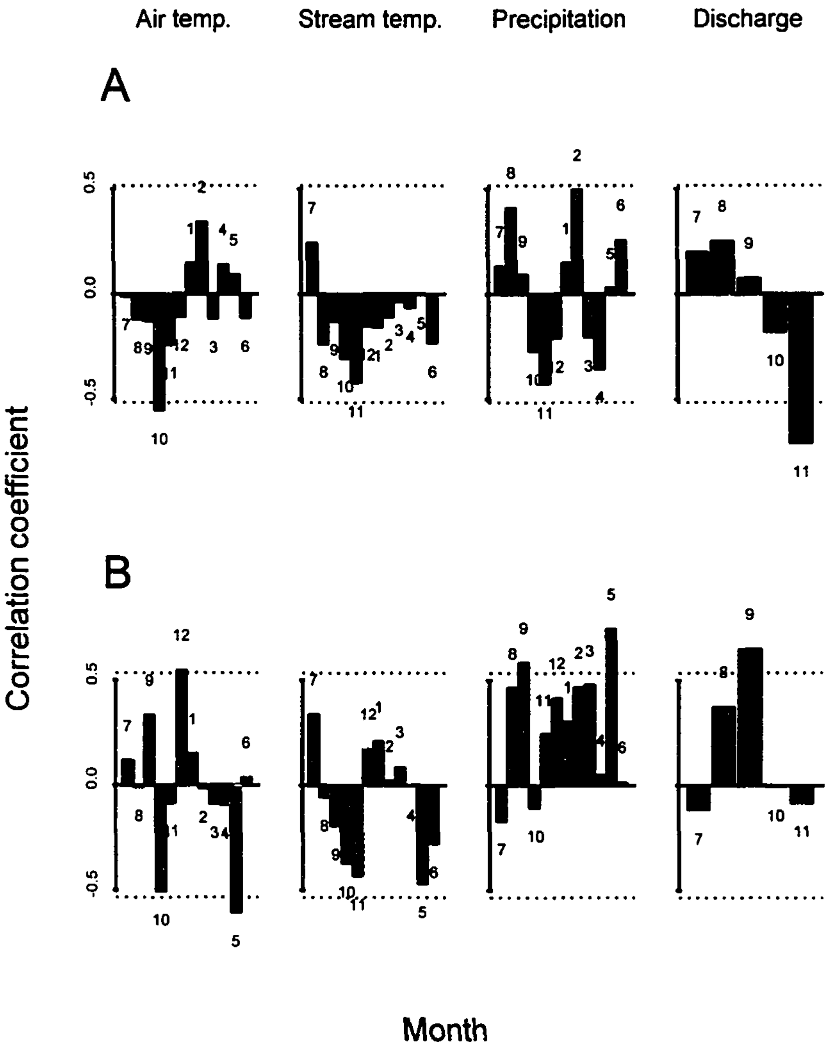

Figure 3.3. Correlations between the residuals of Ricker models and four environmental variables, i.e., air temperature, stream temperature, precipitation and Auke Creek discharge, for pink salmon (A) and sockeye salmon (B) in the Auke Lake system. Dotted lines indicate significant level of correlation at .05.

Sockeye spawner-recruit model with a precipitation variable

The positive effect of May precipitation on sockeye smolt production may provide biologically understandable mechanism. Although the correlation was the highest in May, it is probably preferable to use average precipitation between spawning and emergence (i.e., August to May) because of the consistent positive correlations with precipitation in other months.

Let $P_{t\text{-}1}$ be standardized average precipitation from August in year (t-1) to May in year t. The Ricker model with the precipitation variable becomes

$$\ln(R_t) = a + \ln S_{t-1} - \beta \cdot S_{t-1} + \gamma \cdot P_{t-1} + w_t \qquad (3.9)$$

where w_t is a normally distributed random variable with mean 0 and variance σ^2. Note that addition of precipitation variable into the Ricker model resulted in increased estimates of a and β parameters compared to those without this variable (Table 3.1), suggesting that the true sockeye smolt production may be more productive at small spawning levels but declines more quickly with increasing spawning stock. Distribution of residuals became more homoscedastic around the predicted line after the addition of precipitation (Figure 3.4).

Table 3.3. Parameter estimates, standard errors (±1 SE), residual degrees of freedom d.f., residual sum of squares *RSS*, and coefficients of determination R^2 for the Ricker model with average precipitation for sockeye salmon in the Auke Lake system. Significance level of parameter estimates is ** $p < .01$.

Parameter estimate ± 1 SE					
a	β	γ	d.f.	*RSS*	R^2
3.732E+00** ±2.887E-01	7.369E-04** ±9.237E-05	6.709E-01** ±1.627E-01	11	3.145	.612

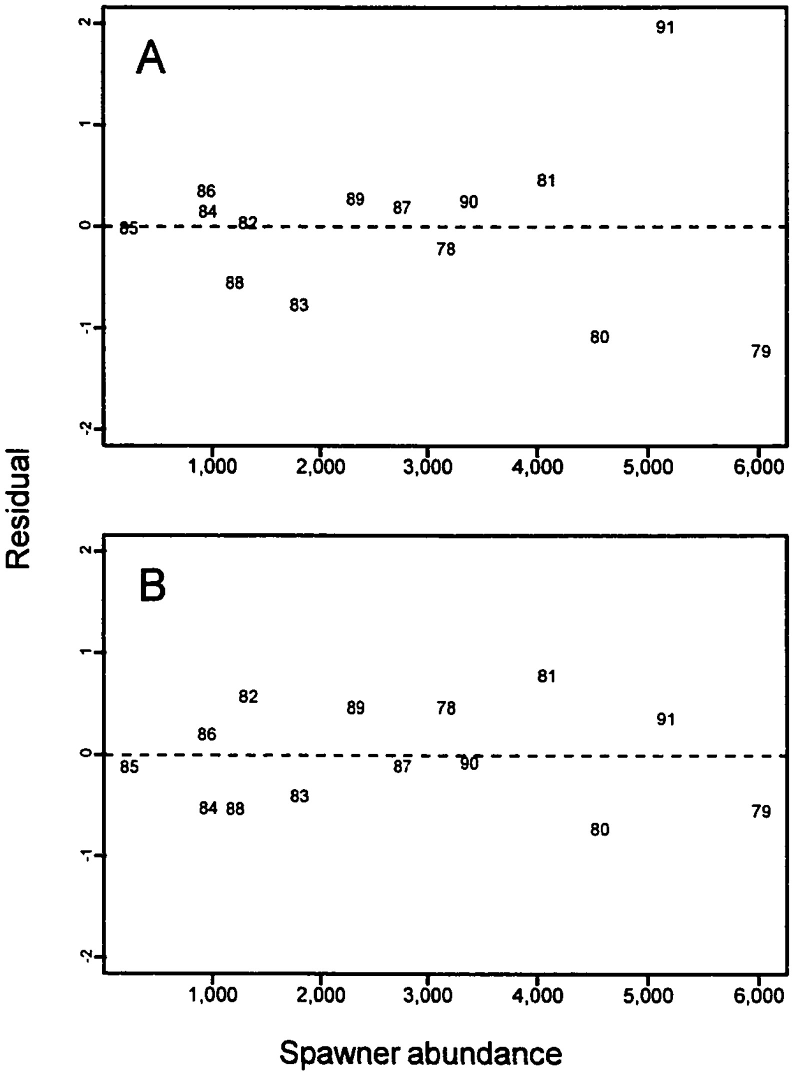

Figure 3.4. Residuals from the Ricker model of sockeye salmon plotted against spawning stock size without any environmental variables (A) and with a precipitation variable (B). Numbers inside plots indicate brood years.

Spawner capacity and maximum fry and smolt production

Despite relatively wide confidence intervals especially toward upper limits, spawner capacity S_{max} and the maximum fry production R_{max} of pink salmon were much greater than those of sockeye salmon (Table 3.3). With the precipitation effect added to the production model, sockeye spawner capacity and the maximum smolt production became S_{max} = 1,357 (95 % C.I. = 1,121-1,747) and R_{max} = 20,853 (95 % C.I. = 14,994-28,670) with average precipitation P during 1978-91. The S_{max} was obtained as the reciprocal of β parameter in (3.9), and the R_{max} was obtained by an equation

$$R_{max} = \frac{1}{\beta} e^{a+\gamma \cdot P-1}. \tag{3.11}$$

The S_{max} and its 95 % C.I. became smaller after the addition of the precipitation variable because of an increased β parameter estimate and reduced variation around the Ricker curve, respectively.

Table 3.4. Estimated spawner capacity S_{max} and the maximum fry and smolt production R_{max} for pink and sockeye salmon. The 95 % confidence intervals (C.I.) were obtained by a bias-corrected percentile method applied to 1,000 bootstrap samples.

		95 % C.I.			95 % C.I.	
	S_{max}	Lower	Upper	R_{max}	Lower	Upper
Pink	21,446	14,031	42,131	153,205	113,072	204,674
Sockeye	1,724	1,237	2,858	17,306	11,231	28,227

Discussion

Density-dependent mortality

Shapes of smolt production curves are a key to understanding mortality mechanisms during spawning, incubation, emergence and freshwater rearing for Pacific salmon. The Ricker curve observed for pink salmon in the Auke Lake system appears to be asymptotic similar to the Beverton-Holt and McNeil-Chapman curves, although with no extreme spawning stock sizes in the observed data it is unclear whether the Ricker curve remains asymptotic or shows overcompensation (i.e., dome shape) for larger spawning stocks. Asymptotic spawner-recruit relationships are known for pink salmon in Sashin Creek, southeast Alaska (Ignell 1988), and for other salmonid populations such as chum salmon (Bonnell 1991) and steelhead trout (Ward and Slaney 1993). On the contrary, some studies revealed that the shape of smolt production curves can be linear, asymptotic or dome-shaped among different populations of the same species or among closely related species (Kennedy and Crozier 1993; Ward and Slaney 1993).

If spawning stock is a regulatory factor of fry and smolt production, production curves could exhibit a dome shape (Ricker 1954). Although egg loss due to redd superimposition can be a major candidate of such density-dependent mortality, there are other possible sources of mortalities for embryos and juveniles of Pacific salmon. For example, if the survival of embryos and alevins is regulated by limited amount of intragravel oxygen, smolt production curves can be dome-shaped because embryo mortality is proportional to the initial abundance of deposited eggs (i.e., spawning stock times average effective fecundity). Rapid oxygen consumption due to both respiration of live embryos and decomposition of dead embryos can cause severe mortality (Heard 1978). Intensive spawning causes a deterioration of the hydrochemical regime of spawning areas; for example accumulation of carbon dioxide and increased acidity due to metabolic byproducts (McNeil 1969; Bailey et al. 1980; Rice and Bailey 1980). Rice and Bailey (1980) reported that ammonia concentrations in salmon streams in southeast Alaska can be expected to reach levels potentially harmful to salmon eggs and alevins.

For sockeye salmon that usually spend more than one year in freshwater after emergence, density-dependence can not only result from limited spawning areas and intragravel oxygen but also from limited food resources in nursery lakes (Kyle et al. 1988; Rieman and Myers 1992). In fact, Taylor et al. (1992) observed the occurrence of reduced fry-to-smolt survival of hatchery stocked sockeye salmon in the Auke Lake system when the stocking size was high (100,000 fry). Ward and Slaney (1993) also found that the most sensitive life stage controlling the recruitment of steelhead trout was from fry to parr and not during spawning or incubation.

Strong overcompensation observed in sockeye smolt production, however, may be misleading because the dome-shaped appearance of the Ricker curve is largely due to two broods 1979 and 1980, during which an environmental condition for the smolt production was not favorable for sockeye salmon (and pink salmon) as indicated by a linearly increasing time trend of freshwater survival since the late 1970s.

Density-independent mortality

Correlation analysis detected a strong negative influence of stream discharge in November on pink salmon fry production. Extremely high stream discharges are detrimental to salmonid embryos because of wash out and mechanical shock caused by gravel movement (Wickett 1958; Thorne and Ames 1987; Scrivener and Brownlee 1989). However, in the Auke Lake system such severe discharge or flooding normally occurs in September and October (Table 2.2) and not in November. Furthermore, by November most of the pink salmon embryos in this system complete an eyed stage (Hebert 1994), after which salmonid embryos are quite resistant to mechanical shocks (Smirnov 1954; Fitzsimons 1994). Therefore, I suspect that the negative correlation between the November discharge and pink salmon production is spurious.

A negative correlation between egg-to-fry survival and run timing of spawners, on the other hand, is a well-known phenomenon for pink salmon in Sashin Creek (Skud 1958; Merrell 1962; McNeil 1968; Heard 1978). This phenomenon is believed to be a survival advantage of early spawned embryos that start development under warmer water temperature than late spawned embryos (Merrell 1962). Such a negative correlation was not observed for pink salmon in the Auke Lake system when fry-per-spawner was used in the analysis, but the correlation became significantly negative when the residual of a spawner-recruit model was used instead. Thus the populations of pink salmon in Sashin and Auke Creeks might be influenced, to some extent, by similar environmental variable(s) associated with run timing. In the Auke Lake system, this (these) variable(s) may be masked by a relatively strong density-dependent mortality.

Correlation coefficients between precipitation and residuals of sockeye smolt production were consistently positive during most of the months between spawning and emergence. Significant correlations at .05 were found for precipitation in September and in May of the following spring. In particular, the 1991 brood apparently benefited from unusually high precipitation during spawning, incubation and the first feeding of emergent fry in the spring of 1992. In fact, annual precipitation in 1991 was the record high at the Juneau Airport since climatological data were initially collected in 1943 by the National Weather Service. Furthermore, precipitation in May 1992 was also more than twice higher than the average May precipitation since 1978. Increased precipitation would enlarge the spawning area, provide continuous water circulation and oxygen transport to developing embryos, and prevent streambeds from freezing (Wickett 1958; Becker et al. 1982; Chadwick 1982; Heard 1991). Indeed, positive effects of precipitation on freshwater survival were reported for coho salmon (Anderson and Wilen 1985) and for Atlantic salmon (Gibson and Myers 1988). Different responses between pink and sockeye salmon to environmental variables may be due to different spawning habitats selected by these species; pink salmon spawn in Auke and Lake Creeks, whereas sockeye salmon mainly spawn on the shore of Auke Lake and in Lake Creek. Nevertheless, it is not fully understandable that environmental conditions which considerably favored smolt production of sockeye salmon in 1991 did not favor pink salmon fry production.

I could not identify environmental variables that had caused an increasing trend in smolt production for pink and sockeye salmon since the late 1970s in the Auke Lake system. Hofmeister (1994) found that pink salmon harvest in southeast Alaska has been increasing since the mid 1970s. He attributes this trend to increased winter air temperature, but I could not confirm this for the Auke Lake area.

CHAPTER 4. DETERMINANTS OF STREAM LIFE, SPAWNING EFFICIENCY, AND HABITAT SELECTION IN PINK SALMON

In the Auke Lake system, pink salmon have two major choices of spawning habitats, the outlet Auke Creek and the major inlet Lake Creek, which offer quite different environments for the spawners and embryos (Chapter 2). The spawning migration of pink salmon in this system occurs during August and September usually with two distinct runs referred to as early and late runs; the peak immigration of the early run spawners normally precedes that of the late run spawners by more than two weeks (Taylor 1980; Gharrett and Smoker 1993). Despite such time lag between the runs and despite a decline from the early immigration peak to the late of more than 5 °C in stream temperature, the emigration of pink salmon fry in the next spring is relatively synchronous. The time span of emigration is not amplified beyond the time span of spawning as might be predicted from consideration of the steeply declining temperature of Auke Creek each autumn (see Tables 2.2 and 2.3).

In this chapter, I analyze data from a tagging study conducted at Auke Creek during 1994 to examine three attributes of pink salmon spawners of different runs. Relation between the findings of the tagging study and fry outmigration timings is discussed. A hypothesis is proposed that each attribute should vary within the season such that synchrony of fry outmigration would be maximized.

Methods

Tagging

Tagging was conducted at the Auke Creek weir from August 23 to September 21, 1994. The period of tagging encompassed more than 90% of the pink salmon run into Auke Creek in 1994. Numbered spaghetti tags (Anchor T-bar tags, Floy Tag Inc.) were emplaced at the (posterior) insertion of the dorsal fin in female pink salmon randomly selected during the weir operation. The number of tagged fish was roughly proportional to the daily escapement of pink salmon.

The tags were recovered each day and recorded from carcasses or as lost tags in Auke Creek, mostly at the weir which eventually trapped all carcasses flushed downstream when stream discharges were sufficiently high. When the stream discharges were low, especially during the early spawning season, daily foot surveys were conducted throughout the entire channel of Auke Creek to collect tagged carcasses stranded on spawning grounds. Thus almost all (more than 95%) of the carcasses of pink salmon in Auke Creek were checked for the presence of tags. However, a small proportion of lost tags were not recovered when the stream discharges were extremely high.

Tag recovery was not conducted in Lake Creek, but the number of spawners in this creek was visually counted during foot surveys on the entire spawning ground (1,250 m long) on 15 occasions throughout the spawning season in order to observe temporal migration pattern of female pink salmon into Lake Creek.

Spawner Attributes

Stream life in Auke Creek L of female pink salmon was recorded from 584 tagged carcasses throughout the spawning season as the time difference between tagging and recovery dates. The tagged carcasses were nearly all recently dead, but some were not. In order to construct as accurate a regression model as possible, any lost tags and old carcasses were excluded from the calculation of stream life. By letting the number of carcasses tagged on the i th day and subsequently inspected for stream life be n_i, L_i was obtained by taking an average of stream lives L_{ij} over n_i carcasses. Thus L_i's should have different weights in the least squares analysis, such that $w_i = 1 / V(L_i)$ where $V(L_i) = \sum_j (L_{ij} - L_i)^2 / (n_i - 1), j = 1,.., n_i$. The L_i's were log-transformed in order to obtain a more linear relationship with predictor variables. Note that, since no tag recovery was conducted in Lake Creek, stream life in this analysis applies only to Auke Creek spawners.

Spawning efficiency E of female spawners was evaluated in terms of the egg retention of carcasses. Four hundred ninety seven tagged carcasses were inspected for egg retention throughout the spawning season in Auke Creek. Instead of counting all the eggs retained in an ovary, egg retention was recorded simply as a binary response, i.e., "*many*" or "*few*" corresponding to egg retention of more than or less than 500 eggs. Letting the number of carcasses tagged on the *i* th day and subsequently inspected for the egg retention be n_i, of which s_i carcasses had less than 500 eggs, the spawning efficiency of the daily cohort of pink salmon on the *i* th day was obtained as $E_i = s_i / n_i$, which again applies to Auke Creek spawners only.

Habitat selection, or the proportion *P* of females recovered in Auke Creek, was obtained as $P_i = r_i / M_i$, where M_i is the number of fish tagged on *i* th day and r_i is the number of tags from M_i subsequently recovered in Auke Creek. Lost tags were included in r_i, since those tags were most likely separated from the body of an Auke Creek spawner when the fish's tissue became softer as it decomposed. The three spawner attributes *L*, *E*, and *P* have 21 observations, as the tagging was conducted for a total of 21 days.

Statistical analysis

Spawning efficiency *E* and habitat selection *P* are binary responses, for which ordinary linear regression is not applicable because of the limited range [0,1] and the unequal variances of response variables. Thus the attributes *E* and *P* were analyzed by a logistic regression model which belongs to a family of generalized linear models. For the logistic models, a response variable μ [0,1] is logit transformed as $\eta = \ln\{\mu/(1-\mu)\}$, so that the η is mapped onto the real line [-∞, ∞]. The model was fit with weights of the inverse of corresponding variances, i.e., $V(E)$ or $V(P)$, and the maximum likelihood estimates of parameters were obtained by iterative reweighted least squares (McCullagh and Nelder 1983). In contrast, stream life *L* was simply log-transformed and analyzed by ordinary linear regression with weighted least squares as described before.

The candidate predictor variables for the spawner attributes *L*, *E*, and *P* were 1) Auke Creek temperature *T*, 2) logarithm of stream discharge ln *D*, 3) spawner abundance *S* in Auke Creek, and 4) freshwater immigration date *X*. One more variable *L* (stream life) was added as a candidate predictor variable for the analysis of spawning efficiency *E*, since *L* and *E* might have a causal relationship. Auke Creek temperature *T* has been measured every morning by the NMFS since the 1960s. Stream discharge *D* was calculated from daily stream gage readings and observed stream discharges at ten contrasting gage heights. Spawner abundance *S* in Auke

Creek was estimated from escapement and tagging data (Appendix II); visual counting of spawners in this creek was not feasible unlike in Lake Creek because of high spawner density, existence of deep pools, and low visibility. The immigration date *X* was counted from August 23, 1994. The actual form of *T*, *D*, and *S* variables was either the 6-day moving average of daily measurements or simply the daily measurements depending on the spawner attributes. The 6-day moving averages were used for the analyses of stream life *L* and spawning efficiency *E*, since these two attributes are probably influenced by average environmental conditions encountered by individual spawners during freshwater residence. In contrast, daily measurements were used for the analysis of habitat selection *P*, assuming that a fish's decision whether to spawn in Auke Creek or in Lake Creek was made soon after immigration. Despite these modifications, the same notations were used for *T*, *D*, and *S* among the different models of spawner attributes.

The selection of predictor variables to be included in regression models was based on a method similar to a stepwise procedure. Firstly, a spawner attribute was regressed against predictor variables one by one, and the one that was significant at the 5 % level and reduced the residual sum of squares (*RSS*) most was selected as the first predictor variable and retained in the regression model. Secondly, another variable which reduced the *RSS* most was selected as the second variable only if both the first and second variables were each significant at the 5 % level. The number of predictor variables included in a model was limited to two, because with such a small number of observations ($n = 21$) it is difficult to give biological interpretation to models with three or more predictor variables even if they happen to have significant coefficients. For the logistic regression models of *E* and *P*, the deviance was to be minimized instead of the *RSS*. All the statistical computation was accomplished using the S data analysis and graphics system (Becker and Chambers 1984; Chambers and Hastie 1992).

Results

Auke Creek temperature was about 5 °C higher than Lake Creek temperature when pink salmon started the migration into Auke Creek but decreased almost linearly from 15 °C to 9 °C throughout the 1994 season so that the temperature difference between the two creeks became 2 °C at the end of the spawning (Figure 4.1A). Stream discharge in Auke Creek was nearly 0 m^3/s until late August when a small freshet on August 23 triggered upstream migration of pink salmon. The estimated spawner abundance in Auke Creek exhibited three modes between late August and late September, whereas spawner counts in Lake Creek appear to have a single mode in early September (Figure 4.1B). Note, however, that the estimated spawner abundance in Auke Creek does not necessarily represent the number of Auke Creek spawners but includes Lake Creek spawners which migrated through Auke Creek.

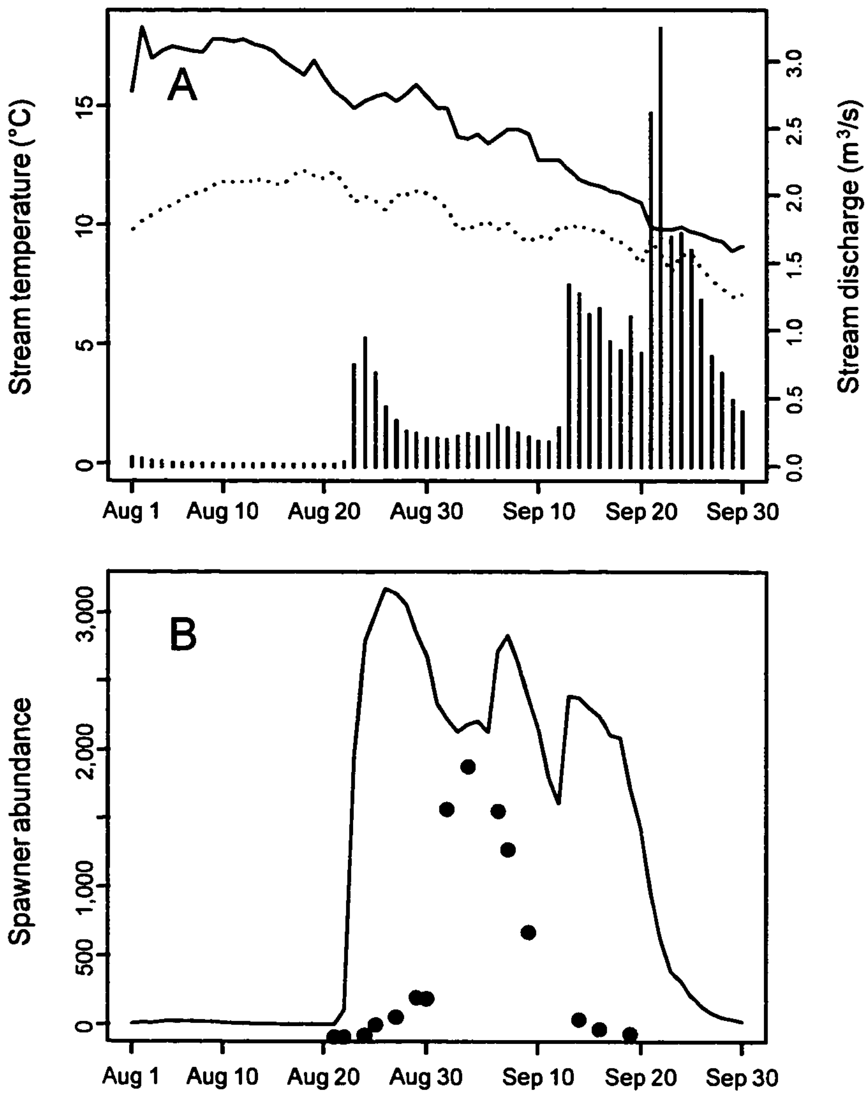

Figure 4.1. Stream temperatures in Auke Creek (solid line) and Lake Creek (dotted line) and stream discharge in Auke Creek (bar plot) (A), and pink salmon spawner abundance in Auke Creek (solid line) and in Lake Creek (closed circles) during the 1994 spawning season (B).

Stream life

Stream life L was 8-10 days at the beginning of the season, decreased to 5-6 days during the mid season, and then rose to about 8 days during the late season (Table 4.1). The average stream life of 584 female pink salmon in Auke Creek was 6.9 days during the 1994 spawning season.

The most parsimonious model contains only one predictor variable $\ln D$ with a positive coefficient, and none of the other variables improved the model fit significantly (Table 4.2). The first four data points of observed stream life show consistently higher values than predicted, but weights for these points are all smaller than average (Figure 4.2A). Except for the data points with small weights, there are no outliers for the model (Figure 4.3).

Spawning efficiency

Spawning efficiency E was considerably low during the early season, so that the majority of the early run spawners retained more than 500 eggs when they died in Auke Creek (Table 4.1). As the season proceeded, E steadily increased with a decreasing stream temperature which is the only predictor variable in the best model (Table 4.2). Although the other variables did not appreciably improve the model fit, the observed spawning efficiencies exhibit relatively high variability around the predicted line (Figures 4.2B and 4.4), suggesting the existence of undetected environmental factors controlling the spawning efficiency of pink salmon.

Habitat selection

The proportion P of daily cohorts spawning in Auke Creek increased substantially from about .3 at the beginning to .7 at the end of the season (Figure 4.2C), indicating that the spawning habitat of pink salmon gradually shifted from Lake Creek to Auke Creek. The estimates of the proportion may be underestimated during the late season, because the higher stream discharges (Figure 4.1A) often made the recovery of lost tags impossible. Thus the actual slope of the increase in Auke Creek spawner proportion may have been even steeper than that observed. It is now apparent that most spawners counted in Lake Creek during foot surveys originated from the first run of pink salmon observed in Auke Creek about 10 days before (Figure 4.1B). This indicates that the Lake Creek spawners had a fairly long stream life similar to the four daily cohorts that died in Auke Creek after a stream life of eight to 10 days (Figure 4.2A).

The most significant variable affecting habitat selection was immigration date *X*, followed by a less significant ($.01 < p < .05$) variable ln *D*. The amount of reduction in the deviance was substantial when ln *D* was added to a model with a single predictor *X* compared to when the other predictor variables were added to the model (Table 4.2). However, the variable *X* implies unknown genetic and/or environmental effects associated with the run timing of pink salmon, so that stream temperature *T*, for example, may possibly replace *X*. The predicted line by variables *X* and ln *D* fits the observed proportions well (Figure 4.2C).

Table 4.1. Summary of the 1994 tagging study, showing daily escapement of pink salmon, the number of tagged pink salmon, the number of tag recovery in Auke Creek, stream life L, its variance $V(L)$, sample size n_l for the stream life measurement, the number of carcasses with less than 500 egg retention (*Few*), those with more than 500 retention (*Many*), and the sample size n_e (= *Few*+*Many*) for the egg retention measurement.

				Stream life			Egg retention		
Tag date	Escape-ment	No. tagged	No. recovered	L (day)	$V(L)$[a]	n_l	*Few*	*Many*	n_e
Aug. 23	5,195	212	75	8.2	11.22	72	22	32	54
24	2,830	113	34	10.6	18.78	31	9	16	25
25	786	50	16	9.3	13.53	16	2	7	9
26	636	41	12	10	8.73	12	2	7	9
27	310	39	10	4.8	1.07	10	2	5	7
28	312	76	33	5	1.78	33	7	21	28
29	298	47	20	5.4	2.69	19	3	10	13
30	282	44	20	4.9	1.06	17	3	11	14
31	349	38	25	5.2	2.18	22	10	7	17
Sep. 1	403	36	19	5.3	.47	18	6	7	13
2	543	-	-	-	-	-	-	-	-
3	666	41	27	6.2	2.81	25	7	16	23
4	575	-	-	-	-	-	-	-	-
5	665	44	19	6.3	4.47	18	11	6	17
6	1,466	40	25	5.8	2.67	24	6	12	18
7	803	94	58	5.2	1.57	53	18	28	46
8	186	-	-	-	-	-	-	-	-
9	310	-	-	-	-	-	-	-	-
10	282	56	35	5	2.03	33	21	10	31
11	245	-	-	-	-	-	-	-	-
12	525	-	-	-	-	-	-	-	-

Table 4.1. (Continued)

				Stream life			Egg retention		
Tag date	Escape-ment	No. tagged	No. recovered	L (day)	V(L)[a]	n_l	*Few*	*Many*	n_e
13	1,890	100	69	7.4	4.06	69	36	29	65
14	571	50	26	8.1	2.41	25	9	15	24
15	220	50	31	7.2	5.06	30	16	13	29
16	165	25	16	7.8	3.8	16	12	4	16
17	54	-	-	-	-	-	-	-	-
18	214	54	37	7.2	3.43	36	25	10	35
19	43	-	-	-	-	-	-	-	-
20	25	-	-	-	-	-	-	-	-
21	22	11	7	8.4	.8	5	4	0	4

[a] The variance formula is given in the text.

Table 4.2. Model selection procedure, showing model terms, parameter estimates and standard errors for only the best models, the degrees of freedom (d.f.), and the residual sum of squares (*RSS*). For spawning efficiency *E* and habitat selection *P*, deviances are shown instead of *RSS*. Significance of model terms is denoted by asterisks, such that * $.01 < p < .05$ and ** $p < .01$.

	Parameter estimates (±1 SE)				
Model	b_0	b_1	b_2	d.f.	*RSS*
Stream life *L*					
$\ln L = b_0 + b_1 \ln D^{**}$	1.97 ± .0415	.202 ± .0333	-	19	.1575
$= b_0 + b_1 \ln D^{**} + b_2 X$				18	.1549
$= b_0 + b_1 \ln D^{*} + b_2 T$				18	.1545
$= b_0 + b_1 \ln D^{**} + b_2 S$				18	.1544
Spawning efficiency *E*					
$\mathrm{logit}(E) = b_0 + b_1 T^{**}$	3.81 ± .752	-.301 ± .0570	-	19	28.25
$= b_0 + b_1 T^{**} + b_2 L$				18	27.92
$= b_0 + b_1 T + b_2 S$				18	26.63
$= b_0 + b_1 T + b_2 \ln D$				18	25.80
$= b_0 + b_1 T^{*} + b_2 X$				18	24.99
Habitat selection *P*					
$\mathrm{logit}(P) = b_0 + b_1 X^{**}$				19	28.93
$= b_0 + b_1 X^{**} + b_2 S$				18	28.19
$= b_0 + b_1 X^{**} + b_2 T$				18	27.18
$= b_0 + b_1 X^{**} + b_2 \ln D^{*}$	-.876 ± .121	.0623 ± .00689	-.187 ± .0835	18	23.90

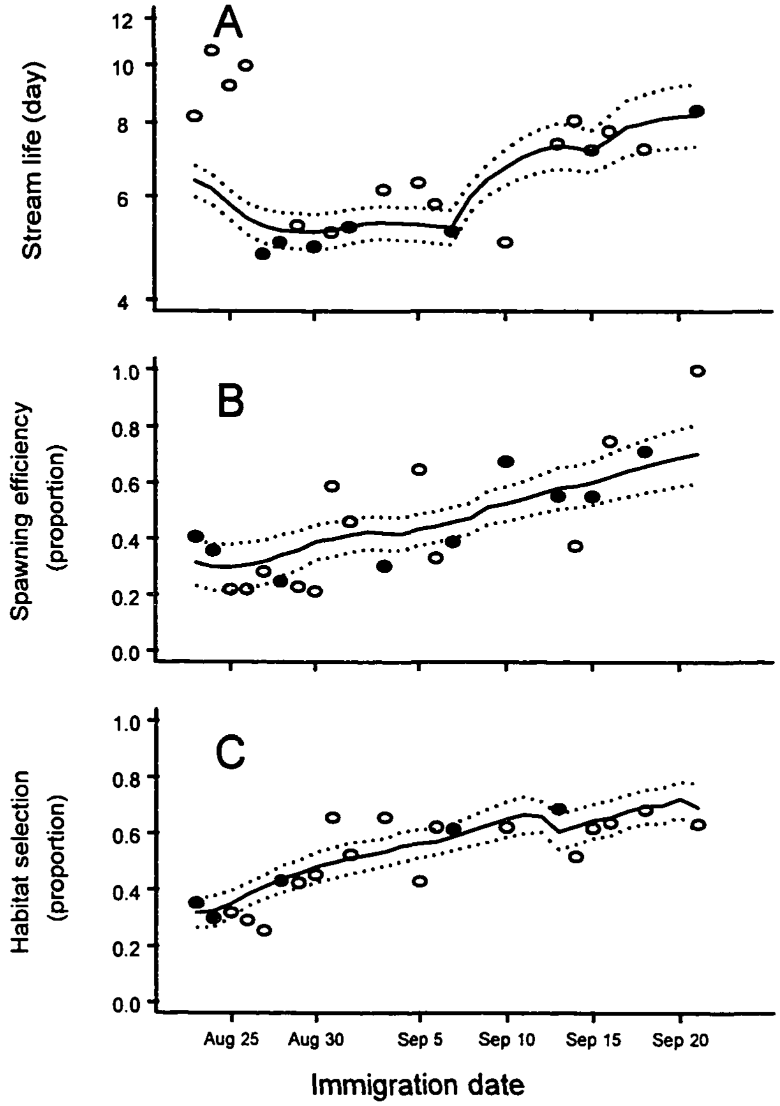

Figure 4.2. Stream life (A), spawning efficiency (B), and habitat selection (C) plotted against the immigration date of tagged female pink salmon. Data points with above and below average weight are marked by closed and open circles, respectively. The predicted line (solid line) is accompanied with pointwise 2 x SE bands (dotted lines).

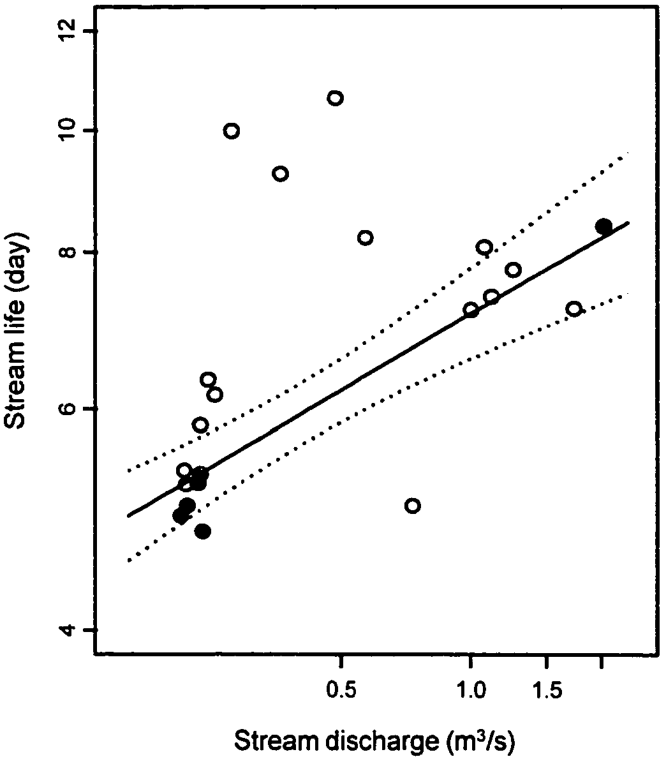

Figure 4.3. The observed and predicted stream life of pink salmon plotted against stream discharge. Data points with above and below average weight are marked by closed and open circles, respectively. The predicted line (solid line) is accompanied with pointwise 2 × SE bands (dotted lines).

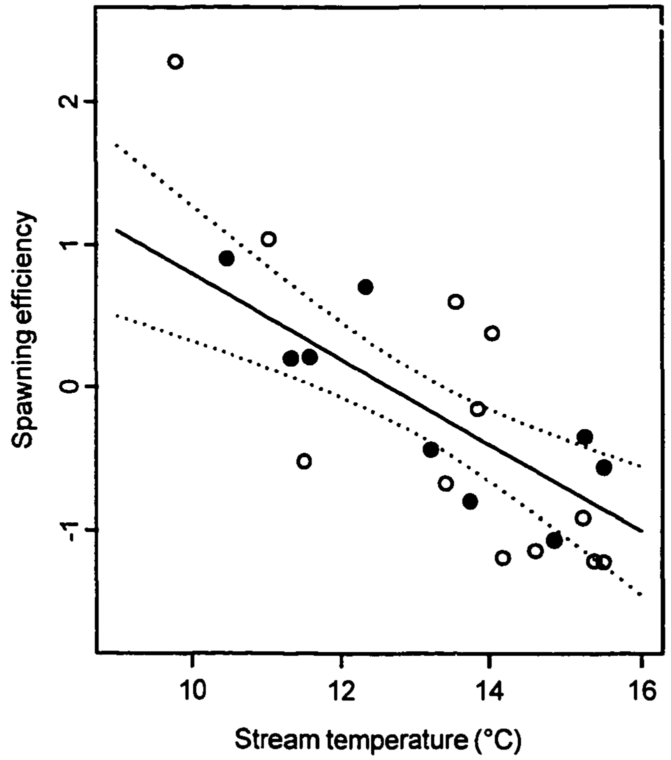

Figure 4.4. The observed and predicted spawning efficiency (logit *E*) of pink salmon plotted against stream temperature. Data points with above and below average weight are marked by closed and open circles, respectively. The predicted line (solid line) is accompanied with pointwise 2 x SE bands (dotted lines).

Discussion

In Pacific salmon, variation of spawning timing between streams within limited geographical areas is such that early runs occur in streams with cooler temperatures than in streams receiving late run spawners (Sheridan 1962; Saunders 1967; Buklis and Barton 1984; Burger et al. 1985; Brannon 1987). Sheridan (1962) found that stream entry and spawning of pink salmon in the southeast Alaska varied with stream temperatures; early runs occurred in mainland streams with lower temperatures, and late runs were mostly found on the outer islands with higher temperatures. Brannon (1987) found that nine stocks of Fraser River sockeye salmon return to their spawning tributaries at a timing directly related to a temperature regime of each tributary. Furthermore, adaptive variation of embryonic development rate, whereby embryos incubating in colder water require fewer accumulated temperature units to complete development, has been observed in Pacific salmon (Koski 1975; Joyce 1986; Brannon 1987; Hebert 1994). The important outcome of such migratory traits and embryonic development patterns is the relatively synchronous emigration of fry and smolts from different run timings into the first feeding area, i.e., an estuary or a lake (Randall et al. 1987). Synchrony of fry and smolt emigration in Pacific salmon in the spring maximizes survival to maturity if the emigration peak coincides with seasonal optimum conditions for their growth; such a match between emigration timing and optimum conditions has been demonstrated for several populations of salmon (Brannon 1987; Taylor et al. *in press*).

The observation of increasing stream life with immigration date in the present study seems to be contrary to other reports of stream life in Pacific salmon (Thomason and Jones 1984; Dangel and Jones 1988; English et al 1992), including my observation of sockeye salmon stream life in the Auke Lake system (Figure 2.5). Increasing stream life tends to de-synchronize fry emigration because embryos experience warmer incubation temperature, on average, than if stream life of early immigrants had been longer. Increasing stream life also separates the spawning events of early- and late-run spawners, de-synchronizing fry emigration. However, it should be recalled that the stream life in this analysis applies only to Auke Creek spawners and does not include Lake Creek spawners which probably had a longer stream life as explained later. Stream discharge was the predictor that best explained the variation of stream life, not date of immigration; the higher the stream discharge the longer the female pink salmon lived. Low discharge probably delayed the entry of spawners into the stream and decreased the oxygen supply to them, thus shortening their lives. Despite a severe freshet during late September, the late run spawners apparently lived longer than the average stream life (Figures 4.1A and 4.2A).

The shorter stream lives of female pink salmon were accompanied by a large pre-spawning mortality caused by high stream temperature above 15 °C in late August. Approximately 70 % of the early run spawners retained more than 500 eggs (Figure 4.2B), which is abnormal in light of typical egg retentions reported for this species (less than 5% of total fecundity; McNeil 1968; Heard 1978). The observations in 1994 may have been anomalous, but similar sustained high temperatures in Auke Creek during late August have been observed in other recent years. Also, similar large scale mortalities of pre-spawning pink salmon have been reported from several streams in southeast Alaska during drought and high temperature (Murphy 1985).

An effect of spawner abundance on habitat selection was not observed. In Sashin Creek, southeast Alaska, higher spawner abundance has been reported to cause pink salmon to migrate farther upstream and seek less crowded spawning ground (Merrell 1962; McNeil 1966, 1968; Heard 1978). Merrell (1962) and McNeil (1966, 1968) observed that pink salmon tended to spawn in the lower area of Sashin Creek in years when the spawner abundance is low, while in years of high spawner abundance a large number of spawners used intensively the upper area of the creek as well as the lower area.

The most significant predictor variable for habitat selection of the 1994 pink salmon spawners was immigration date from the sea; most of the early run pink salmon spawned in the inlet tributary Lake Creek, whereas the late run pink salmon spawned in the outlet Auke Creek. This pattern may or may not be typical for Auke Creek, but such a habitat shift from upstream to downstream during a spawning season would not be peculiar to the pink salmon population in the Auke Lake system. It has been observed for other populations of pink salmon and even for other salmonid species (Briggs 1955; McNeil 1966, 1968; Saunders 1967; Burger et al. 1985; Fukushima 1994). Briggs (1955) hypothesized that in anadromous or potamodromous fishes the earliest arrivals in a particular spawning tributary will travel to the farthest reaches of the acceptable breeding area, the later arrivals occupying territories closer to the mouth of the stream. The consequence of such a migratory trait would be directly related to different developmental rates of embryos spawned in different temperature regimes. In general, upstream water temperatures are lower than downstream temperatures in most stream systems and especially so in lacustrine systems (Burger et al. 1985). In Auke Creek, for example, despite the higher stream temperature encountered by the early run spawners when they first entered freshwater, their embryos actually started development at similar or even lower temperatures in the inlet Lake Creek than the late-run embryos spawned in the outlet Auke Creek (Figure 4.1A). Thus I may rephrase the Briggs' hypothesis to say that early run spawners of salmonids generally select colder water for egg deposition than do later spawners.

If salmonid fish immigrating over extended periods indeed follow the migratory rule hypothesized by Briggs (1955), synchronous outmigration of salmonids can result not only from developing under different incubation temperatures in upstream and downstream habitats but also from another factor associated with their migratory rule, viz., additional traveling time required by early run spawners and their fry to reach an upstream spawning ground and to reach an estuary from the spawning ground, respectively. In the Auke Lake system, for example, actual spawning in Lake Creek by the early run was delayed more than a week after freshwater immigration (Figure 4.1B), whereas spawning in Auke Creek by the late run took place soon after the immigration. Thus, Figure 4.1B implies that stream life of pink salmon population in the whole system of Auke Lake was longer for the early run than for the late run.

The spawning habitat shift observed in the Auke Lake system may be best explained by the adaptation to synchronous fry outmigration as discussed above. However, since the variables X (immigration date) and T (temperature) are indistinguishable in their effects on habitat selection because of their strong colinearity ($r = -.956, p < .0001$), the habitat selection could have been equally well explained by the stream temperatures instead of immigration date. It is thus uncertain whether the shift of spawning habitat is related to a genetic trait specific to the different runs of pink salmon or it is a behavioral response to environmental factors showing a linear trend such as stream temperature. In this regard it is worth noting that variation of run timing has been shown to have a significant basis in genetic variation in odd-year pink salmon in the Auke Lake system (Smoker et al. *in press*). Note how similar were the trends of spawning efficiency and habitat selection (Figures 4.2B and 4.2C). Evidently, it was impossible for the early run spawners to accomplish normal egg deposition in Auke Creek when the temperatures were above 15 °C.

CHAPTER 5. ESTIMATION OF EGG LOSS FROM THE SPAWNING GROUND OF PINK SALMON

Unlike most Pacific salmon, pink salmon use the freshwater environment only for spawning and incubation of embryos. I hypothesize that the density-dependent pink salmon fry production observed in Auke Creek is largely attributable to redd superimposition during spawning. This hypothesis is in part based on an asymptotic production curve of pink salmon fry observed in Auke Creek (Chapter 3) and in the similar stream Sashin Creek (Ignell 1988). This chapter describes an unique method that can quantitatively evaluate a magnitude of egg loss during pink salmon spawning from the streambed using a mark and recapture technique and the maximum likelihood method.

Methods

Mark and recapture experiments

The study area is the major spawning ground of pink salmon in Auke Creek, which extends about 125 m downstream from the outlet of Auke Lake. A total of six small wooden weirs installed in the 1960's to trap the gravel and enhance the spawning habitat segregate the study area into seven sections.

Mark and recapture experiments were performed from August 24 to October 12, 1994 to estimate amounts of eggs dislodged from the spawning ground. Thousands of salmon eggs dyed with food color were released and recaptured along with natural eggs. Combinations of several different colors and two sizes of eggs increased available numbers of marks; eggs of pink and chum salmon prepared from those discarded at nearby hatchery served as small marks, whereas eggs of chinook salmon prepared at the Auke Creek weir served as large marks. The size difference between the two marks was obvious enough to be easily distinguished.

A total of eleven experiments were conducted, each of which consisted of three-day multiple mark and recapture. First, the numbers of spawners, mostly pink salmon, were counted on each section of the study area for a total of eight days between August 25 and September 7 when the visibility of stream water was sufficiently high. During the eleven experiments (i.e., 33 days), five thousand marked eggs were distributed each day, except on September 23 when the number was 4,670, on the seven stream sections in proportion to the spawner count on each section in order to facilitate a random mixture of the marked and the natural eggs. When the visibility of stream water was low due to high stream discharge later in the season, the proportions of eggs released were approximated by the latest observation. The color and/or the size of marked eggs were varied from day to day and, if necessary, from experiment to experiment to avoid mistakenly counting marked eggs from previous experiments.

Drift nets (opening size, .3 x .3 m) were installed in advance of the mark release at the downstream end of the last section from upstream and left in place for 24 hours. The number of nets was not fixed among the experiments but varied from two to five depending on discharge level; when the discharge was low, more nets were required to obtain a large enough sample. Stream discharges were measured each day in Auke Creek throughout the spawning season by the method described in Chapter 4.

Salmon eggs cannot move independently in any direction. Eggs drift in the water only in one direction, from upstream to downstream, so that egg sampling is dependent on stream flow. If stream flow is low, eggs may stop, accumulate in the interstices of gravel because of their somewhat greater specific gravity than the water, and never be subject to capture. The statistical model for the experiment needs to be an open population model, because both marked and natural eggs are continuously flowing out of the study area during the sampling period. In addition, salmon eggs might be subject to predation by other fish such as Dolly Varden. Fortunately, however, the geographical situation of the study area precludes the immigration of eggs from upstream, as there was no spawning ground above the study area, i.e., the outlet area of Auke Lake.

Examination of embryonic developmental stages of sampled eggs

Salmon eggs sampled by the drift nets were subsampled at Auke Creek and preserved into Stockard solution. The developmental stages of sampled eggs were later identified under the microscope based on Ballard (1973). This information was utilized to discuss possible mechanisms of egg loss.

Statistical models

The goals of this analysis are to 1) find the most realistic and robust model that describes egg movement and capture, 2) obtain reliable estimates and standard errors of catchability coefficients, and 3) apply the coefficients to the observed numbers of natural eggs to estimate the amount of egg loss from the pink salmon spawning ground. The estimation of egg loss used the maximum likelihood method of Hilborn (1990). This method estimates movement-related parameters of fish populations based on mark and recapture data. His approach has three elements: 1) a population dynamics and movement model, 2) an observation model for recaptured marks, and 3) maximum likelihood theory to estimate parameters.

For the eleven three-day mark and recapture experiment, let k denote experiment number ($k = 1, ..., 11$), i denote the number of mark group within an experiment ($i = 1, 2$ and 3), and t denote days after the mark release ($t = 1, 2$ and 3). For the k th experiment, let

$M_{i,t0,k}$ = the initial number of marked eggs for group i ($i = 1, 2$ and 3) released on day $t0$
$M_{i,t,k}$ = the number of marked eggs remaining on the study area on day t ($t = 1, 2$ and 3)
$l_{i,t,k}$ = the remaining rate of marked eggs on the study area between days (t-1) and t
$E_{i,t,k}$ = the number of marked eggs from group i that move out between days (t-1) and t
$L_{t,k}$ = the number of natural eggs that move out during the same period as $E_{i,t,k}$
$p_{t,k}$ = the probability of capture of eggs on day t
$m_{i,t,k}$ = the number of sampled marked eggs from $E_{i,t}$ on day t, and
$u_{t,k}$ = the number of sampled natural eggs from $L_{t,k}$ on day t.

Within each experiment k, $M_{i,t}$, $l_{i,t}$, $E_{i,t}$ and $m_{i,t}$ are expressed as three by three triangular matrices with six elements, whereas the L_t, p_t and u_t are vectors of length three. Total numbers of observation for mark recapture $m_{i,t,k}$ and natural eggs $u_{t,k}$ are, therefore, 66 (= 6 x 11) and 33 (= 3 x 11), respectively.

The equation for $M_{i,t+1,k}$ in terms of $M_{i,t,k}$ and $l_{i,t,k}$ can be written

$$M_{i,t+1,k} = M_{i,t,k} l_{i,t,k} \cdot \tag{5.1}$$

In order to reduce the number of parameters in (5.1) and to connect information among eleven experiments, it was assumed that the rate of movement is a function of both time elapsed since mark release and stream discharge on day *t*. Marked eggs would probably become less movable as time elapses because eggs are subsequently caught into the interstices of gravel due to their greater specific gravity than water. On the other hand, it is quite obvious that eggs move more easily when the discharge is greater. In other words, the remaining rates of marked eggs are large when the inverse of discharge is greater. Thus $l_{i,t,k}$ should be proportional to time since release and to the inverse of discharge. Mathematically, $l_{i,t,k}$ is described as

$$\begin{aligned} \left\{ l_{i,t,k} \right\} &= \begin{bmatrix} l_{1,1,k} & l_{1,1,k} & l_{1,3,k} \\ & l_{2,2,k} & l_{2,3,k} \\ & & l_{3,3,k} \end{bmatrix} \\ &= \begin{bmatrix} f_1 d_{1,k} & f_2 d_{2,k} & f_3 d_{3,k} \\ & f_1 d_{2,k} & f_2 d_{3,k} \\ & & f_1 d_{3,k} \end{bmatrix} \end{aligned} \tag{5.2}$$

where f_1, f_2 and f_3 are parameters that represent time-dependent movement, and $d_{1,k}$, $d_{2,k}$ and $d_{3,k}$ are the reciprocals of observed stream discharge on corresponding days. During the likelihood maximization $d_{t,k}$ were scaled by multiplying the minimum observed stream discharge throughout the eleven experiments, so that the $d_{t,k}$ and $l_{i,t,k}$ in (5.2) never exceed one, given a constraint on f such that $0 < f < 1$. Note that the three f parameters were fixed among experiments, since they were only dependent on time after mark release and not dependent on days.

The number of marked eggs that move out between days (t-1) and t is the difference between two successive values of (5.1), so that

$$\hat{E}_{i,t,k} = M_{i,t,k} - M_{i,t+1,k}\,. \tag{5.3}$$

Then the predicted number of eggs sampled is

$$\hat{m}_{i,t,k} = p_{t,k}\hat{E}_{i,t,k}\,. \tag{5.4}$$

To further reduce the number of parameters in the model, the $p_{t,k}$ were assumed to be proportional to the diagonal elements $m_{t,t,k}$ of observed mark recapture matrices (i.e., mark recaptures on the first day after the releases of 5,000 marks reflect the capture probabilities). Thus,

$$p_{t,k} = \frac{m_{t,t,k}}{m_{max}} q_k \tag{5.5}$$

where m_{max} is the maximum observed mark recapture of $m_{t,t}$ throughout the eleven experiments and q_k is a catchability coefficient (parameter) for the k th experiment. The m_{max} was required to keep p less than one during the likelihood maximization, given a constraint on q such that $0 < q < 1$. By incorporating (5.2), (5.3) and (5.5) into (5.4), the predicted number of marked eggs in a sample can be expressed by the initial number of mark releases $M_{i,t0,k}$, observed stream discharges $1/d_{t,k}$, observed mark recaptures $m_{t,t,k}$, and model parameters f's and q's.

The likelihood of predicted mark recaptures $\hat{m}_{i,t,k}$ given observed mark recaptures $m_{i,t,k}$ is then calculated using a Poisson probability, assuming the more explicit multinomial distribution can be approximated by Poisson distribution due to small numbers of mark recaptures in the present study. The likelihood is written as

$$\boldsymbol{L}_{i,t,k} = \boldsymbol{L}\left(\hat{m}_{i,t,k} \middle| m_{i,t,k}\right) = \frac{e^{-\hat{m}_{i,t,k}}\,\hat{m}_{i,t,k}^{\;m_{i,t,k}}}{m_{i,t,k}!} \tag{5.6}$$

and the total likelihood is the product of (5.6) throughout eleven k's, three t's and three i's.

$$\boldsymbol{L} = \prod_{i}^{3} \prod_{t}^{3} \prod_{k}^{11} \boldsymbol{L}_{i,t,k} \,. \tag{5.7}$$

The logarithm of above likelihood was used during a function maximization procedure.

Finally, the estimates of egg loss for day t of k th experiment can be obtained as

$$\hat{L}_{t,k} = u_{t,k} \,/\, p_{t,k} \,. \tag{5.8}$$

The standard errors of model parameters were obtained by performing bootstrapping (Efron 1982). During each replication, 1) Poisson random numbers $m^*_{i,t,k}$ were generated for each of the 66 (= 6 x 11) observations of mark recapture with Poisson parameter $\lambda = m_{i,t,k}$, and 2) the maximum likelihood estimates of parameters were obtained. After repeating this procedure 500 times, the standard deviations of the 500 sets of bootstrap parameter estimates were calculated to approximate the standard errors of original parameter estimates.

The numbers of natural eggs u_t sampled by the drift nets were also assumed to be distributed as Poisson. The standard error of $\hat{L}_{t,k}$ was obtained by separately generating Poisson random numbers $u^*_{t,k}$ for each of the 33 (= 3 x 11) observations of natural egg loss with $\lambda = u_{t,k}$ and by dividing each of them by each of the corresponding 33 $p^*_{t,k}$'s ($= \frac{m^*_{t,t,k}}{m^*_{max}} q^*_k$). The 33 $u^*_{t,k}$'s were generated 500 times and the 33 $p_{t,k}{}^*$'s were chosen randomly from the 500 sets of bootstrap estimates obtained above.

I developed three models for movement and capture of marked eggs from Auke Creek spawning ground. The first model (Model 1) is a full model with 14 parameters, and the second (Model 2) and the third (Model 3) are reduced models with the number of parameters 12 and 4, respectively. The parameters in Model 1 are time-dependent movement parameters (f_1, f_2 and f_3) and catchability coefficients (q_1 through q_{11}) that may differ among experiments.

The parameters in Model 2 are one *f* and eleven *q*'s; the time-dependence in (5.2) was ignored, and the remaining rates of eggs $l_{i,t,k}$ are only dependent on stream discharges. In Model 3, the time-dependence in egg movement was adopted, but catchability coefficients q in (5.5) were held constant throughout experiments, so that this model has three *f*'s and one *q*. The probabilities of capture in this model are simply dependent on the ratio of mark recaptures on the first day after mark releases, i.e., $m_{t,t,k}$ in (5.5). For Models 1, 2 and 3, identical (500) sets of Poisson random numbers were used both for $m_{i,t,k}$ and $u_{t,k}$ during the bootstrapping.

Comparison between the models was done using the likelihood ratio test. The test statistic is

$$\chi^2 = -2\left(\ln \boldsymbol{L}_R - \ln \boldsymbol{L}_F\right) \tag{5.9}$$

where ln $\boldsymbol{L}_R$ and ln $\boldsymbol{L}_F$ are log-likelihoods of full and reduced models, respectively. The asymptotic distribution of above statistic is chi-square distribution with degrees of freedom equal to the difference in the degrees of freedom between the full and reduced models (Quinn and Deriso *in press*).

Results

Model selection

The number of recaptures m was usually more than 100, whereas the number of captures of natural eggs u had a large range from one on October 13 to 3,333 on September 13 (Table 5.1). Common parameters and their standard errors among Models 1, 2 and 3 were quite similar to one another (Table 5.2). The coefficients of variation (CV) were all less than 10 %. It is noted that the CV of the catchability coefficient in Model 3 (6.13 %) was smaller than the CV of any catchability coefficients estimated for Models 2 and 3.

Contrary to the original prediction, the movement parameters f_1, f_2 and f_3 did not monotonically increase but decreased to a considerably small value for the third day of recapture for both Models 1 and 3. This was largely due to the fact that the $m_{1,3,k}$ (i.e., mark recapture on the third day from the first group of mark release) were similar to $m_{1,2,k}$. Namely, in order for such relatively large numbers of marked eggs to be captured on the third day, most of the remaining marked eggs needed to move out, in the models, between the second and the third days, or equivalently f_3 needed to be as small as 0. Obviously, there is no biological or physical mechanism that support such movement pattern of salmon eggs, and the egg movement in waterflow is apparently more complicated than that predicted by time and stream discharge. Based on estimated parameters, remaining rates $l_{i,t,k}$ and probabilities of capture $p_{t,k}$ were calculated in Appendix III.

The estimated catchability coefficients were highly correlated to each other for Models 1 and 2, suggesting parameter instability (Table 5.3). Correlations both between movement parameters f and between f and q were negligible in all models, and the four estimated parameters in Model 3 were quite stable.

Table 5.1. The observed numbers of marked recaptures and natural eggs during the eleven experiments in Auke Creek, 1994.

		Mark recapture					Mark recapture		
Experiment	Date	m_{i1}	m_{i2}	m_{i3}	Experiment	Date	m_{i1}	m_{i2}	m_{i3}
Exp. 1	Aug. 24	98	10	4	Exp. 5	Sep. 16	143	10	9
	25	-	120	5		17	-	83	8
	26	-	-	96		18	-	-	109
	u_t	96	557	851		u_t	2,036	1,899	1,039
Exp. 2	Sep. 1	27	19	8	Exp. 6	Sep. 19	119	5	6
	2	-	50	18		20	-	37	4
	3	-	-	55		21	-	-	65
	u_t	943	2,552	1,814		u_t	1,175	803	808
Exp. 3	Sep. 7	42	9	12	Exp. 7	Sep. 23	113	5	2
	8	-	25	23		24	-	193	2
	9	-	-	92		25	-	-	199
	u_t	1,195	1,804	2,415		u_t	97	71	15
Exp. 4	Sep. 12	125	9	7	Exp. 8	Sep. 26	208	4	2
	13	-	104	9		27	-	110	3
	14	-	-	72		28	-	-	62
	u_t	3,333	2,759	1,192		u_t	28	12	13

Table 5.1. (Continued)

		Mark recapture					Mark recapture		
Experiment	Date	m_{i1}	m_{i2}	m_{i3}	Experiment	Date	m_{i1}	m_{i2}	m_{i3}
Exp. 9	Oct. 1	50	11	16	Exp. 11	Oct. 10	204	7	1
	2	-	51	18		11	-	122	9
	3	-	-	56		12	-	-	103
	u_t	5	26	53		u_t	21	8	1
Exp. 10	Oct. 4	101	1	2					
	5	-	169	3					
	6	-	-	247					
	u_t	38	31	48					

Table 5.2. Parameter estimates, standard errors and the coefficients of variation for Models 1, 2 and 3.

	Estimate	SE	CV(%)
Model 1			
f_1	3.746E-01	2.001E-02	5.34
f_2	6.119E-01	4.802E-02	7.85
f_3	1.000E-04	1.661E-07	.17
q_1	5.595E-02	3.565E-03	6.37
q_2	7.444E-02	6.272E-03	8.43
q_3	7.371E-02	5.633E-03	7.64
q_4	5.579E-02	3.624E-03	6.50
q_5	5.536E-02	3.476E-03	6.28
q_6	5.392E-02	3.414E-03	6.33
q_7	5.168E-02	3.179E-03	6.15
q_8	5.309E-02	3.310E-03	6.24
q_9	6.464E-02	4.962E-03	7.68
q_{10}	5.056E-02	3.107E-03	6.15
q_{11}	5.527E-02	3.442E-03	6.23

Table 5.2. (Continued)

		Estimate	SE	CV(%)
Model 2				
	f	4.184E-01	2.375E-02	5.68
	q_1	5.622E-02	3.585E-03	6.38
	q_2	7.557E-02	6.552E-03	8.67
	q_3	7.571E-02	5.982E-03	7.90
	q_4	5.601E-02	3.655E-03	6.53
	q_5	5.556E-02	3.490E-03	6.28
	q_6	5.406E-02	3.427E-03	6.34
	q_7	5.174E-02	3.183E-03	6.15
	q_8	5.333E-02	3.328E-03	6.24
	q_9	6.474E-02	4.986E-03	7.70
	q_{10}	5.062E-02	3.110E-03	6.14
	q_{11}	5.562E-02	3.469E-03	6.24
Model 3				
	f_1	3.615E-01	1.848E-02	5.11
	f_2	5.875E-01	4.835E-02	8.23
	f_3	1.000E-04	5.331E-08	.05
	q	5.557E-02	3.406E-03	6.13

Table 5.3. The correlation coefficients between the parameters of Models 1, 2 and 3 obtained from the 500 bootstrap replicates. The coefficients greater than .8 are shown in bold face.

Model 1

	f_1	f_2	f_3	q_1	q_2	q_3	q_4	q_5	q_6	q_7	q_8	q_9	q_{10}	q_{11}
f_1	1.00	.10	.04	.08	.33	.31	.12	.08	.07	.00	.05	.23	.00	.08
f_2		1.00	.07	.01	-.12	-.09	.03	.01	.02	-.02	.00	.08	-.02	-.02
f_3			1.00	.07	.07	.09	.08	.09	.10	.08	.08	.05	.08	.08
q_1				1.00	.78	**.83**	**.93**	**.94**	**.94**	**.97**	**.97**	**.81**	**.97**	**.97**
q_2					1.00	.69	.76	.77	.76	.78	.79	.67	.78	.79
q_3						1.00	.79	**.81**	**.82**	**.83**	**.84**	.71	**.83**	**.85**
q_4							1.00	**.92**	**.91**	**.94**	**.94**	.78	**.94**	**.93**
q_5								1.00	**.92**	**.96**	**.96**	.79	**.96**	**.95**
q_6									1.00	**.95**	**.95**	.79	**.96**	**.95**
q_7										1.00	**.99**	**.81**	**.99**	**.98**
q_8											1.00	**.82**	**.99**	**.98**
q_9												1.00	**.82**	**.82**
q_{10}													1.00	**.98**
q_{11}														1.00

Table 5.3. (Continued)

Model 2

	f	q_1	q_2	q_3	q_4	q_5	q_6	q_7	q_8	q_9	q_{10}	q_{11}
f	1.00	.09	.34	.35	.13	.09	.08	.00	.05	.25	.00	.09
q_1		1.00	.76	**.81**	**.92**	**.94**	**.93**	**.97**	**.97**	**.80**	**.97**	**.97**
q_2			1.00	.71	.75	.76	.74	.76	.77	.66	.76	.78
q_3				1.00	.77	**.80**	**.80**	**.81**	**.82**	.71	**.81**	**.83**
q_4					1.00	**.91**	**.90**	**.93**	**.94**	.77	**.93**	**.93**
q_5						1.00	**.92**	**.96**	**.96**	.79	**.96**	**.95**
q_6							1.00	**.95**	**.95**	.79	**.96**	**.95**
q_7								1.00	**.99**	**.81**	**.99**	**.98**
q_8									1.00	**.82**	**.99**	**.98**
q_9										1.00	**.81**	**.82**
q_{10}											1.00	**.98**
q_{11}												1.00

Model 3

	f_1	f_2	f_3	q
f_1	1.00	.05	-.04	.08
f_2		1.00	-.07	-.02
f_3			1.00	-.08
q				1.00

The likelihood ratio tests revealed that Model 1 outperformed the other two models with a significantly higher likelihood value than Models 2 and 3 ($p < .005$, chi-square test). The difference between Models 2 and 3 was not significant ($p > .1$, chi-square test; Table 5.4). The significant difference between Models 1 and 2 is attributable to ignoring time-dependent egg movement in Model 2 despite the fact that the f's were indeed largely variable within experiments as shown in the other two models (Table 5.2). Note that the values of log-likelihoods in Table 5.4 do not include the denominator of likelihood function (5.6) which is constant among the three models and thus does not influence the likelihood ratio tests. Despite the significant difference between Models 1 and 2, the estimated numbers of egg loss L were almost identical (Table 5.5), since the L's are dependent only on parameter p's which are similar between the models (Appendix III). The egg loss estimates and the standard errors in Model 3 were much greater than those in the other two models during Experiments 2 and 3, but coefficients of variation were consistently smaller throughout most experiments for Model 3 than for Models 1 and 2.

The smaller egg losses in Models 1 and 2 compared to those in Model 3 during Experiments 2 and 3 are attributable to exceptionally larger catchability coefficients q_2 and q_3 in Models 1 and 2 than q in Model 3 (Table 5.2). The mark recapture data during Experiments 2 and 3 showed apparently different patterns from the data during the other experiments (Table 5.1); mark recaptures on the first days after release were almost half or less than those in the other experiments, but recaptures on the second and the third days were comparable to the others. Models 1 and 2 are probably overparameterized because estimated parameters in these models were less reliable and highly correlated, which resulted in large CV's in egg loss estimates. On the other hand, Model 3 may lack some flexibility that was required for the situations like the two experiments described above. It is difficult to choose the best model from Models 1, 2 and 3.

Table 5.4. The likelihood ratios tested by chi-square statistic among Model 1, 2 and 3 of egg loss estimation.

	Model 1	Model 2	Model 3
Log-likelihood	13,346	13,331	13,326
Residual d.f.	52	54	62

Likelihood ratio

	Model 1	Model 2	Model 3
Model 1	-	29.91	40.95
Model 2	-	-	11.04
Model 3	-	-	-

Difference of d.f.

	Model 1	Model 2	Model 3
Model 1	-	2	10
Model 2	-	-	8
Model 3	-	-	-

Chi-square critical values ($\alpha = .05$)

	Model 1	Model 2	Model 3
Model 1	-	5.99	18.31
Model 2	-	-	15.51
Model 3	-	-	-

Table 5.5. The estimated numbers of egg loss $L_{t,k}$, the standard errors SE, and the coefficients of variation CV for Models 1, 2 and 3.

	Model 1			Model 2			Model 3		
	$L_{t,k}$	SE($L_{t,k}$)	CV(%)	$L_{t,k}$	SE($L_{t,k}$)	CV(%)	$L_{t,k}$	SE($L_{t,k}$)	CV(%)
Exp. 1	4,776	579	12.1	4,753	576	12.1	4,809	578	12.0
	22,588	1,713	7.6	22,478	1,705	7.6	22,742	1,680	7.4
	49,479	3,481	7.0	49,239	3,465	7.0	49,817	3,392	6.8
Exp. 2	126,676	11,193	8.8	124,790	11,260	9.0	169,698	11,651	6.9
	149,291	12,313	8.2	147,068	12,422	8.4	199,995	12,639	6.3
	137,070	11,355	8.3	135,029	11,439	8.5	183,622	11,654	6.3
Exp. 3	112,233	9,150	8.2	109,275	9,155	8.4	148,879	10,019	6.7
	300,353	23,741	7.9	292,437	23,759	8.1	398,422	26,025	6.5
	82,671	6,476	7.8	80,492	6,483	8.1	109,664	7,038	6.4
Exp. 4	116,052	7,748	6.7	115,591	7,746	6.7	116,506	7,428	6.4
	134,881	9,114	6.8	134,344	9,109	6.8	135,409	8,735	6.5
	70,355	4,864	6.9	70,075	4,862	6.9	70,630	4,655	6.6
Exp. 5	73,549	4,917	6.7	73,296	4,900	6.7	73,278	4,800	6.6
	138,224	9,043	6.5	137,748	9,017	6.5	137,715	8,797	6.4
	40,863	2,810	6.9	40,722	2,802	6.9	40,712	2,755	6.8
Exp. 6	49,865	3,515	7.0	49,730	3,508	7.1	48,382	3,310	6.8
	98,078	7,319	7.5	97,813	7,306	7.5	95,161	6,879	7.2
	60,392	4,330	7.2	60,228	4,322	7.2	58,596	4,086	7.0
Exp. 7	4,969	601	12.1	4,963	600	12.1	4,621	558	12.1
	1,963	258	13.1	1,961	257	13.1	1,825	240	13.1
	370	103	27.9	369	103	27.9	344	96	27.9
Exp. 8	705	144	20.4	702	143	20.4	673	137	20.4
	496	149	30.0	494	148	30.1	474	142	30.0
	1,066	303	28.4	1,061	302	28.4	1,019	289	28.3

Table 5.5.(Continued)

	Model 1			Model 2			Model 3		
	$L_{t,k}$	SE($L_{t,k}$)	CV(%)	$L_{t,k}$	SE($L_{t,k}$)	CV(%)	$L_{t,k}$	SE($L_{t,k}$)	CV(%)
Exp. 9	444	201	45.3	444	201	45.3	517	234	45.4
	2,088	451	21.6	2,085	450	21.6	2,429	514	21.2
	4,518	706	15.6	4,511	706	15.6	5,255	795	15.1
Exp. 10	1,896	345	18.2	1,894	344	18.2	1,726	313	18.1
	941	175	18.6	940	175	18.6	856	159	18.6
	949	145	15.3	948	145	15.3	864	132	15.2
Exp. 11	456	108	23.6	453	107	23.6	453	107	23.6
	283	103	36.4	281	102	36.4	282	102	36.4
	42	43	102.5	41	43	102.5	42	43	102.6

Amount and patterns of egg loss

The egg loss estimates from Models 1 and 3 were plotted against sampling dates together with the plots of estimated spawner abundance of pink salmon and stream discharge during the same period (Figure 5.1). Model 2 is not shown in this figure, as it was indistinguishable with Model 1 (Table 5.5). Since the visual counting of spawners in the study area was discontinued on September 10 when the visibility was reduced due to increased streamflow, the estimated Auke Creek pink salmon abundance (Appendix II) was used instead in Figure 5.1. Note that the visual counts in the study area during eight days of early experiments (Table 5.6) were only about one third of the estimated spawner abundance in Auke Creek; obviously, the latter included not only spawners in the study area (125 m) but also spawners outside the area such as those congregating near the weir or those up-migrating to Auke Lake.

Note that egg losses were only observed when pink salmon were present in Auke Creek, and the maximum daily egg loss (300,353 ±23,741 eggs in Model 1 and 398,422 ± 26,025 eggs in Model 3) appears to correspond to the second peak of pink salmon run. Despite two relatively large freshets (3.0 m^3/s) during late September and early October, salmon eggs did not emerge from the gravel and thus were not lost from the spawning ground.

Table 5.6. Pink salmon count in the Auke Creek study area during eight days in the early spawning season.

Aug. 25	Aug. 27	Aug. 28	Aug. 29	Sep. 1	Sep. 3	Sep. 7	Sep. 10
320	1,009	818	1,035	561	690	813	560

Developmental stages of sampled natural eggs washed out from Auke Creek showed a tendency to increase as the spawning season progressed (Table 5.7). Most eggs from earlier samples (Experiments 1-3) were apparently dead judging from their opaque color at sampling, whereas most eggs from later samples (Experiments 6 and after) were eyed (Stage > 18) and alive; embryos were occasionally seen moving inside the egg shell. The stages of most eggs from early samples could not be identified, but they must be either in very early stages or unfertilized. Salmonid eggs of early stages are easily destroyed due to mechanical shock of streamflow and become extremely difficult for stage identification.

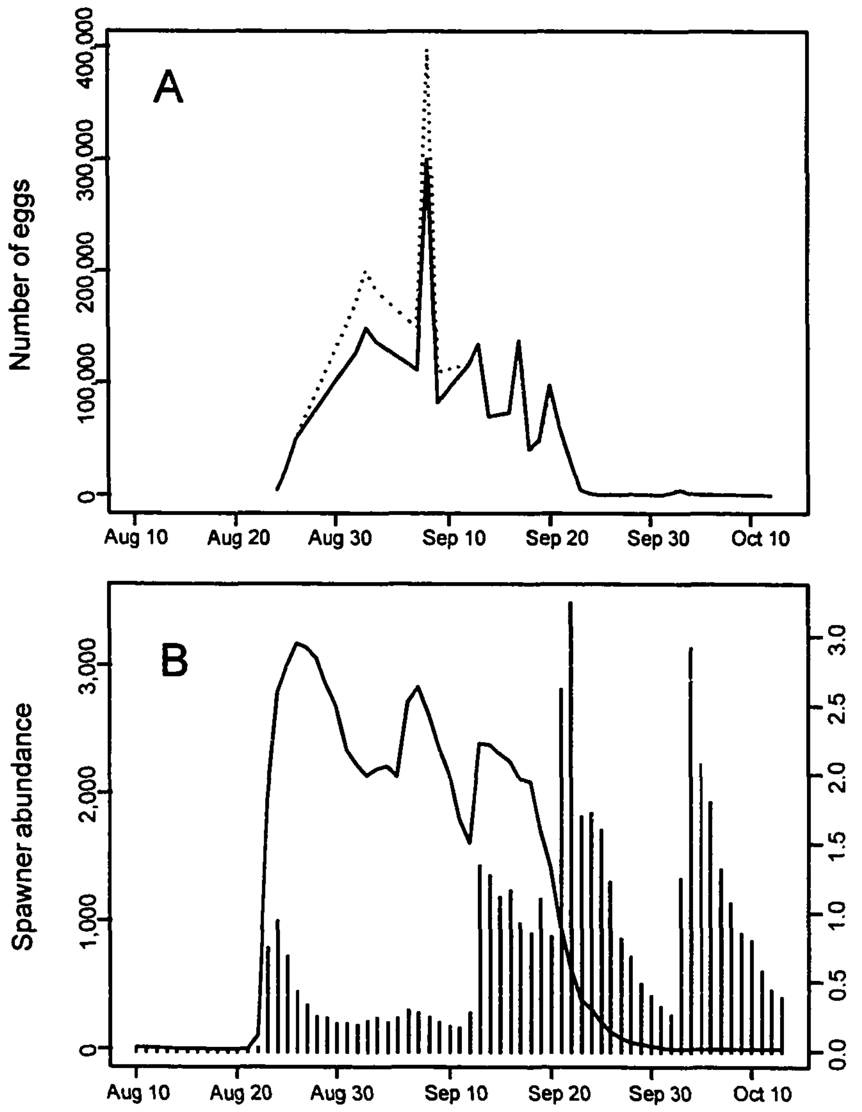

Figure 5.1. Numbers of egg loss from the Auke Creek spawning ground estimated by Model 1 (solid line) and Model 3 (dotted line) plotted against sampling dates (A), and pink salmon spawner abundance (solid line) and Auke Creek discharge (bar plot) during the same period (B).

Table 5.7. Embryonic developmental stages of pink salmon eggs lost from the Auke Creek spawning ground during 1994. The stages of development are based on Ballard (1973).

				Developmental stage													
	Date	*n*	UN[a]	<11	11	12	13	14	15	16	17	18	19	20	21	22	23
Exp. 1	Aug. 24	19	13	6													
	25	55	20	6													
	26	56	28	28													
Exp. 2	Sep. 1	69	66	3													
	2	72	62	10													
	3	74	73						1								
Exp. 3	Sep. 7	79	74						2			1	2				
	8	No samples															
	9	78	76		1					1							
Exp. 4	Sep. 12	72	60							1	2	1	8				
	13	78	72	1						1		1	3				
	14	77	66									5	5	1			
Exp. 5	Sep. 16	95	84					2	2	1		1	1	3	1		
	17	86	73	2					4			1	1		5		
	18	83	64				1			1		2	4	5	6		
Exp. 6	Sep. 19	79	67									4	3	3	2		
	20	88	69			1			1			4	3	1	9		
	21	81	71						1				5	2	2		
Exp. 7	Sep. 23	70	46	1	1			2	2	4	3	4	2	1	2	2	
	24	54	35	1	1							2	2	11	2		
	25	11	7									1	1		2		
Exp. 8	Sep. 26	23	11									2	1	1	8		
	27	10	6										2		2		
	28	10	5									1		2	1	1	
Exp. 9	Oct. 1	No samples															
	2	No samples															
	3	30	15			2						4	2	1	3	1	2
Exp. 10	Oct. 4	33	10									2	8	6	5	1	
	5	26	3								1	5	3		9	3	2
	6	38	7									8	5	7	7	4	
Exp. 11	Oct. 10	15	1								1	1	6		6		
	11	6	1										1	3	1		
	12	No samples															

[a] Eggs of unknown stages

Discussion

The estimated numbers of egg loss were quite large. Since average fecundity of pink salmon in Auke Creek is about 1,400 eggs (W.W. Smoker, University of Alaska Fairbanks unpublished data), the maximum daily loss of 300,000-400,000 eggs estimated during September 8 and 9 is equivalent to a mortality of about 200-300 female pink salmon. If significant egg loss (i.e., mortality) due to retention is taken into account (Chapters 2 and 4), actual mortality of spawners could become even larger. During the first two weeks of September when the daily egg loss was particularly large (> 100,000 eggs), the visual counts of pink salmon spawners in the study area was at most 800 fish (Table 5.6). Assuming the sex ratio of pink salmon to be .5, the average egg retention to be 400, and the average Auke Creek life to be seven days (Chapter 4), the number of eggs successfully deposited by the female pink salmon daily in the study area would become $800(.5)(1{,}400 - 400)/7 \cong 57{,}000$. Although this calculation may be oversimplified, the number of eggs lost from the spawning ground could have exceeded the number of eggs deposited by later spawners of pink salmon.

Three mechanisms originally considered as possible causes of egg loss were redd superimposition, egg spill (i.e., unsuccessful deposition), and streambed scouring due to high stream discharges. In the Auke Creek system, there has been no indication that high stream discharges during spawning adversely influence fry production of Auke Creek pink salmon (Chapter 3). The effect of stream discharges on the loss of salmon eggs is apparently negligible, at least, for the discharge levels observed during the 1994 spawning season in Auke Creek. The egg loss was roughly proportional to abundance of pink salmon spawners in the study area. If redd superimposition was the primary mechanism for the egg loss, the estimates of egg loss should be high when both daily spawner abundance and egg density in the study area were high. If, on the other hand, egg spill was the true mechanism, the estimates should be an approximately linearly increasing function of daily spawner abundance regardless of the egg density in the streambed, since each female spawner would have spilled some expected number of eggs from her redd. There are published field observations both supporting (Vronskiy 1972) and minimizing (Briggs 1953; Healey 1991) the significance of egg spill in Pacific salmon. The present study lacks data on egg density in the streambed, so that it was not possible to analyze the functional relationship among these variables. However, the finding that the natural eggs sampled by drift nets showed more advanced developmental stages as the season progressed can be taken as direct evidence for redd superimposition. If the eggs were simply spilled out of the redds, they would have been expected to be unfertilized or at very early developmental stages throughout the season because salmonid eggs are sensitive to mechanical shock soon after fertilization until after epiboly (Smirnov 1954; Fitzsimons 1994).

The observation of more advanced developmental stages found in later samples demonstrates another important attribute of pink salmon mortality in Auke Creek, viz., eggs spawned by earlier pink salmon suffer higher mortality due to redd superimposition than eggs by later pink salmon. Actual mortality of the early spawned eggs can be even greater because eggs may die from mechanical shock caused by digging activity of later spawners even though the eggs are not removed from the streambed (Heard 1991).

In Auke Creek, pink salmon escapements recently have been around 20,000 in even years and around 5,000 in odd years. The 1994 escapement (21,312 fish) was the third highest since reliable escapement data were first obtained in 1971 and is about the level of estimated spawner capacity S_{max} of this species in the Auke Lake system (Chapter 3). At this level of escapement, density-dependent mortality is so high that the fry production is only about seven fry per spawner (Chapter 3). Historical escapements of pink salmon into Auke Creek may not be remarkably large compared to other streams producing this species. However, throughout the 1994 season approximately 60 % of the total escapement spawned in the small study area (125 m long) of Auke Creek rather than in upstream tributaries (Chapter 4). Thus, the spawner density must have been extremely high at the peak spawning in this creek, and there was a potential for redd superimposition to be a major source of density-dependent mortality, especially in the 1994 season.

The magnitude of redd superimposition and consequent egg mortality have never been fully understood. Thorsteinson et al. (1971) conducted an experiment to measure egg dislodgment from the spawning ground of pink salmon, in which they buried marked eggs in the gravel and monitored the amount of eggs subsequently dislodged. They found that the egg dislodgment increased as the number of spawners, the density of eggs in the spawning ground, and stream discharge increased. Van den Berghe and Gross (1989) found that coho salmon superimposed their redds and destroyed 28 % of 97 redds constructed by earlier spawners in one year and 20 % of 113 redds in the following year. On the contrary to the negative effects of redd superimposition, Smirnov (1947) considered the “digging up” of the spawning grounds as a positive effect in the process of salmon reproduction. He believed the spawning grounds which are not dug up become unfit for salmon reproduction because the digging activity frees accumulated fine sediment and metabolic waste material from the gravel, increasing oxygen supply to embryos.

CHAPTER 6. SPECIES INTERACTION BETWEEN SOCKEYE AND PINK SALMON DURING SPAWNING

This chapter analyses intra- and interspecific interaction within and between pink and sockeye salmon in Lake Creek. It uses a multivariate statistical technique which is widely used by ecologists to study multi-dimensional niche overlap among sympatric species (e.g., Green 1971; M'Closkey 1976; Dueser and Shugart 1978, 1979; Malmqvist 1980; Porter and Dueser 1982; Reinert 1984; Adler 1985; Munro and Rounds 1985; Shenbrot et al. 1991; Scott and Dueser 1992). Multivariate statistics are useful for habitat studies because there is no single variable that can fully describe the habitat of any organism and because habitat variables are more or less correlated with each other; for example, velocity, depth and gravel size in a stream are all three interrelated.

Methods

Spatiotemporal spawner distribution

Lake Creek was equally divided into 50-m sections from the mouth to 1,200 m upstream where the migration of spawners has been blocked by an impassable log jam. An observer recorded the numbers of both pink and sockeye salmon in each section while walking along the stream from the uppermost section toward downstream. The stream was surveyed throughout spawning seasons (early August to late September) of 1992-94 on an average interval of one to three days depending on the year. The survey covered the entire spawning area and included all the active spawners but did not include postspawners that could not maintain position in the streamflow.

Systematic sampling of active redds for microhabitat measurement

During the spawning season in 1994, microhabitat selection by the spawners of pink and sockeye salmon was investigated in sections 7, 8 and 9 (150 m) of Lake Creek where the co-spawning of the two species had been most intensive. The microhabitat was evaluated in terms of hydrological and geomorphological variables that were measured at randomly selected redds. The measurements were repeated on August 24, 26, 31, September 4 and 8 because habitat selection might have differed not only between species but also among different spawning timings within species due to different availability of microhabitats or due to different spawner abundances.

Active redds were selected for microhabitat measurements by a systematic sampling that allowed samples to be taken evenly over the population. Active redds were identified as those on which a female was observed actively digging the gravel at the time of measurement. Firstly, spawners of both sexes were enumerated from upstream to downstream in sections 7, 8 and 9. After disturbed spawners returned to their redds to resume digging (about 10-15 min later), spawners were enumerated once again from downstream, and every *k* th spawner was selected, where the *k* value was calculated by dividing the total number of spawners by the appropriate sample size. If the selected spawner was a female, a redd being dug by the female was marked with a peg attached with a flag. If the selected spawner was a male, a redd being dug up by a female mating with the male was marked. To minimize the disturbance to spawners, the pegs were thrown from nearby riparian vegetation and, later, adjusted to the exact sampling location if necessary. This procedure was applied both to pink and sockeye salmon simultaneously but using different colors for the flag on the pegs to distinguish the species. A target sample size was 30 for each species on each measurement date, but due to a limited man power and limited availability of spawners the sample sizes were smaller for some dates.

Measurement of variables

The four variables measured from each of the randomly selected redds were: 1) water depth *Dep*, 2) current velocity *Vel*, 3) local channel gradient *Grd* and 4) gravel size *Grv* (Figure 6.1). The water depth was measured, to the nearest .5 cm, with a meter stick at the upstream lip of the redd. The current velocity was measured approximately at the depth of female's snout with a Marsh-McBirney Model 201 current meter. The local channel gradient was measured by a carpenter's (Stanley-tm) quick square attached to level and placed upon a rectangular frame (120 x 60 cm) so that the gradient could be read above the water. The frame was placed approximately one meter upstream from the redd parallel to the stream current. A positive local gradient indicated streamwater flowing downward, whereas a negative gradient indicated locally upwelling streamwater relative to the static water level. Gravel size was represented by the average size, to the nearest millimeter, of the first three largest gravels sampled at the middle of the redds by a cylindrical plastic pipe-corer with a diameter of 12.7 cm.

In addition to the habitat variables measured at the redds, water depth and current velocity were also measured during each measurement at a total of six reference points set up on three transects, each of which was installed in each stream section (50 m apart) and provided two reference points. The measurements at the reference points were used as indices of habitat availability on a particular date and were used to adjust the depth and velocity measurements of habitat selection to make the data from different dates amenable to statistical comparison (Baldrige and Amos 1982; Orth et al. 1982). Availability of a habitat variable is determined from its prevalence in the habitat, which is adjusted to eliminate areas where other variables are beyond the tolerance range of the species (Baldrige and Amos 1982). The availability of water depth and velocity for spawners of pink and sockeye salmon can be considerably different through the season, being largely influenced by the preceding weather, especially by the amount of rainfall, but channel gradient and gravel size may be assumed to be invariable.

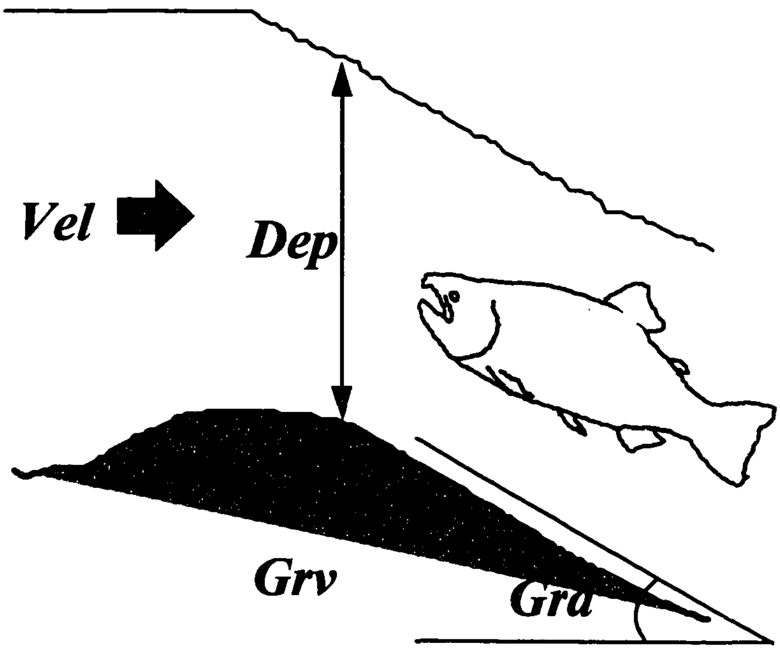

Figure 6.1. Four microhabitat variables *Dep*, *Vel*, *Grd* and *Grv* measured at each of the randomly selected redds of pink and sockeye salmon.

Statistical analyses of microhabitat

The measurements of depth and velocity were weighted by the index of availability of the corresponding variables as follows. Let x_i be the measurement of either depth or velocity at the six reference points on i th of the five days of measurement. The weight W_i was obtained as

$$\begin{aligned} X_i &= \left(x_{i1} + \ \ldots \ + x_{i6}\right) / 6, \quad i = 1, \ldots, 5 \\ \bar{X} &= \left(X_1 + \ \ldots \ + X_5\right) / 5 \\ W_i &= X_i \ / \ \bar{X}. \end{aligned} \tag{6.1}$$

Each measurement of depth and velocity from redds was divided by the corresponding weight for that day. Thus, the depth and velocity measurements were amplified in proportion to the reciprocal of the weight when the available depth and velocity in Lake Creek were small due to a low water level, whereas the measurements were reduced proportionately when the available depth and velocity were great.

The marginal frequency distributions of the observations on each variable were inspected to find whether they were normally distributed. If not, an appropriate transformation was applied to the variable. Any multivariate outliers identified in the pooled data were eliminated from subsequent analyses by visually inspecting the four variables simultaneously using brushing and spinning techniques (Cleveland and McGill 1988).

In order to geometrically examine the four-dimensional multivariate data, multidimensional scaling was applied for each pair of pink and sockeye salmon data from each measurement date. Multidimensional scaling for the present case finds a configuration of observations in fewer dimensions than actually observed such that distances in the new dimensions best match the original distances of the observations (Johnson and Wichern 1992). To test the hypothesis that microhabitat selection by pink and sockeye salmon was the same in terms of the multivariate mean of the four variables, Hotelling's T^2 tests were applied to each pair of groups from the same measurement date and to a pair of groups in the pooled data.

Principal components (PC) were obtained for the pooled data sets of each species from different measurement dates to explain the sample variations of multivariate observations and to compare the variation between the species. The four variables were scaled, in advance, such that each variable had a mean 0 and a standard deviation 1. Linear discriminant function (DF) analyses were performed to identify the linear combinations of the four variables that most efficiently separate microhabitat selection both between the species (DFA1) and among the groups of different species and different measurement dates (DFA2). In the discriminant function analyses, the four variables of microhabitat were scaled in order for the coefficients of DF's to be interpretable. The procedure of scaling was: 1) to pool the data of all species and dates, 2) to scale observations for each variable to have mean 0 and standard deviation 1, and once again 3) to separate the scaled multivariate data into two sets of pink and sockeye salmon (DFA1) or into the groups of species and measurement dates (DFA2).

Multivariate analysis of variance (MANOVA) was used to test if microhabitat selection differs through the spawning season for each species; i.e., MANOVA was performed for the pooled data of pink salmon and those of sockeye salmon separately. A test statistic for this analysis is given by Manly (1986) as

$$\phi = \left[n - 1 - \frac{1}{2}(p + g)\log\left[|\mathbf{T}|/|\mathbf{W}|\right] \right] \tag{6.2}$$

where n is the total number of observations, p is the number of variables, g is the number of groups, $|\mathbf{T}|$ is the determinant of the total sum of squares and cross-products matrix, and $|\mathbf{W}|$ is the determinant of the within-sample sum of squares and cross-products matrix. This statistic was tested for significance by comparison of the chi-squared distribution with $p(g-1)$ degrees of freedom.

The niche breadth of pink and sockeye salmon was represented by the determinants or "generalized variance" of variance-covariance matrices for each group of species and measurement date. The variance-covariance matrices were obtained from the scaled species-date groups that were previously used in the second analysis of DF above.

All the statistical and graphical analyses were done using the S data analysis and graphics system (Becker and Chambers 1984).

A preliminary experiment in 1992

In 1992, microhabitats of pink and sockeye salmon were studied during three days of spawning season in the sections 1-15 of Lake Creek by measuring just two habitat variables, water depth and current velocity. Sampling of redds and measurement of variables were done exactly by the same method described above. The results of this experiment are presented before those of the 1994 experiment, but detailed analysis (such as discriminant function analysis) was not performed for this data set because of the smaller dimensionality.

Results

Spatiotemporal spawner distribution

The run timing of sockeye salmon into Lake Creek was always earlier than that of pink salmon, but its duration was almost the same for both species each year (Figure 6.2). Lack of rainfall in 1994 hindered upstream migration of sockeye salmon and, to a lesser extent, of pink salmon, so that the duration of spawning was much shorter but the observed daily spawner abundance was higher than in the other two years. Sockeye salmon spawned widely over the middle to upper part of the creek, whereas pink salmon mostly selected a lower part (Figure 6.3). In particular, pink salmon constantly preferred sections 1 and 2 despite a large variation in the run sizes among the years, whereas sockeye salmon preferred sections 7 and 9.

The spatiotemporal distribution of spawners was relatively constant throughout spawning seasons (Figure 6.4). It appears, however, that pink salmon in 1992 and 1993 and sockeye salmon in 1993 extended their spawning areas toward upper sections in the middle part of the seasons. The extension by pink salmon roughly coincided with the end of the peak spawning activity of sockeye salmon at sections 7 to 9 (Figure 6.4).

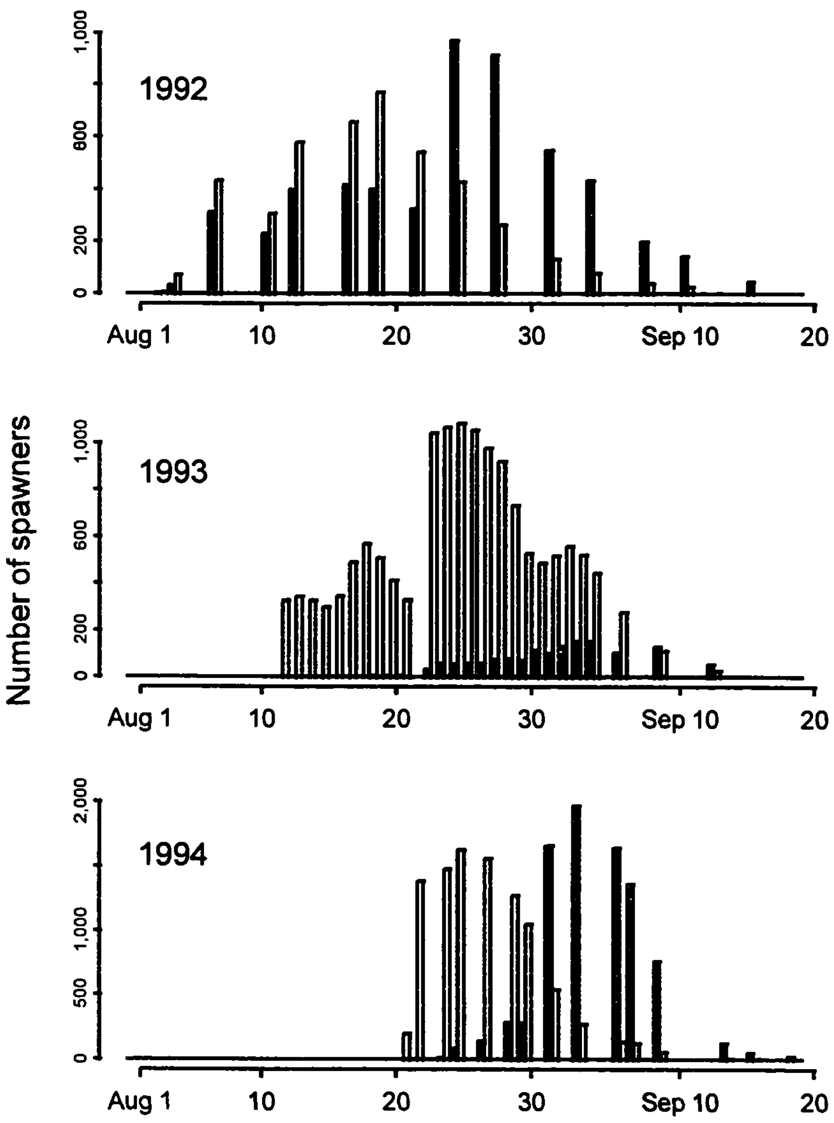

Figure 6.2. Abundance of spawning pink (solid bar) and sockeye (open bar) salmon during the 1992-94 spawning seasons in Lake Creek.

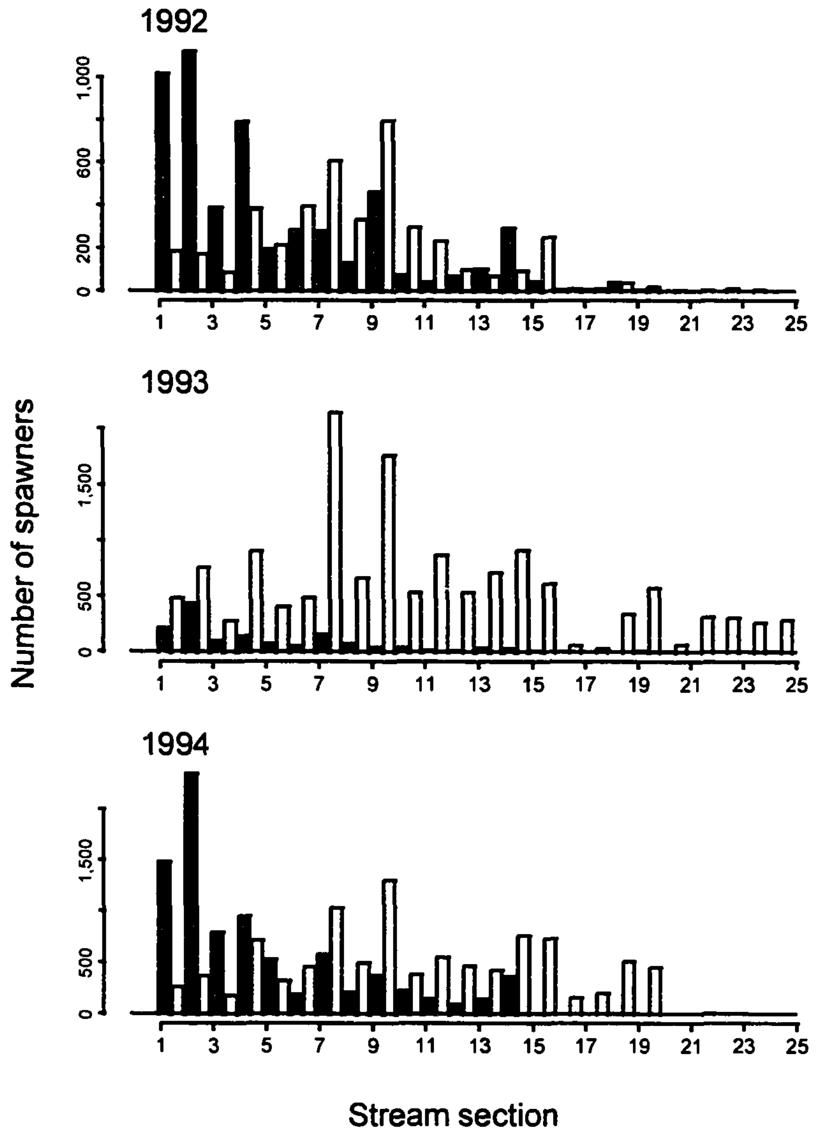

Figure 6.3. Abundance of spawning pink (solid bar) and sockeye (open bar) salmon in study sections during the 1992-94 spawning seasons in Lake Creek. The 50-m sections were located from the mouth to 1,250 m upstream.

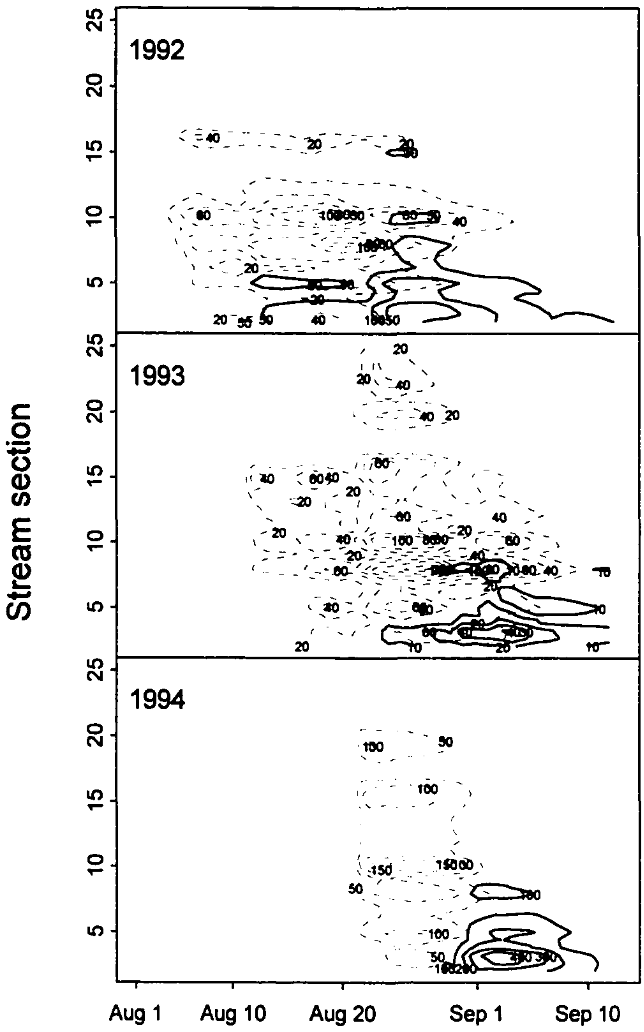

Figure 6.4. The spatiotemporal distribution of spawning pink (solid line) and sockeye (broken line) salmon during the 1992-94 spawning seasons in Lake Creek. The numbers in contours indicate the observed abundance of species.

Microhabitat selection

The spawner abundance of pink and sockeye salmon showed various degrees of contrast during habitat measurements in both 1992 and 1994 (Figure 6.5). In 1994, since pink salmon were almost absent from the study area during the first two days of measurement (August 24 and 26), no redds were sampled on these days for pink salmon.

Microhabitat selection in 1992

The 1992 microhabitat data consist of six groups: three groups for pink salmon and three groups for sockeye salmon obtained on August 18, 26 and September 2. Pink salmon selected shallower sites, at least on the second and third days, with much faster current velocity for spawning than sockeye salmon during the three days of measurement (Table 6.1).

Table 6.1. Means of four microhabitat variables measured from pink and sockeye salmon redds in sections 1-15 of Lake Creek in 1992.

	Water depth (cm)		Velocity (cm/s)		Sample size	
	Pink	Sockeye	Pink	Sockeye	Pink	Sockeye
Aug. 18	17.0	17.0	40	25	16	39
Aug. 26	14.0	18.5	33	20	71	49
Sep. 2	17.0	22.5	37	26	82	14

The bivariate distributions of microhabitat observations, i.e., water depth and current velocity, were not significantly different on August 18 ($T^2 = 9.69, p > .5$), but they were different on August 26 ($T^2 = 45.42, p < .0000$) and on September 2 ($T^2 = 20.82, p < .005$). These observations were largely overlapping between the species, however, during the three days of measurements (Figure 6.6). The significant differences on the second and the third days of measurement were primarily caused by a few observations with relatively deep spawning sites (> 30 cm) selected by sockeye salmon. Sockeye salmon had larger variation in water depth selection at spawning than pink salmon.

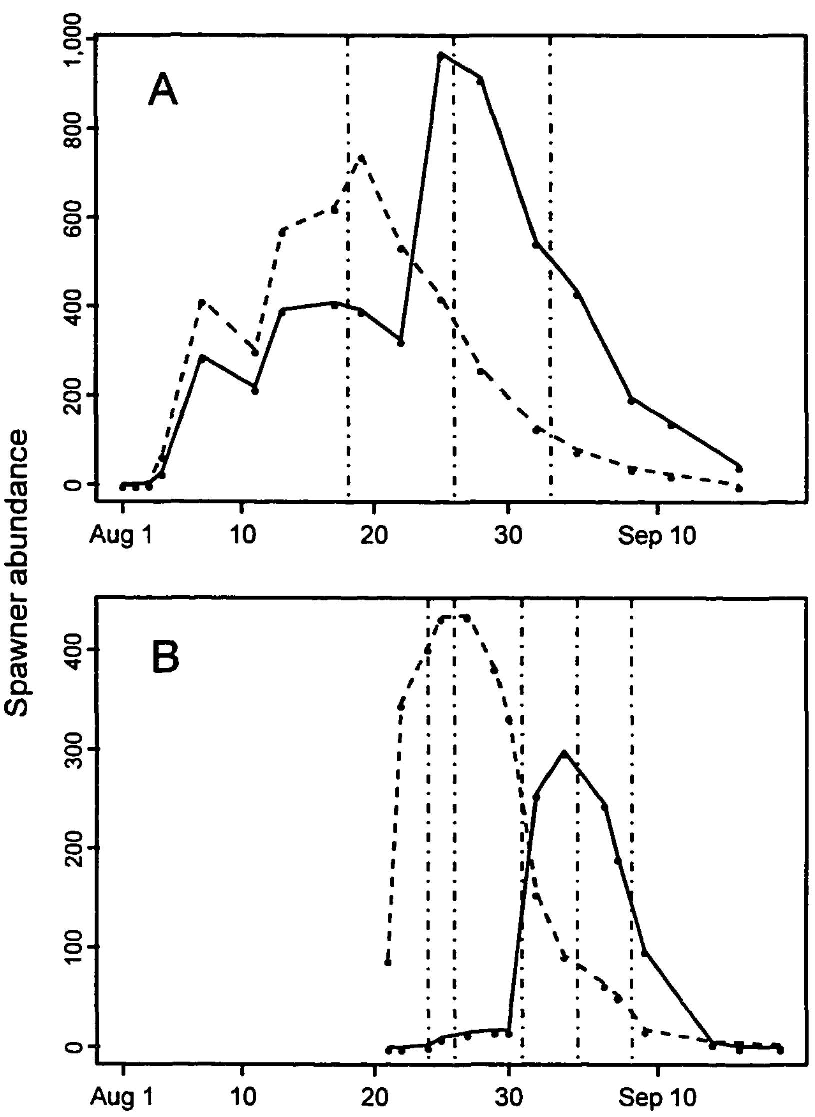

Figure 6.5. The abundance of spawning pink salmon (solid line) and sockeye salmon (broken line) during microhabitat measurements in 1992 (A) and 1994 (B). The study area of Lake Creek was located in sections 1-15 in 1992 and in sections 7-9 in 1994. Vertical lines crossing indicate the dates of measurements.

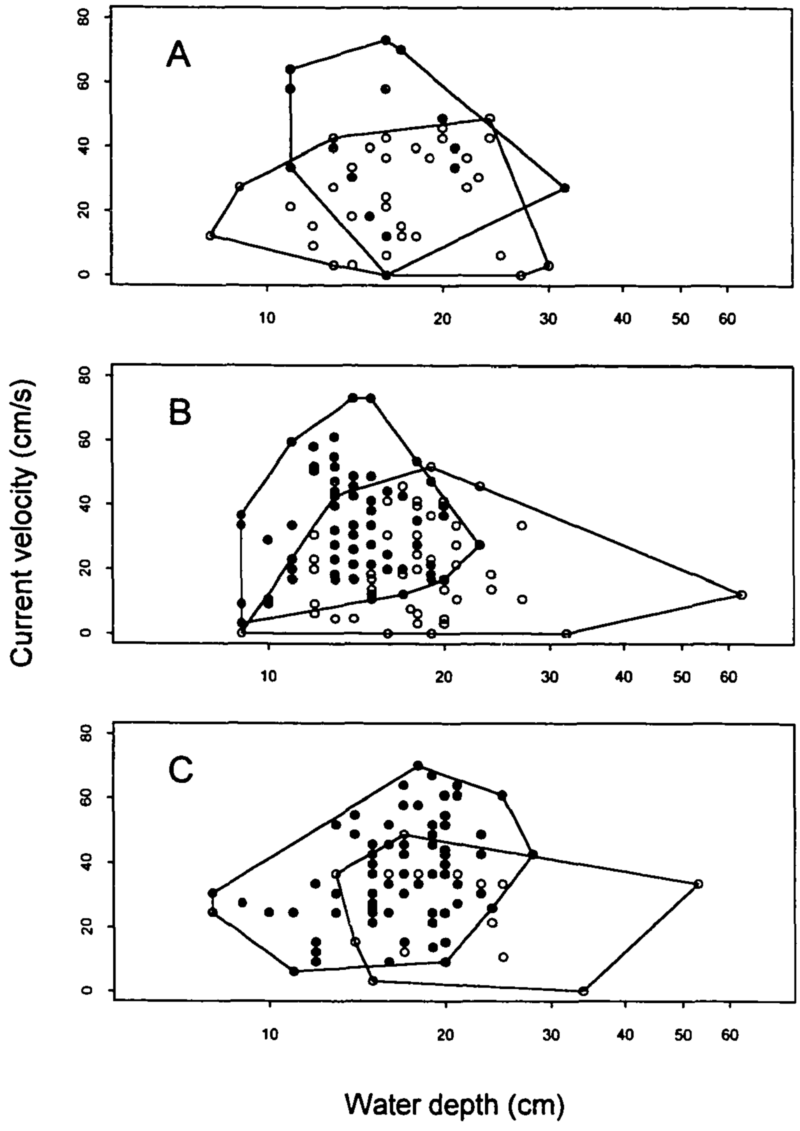

Figure 6.6. Comparisons of microhabitat data in 1992 between pink salmon (closed circles) and sockeye salmon (open circles) plotted against water depth on the x-axis and current velocity on the y-axis. The dates of measurements are August 18 (A), August 26 (B), and September 2 (C).

Microhabitat selection in 1994

Microhabitat data in 1994 consist of eight groups: three groups obtained from pink salmon redds on August 31, September 4 and 8; and five groups obtained from sockeye salmon redds on August 24, 26, 31, September 4 and 8. Means of water depth and current velocity measurements selected by these Pacific salmon were similar to those obtained in 1992. Also, a similar difference in habitat preferences to those in 1992 was observed in 1994, in which pink salmon selected relatively shallower sites with faster water flow (Table 6.2). Channel gradient at sockeye salmon redds varied greatly among different dates of measurement and decreased substantially toward the end of the season.

Habitat availability changed continuously throughout the spawning season due to the drier weather later in the season, and thus water depth and current velocity available for spawners generally showed a decreasing trend (Table 6.2). It appears that the selection of current velocity by pink and sockeye salmon and of channel gradient by sockeye salmon was influenced by the availability of water depth and current velocity.

Table 6.2. Means of four microhabitat variables measured in sections 7-9 in Lake Creek 1994 from pink and sockeye salmon redds. The means of habitat availability (i.e., measurements at six reference points) for water depth and current velocity are also shown for each measurement date.

Date	Depth (cm)	Velocity (cm/s)	Gradient (degree)	Gravel size (cm)	Sample size *n*
Habitat selection					
Pink salmon					
Aug. 24	-	-	-	-	0
26	-	-	-	-	0
31	16.0	39	2.0	8.9	20
Sep. 4	16.0	29	.8	9.0	25
8	14.0	21	1.5	8.4	25
Sockeye salmon					
Aug. 24	20.5	24	1.6	8.1	30
26	17.0	22	1.3	8.2	30
31	22.0	23	.6	7.3	23
Sep. 4	21.5	19	-1.1	7.2	25
8	21.0	17	-1.9	8.3	17
Habitat availability					
Aug. 24	30.5	41			
26	22.5	20			
31	26.5	35			
Sep. 4	21.5	25			
8	19.5	20			

One multivariate outlier was detected in the sockeye salmon data on September 4, 1994. The outlier was due to an unusually large negative measurement of channel gradient, which was probably caused by accidentally placing the gradient meter on a large boulder in front of the sampled redd. The outlier was eliminated from the following analyses. Depth measurements were log-transformed to attain multivariate normality. The sample variances and covariances of microhabitat data were similar between pink and sockeye salmon, although the variances for sockeye salmon were somewhat larger than those for pink salmon (Table 6.3). In particular, the variance of water depth for sockeye salmon was twice larger, in logarithmic scale, than that for pink salmon. In addition, the signs of correlation coefficients between gravel size and the other three variables were opposite between the species.

Table 6.3. The sample variance-covariance matrices of microhabitat data for pink and sockeye salmon.

Pink salmon (n = 70)

	Dep	*Vel*	*Grd*	*Grv*
Dep	.066	-	-	-
Vel	-1.183	230.477	-	-
Grd	-.079	1.152	7.009	-
Grv	.039	-.591	-.126	2.878

Sockeye salmon (n = 125)

	Dep	*Vel*	*Grd*	*Grv*
Dep	.130	-	-	-
Vel	-.778	256.655	-	-
Grd	-.249	7.433	7.312	-
Grv	-.029	5.177	.354	2.484

The pairs of multivariate habitat data for August 31, September 4 and 8, 1994, showed large overlaps similar to the 1992 data between the species, and the sample variations represented by multidimensional scaling were quite comparable between the species for the three dates (Figure 6.7). Despite these overlaps, the multivariate distributions of microhabitat observations were significantly different between pink and sockeye salmon for any pair of groups; i.e., August 31 ($T^2 = 27.68, p < .0005$), September 4 ($T^2 = 36.08, p < .0001$) and September 8 ($T^2 = 60.03, p < .0000$), and for a pair of the pooled groups ($T^2 = 35.20, p < .0000$).

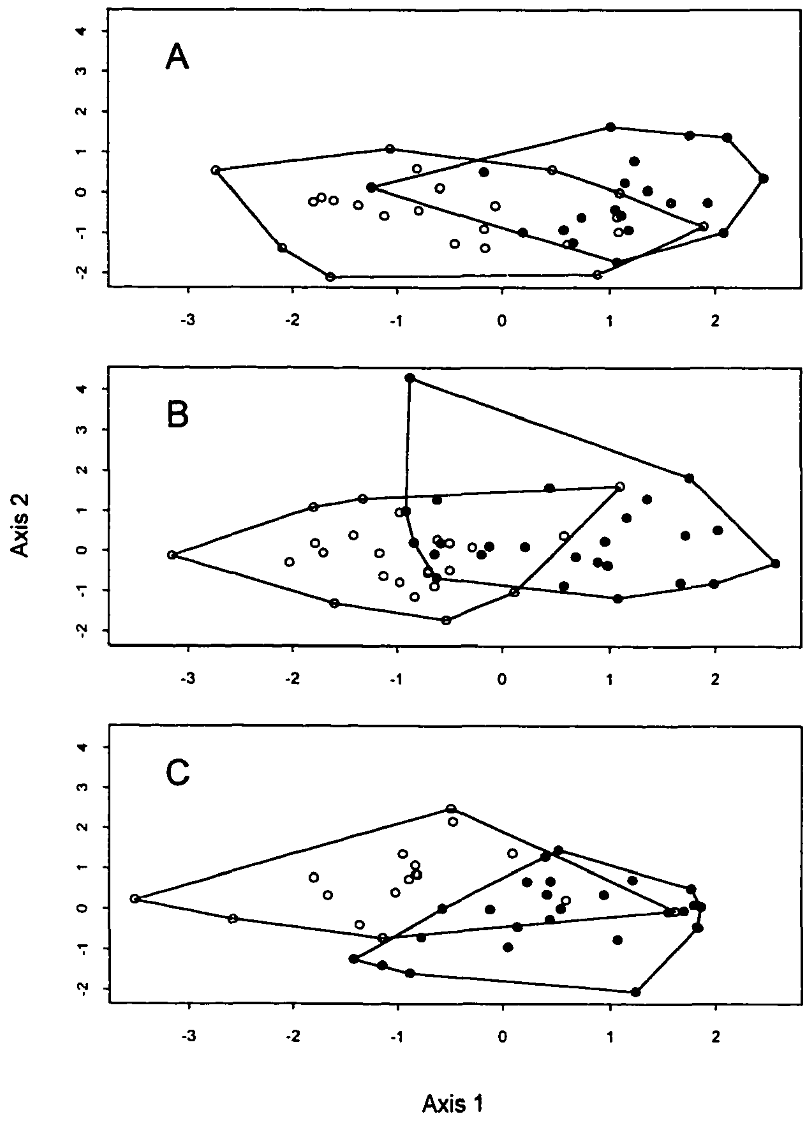

Figure 6.7. Comparisons of microhabitat data in 1994 between pink salmon (closed circles) and sockeye salmon (open circles) by multidimensional scaling. The dates of measurements are August 31 (A), September 4 (B) and September 8 (C). Axes 1 and 2 are nonlinear combinations of four habitat variables.

The first PC for pink salmon was mainly a contrast between water depth and current velocity, in which the selection of spawning habitat varied from deeper and slower water to shallower and faster water (Table 6.4). The first PC for sockeye salmon was similar to pink salmon, but the variation of channel gradient played a more important role than those of depth and velocity. Also, the signs of the coefficient for gravel size were opposite between the first PC's of the two species, which apparently reflected the different covariance matrices described above. The variances explained by each PC were relatively uniform for both species due to small correlation between the four variables; the first two PC's explained only about 60 % of total variance. Thus the sample variation of microhabitat could not be explained with only a few linear combinations of the four variables.

Table 6.4. The principal components of the 1994 microhabitat data for pink and sockeye salmon, showing variances (or eigen values λ), cumulative percentages of the total variance (CPV), and the coefficients of four variables.

	Principal component			
	I	II	III	IV
Pink salmon				
Variance (λ)	1.357	.995	.971	.677
CPV (%)	33.93	58.80	83.08	100.00
Coefficient *Dep*	.686	.097	-.016	.721
Vel	-.622	-.419	.115	.651
Grd	-.293	.520	-.779	.191
Grv	.237	-.738	-.616	-.139
Sockeye salmon				
Variance (λ)	1.459	1.024	.776	.740
CPV (%)	36.49	62.10	81.50	100.00
Coefficient *Dep*	.508	-.502	-.280	.642
Vel	-.531	-.361	-.743	-.187
Grd	-.552	.377	.025	.743
Grv	-.394	-.689	.607	.037

The discriminant function between the pooled groups of pink and sockeye salmon (DFA1) was

$$\mathrm{DF} = -0.464Dep + 0.476Vel + 0.235Grd + 0.577Grv\,. \tag{6.3}$$

The means and standard deviations (in parentheses) of discriminant scores were 19.031 (±7.346) for pink salmon and 13.981 (±8.025) for sockeye salmon. Thus, the microhabitat of pink salmon spawning sites may be characterized by relatively larger gravel, faster current velocity and shallower water depth compared to those of sockeye salmon. Local channel gradient was the least important variable separating the species. However, as indicated by the large standard deviations and by a large overlap in the densities of the discriminant scores (Figure 6.8), it remains difficult to discriminate their habitat selection despite a significant difference ($p < .0000$, T^2-test) in the multivariate means between the species.

A discriminant function analysis among eight groups of species and dates (DFA2, i.e., three groups of pink salmon and five groups of sockeye salmon) revealed that the first DF, which explained the variation of the eight groups most (67.88 %, Table 6.5), mainly separated different groups of sockeye salmon rather than separating species (Figure 6.9). In other words, difference in microhabitat selection was even larger among different spawning timings within sockeye salmon than between species, although convex hulls surrounding the multivariate means of individual species did not cross at any point. Note that the first discriminant score for sockeye salmon appeared to increase with the spawning season (Figure 6.9). As the season progressed, they shifted spawning sites to deeper places with less steep channel gradient as implied by relatively large positive and negative coefficients in the first DF for water depth and channel gradient, respectively (Table 6.5). On the other hand, the second discriminant score that was mainly explained by variation of current velocity showed a trend to decrease with the spawning season, except for "S2" (i.e., habitat selection on August 26, 1994). Recall that the measurements of depth and velocity were weighted by habitat availability at measurement. Since the variation of water depth and current velocity in DF1 and DF2, respectively, showed a roughly opposite trend to the variation of these variables in availability (Table 6.2), the habitat shift toward deeper and faster water shown in Figure 6.9 was probably caused by decreased availability of these variables later in the season. Despite all the attempts to discriminate spawning groups of pink and sockeye salmon, however, differences in multivariate means among measurement dates were not statistically significant both for pink and sockeye salmon because of much larger within-group variation than among-group variation (*p* > .5, MANOVA).

Niche breadths measured by the determinants of variance-covariance matrices showed comparable values between pink and sockeye salmon except for an extremely large value for sockeye salmon observed on August 26 (Figure 6.10). It is now apparent that relatively larger variances in the four variables of sockeye data were largely due to the measurements on this date.

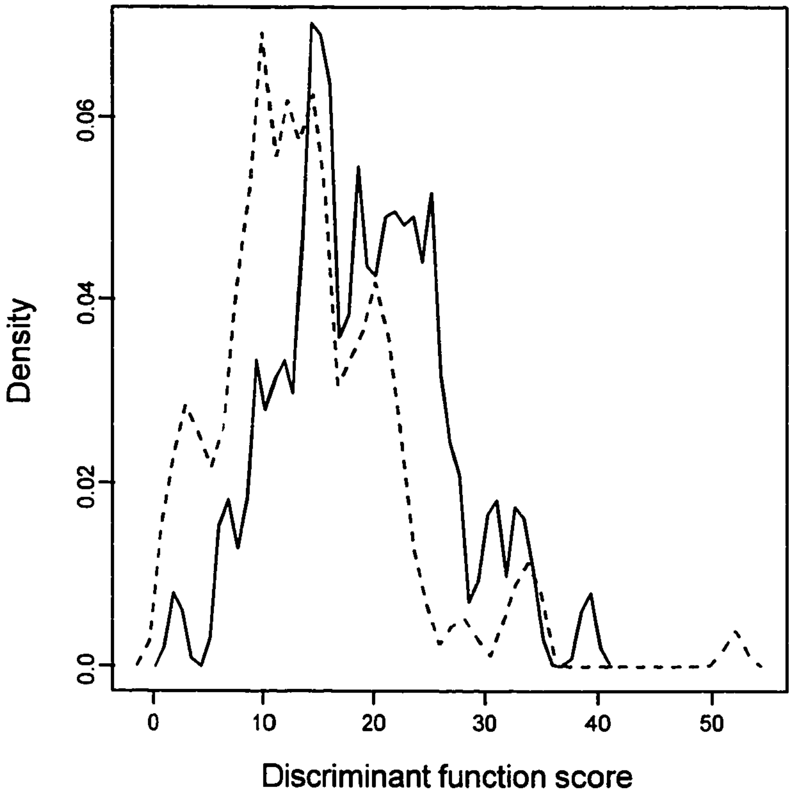

Figure 6.8. Density plots for the discriminant scores of pink (solid line) and sockeye (broken line) salmon microhabitat data in 1994.

Table 6.5. Discriminant functions of eight species-date groups in 1994 showing the percentages of variance explained by each discriminant function and the coefficients of four variables.

	Discriminant function			
	I	II	III	IV
Percentage of variance	67.88	25.81	6.09	.22
Coefficient				
Dep	.909	-.231	.216	-.704
Vel	.142	-.926	.586	.232
Grd	-.608	.214	.507	-.751
Grv	-.325	-.511	-.796	-.391

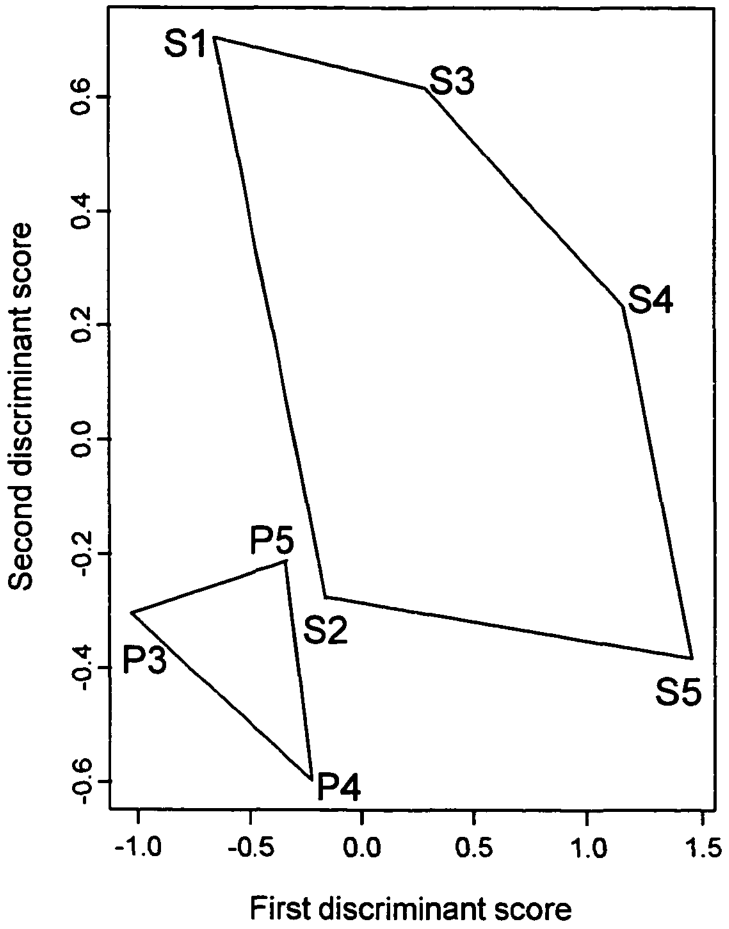

Figure 6.9. Multivariate means of eight species-date groups in 1994 plotted against the first and the second discriminant functions of microhabitat measurements. The letters, "P" and "S", in each data label represent pink and sockeye salmon, respectively; numbers 1-5 indicate the measurement dates: 1) August 24, 2) August 26, 3) August 31, 4) September 4, and 5) September 8.

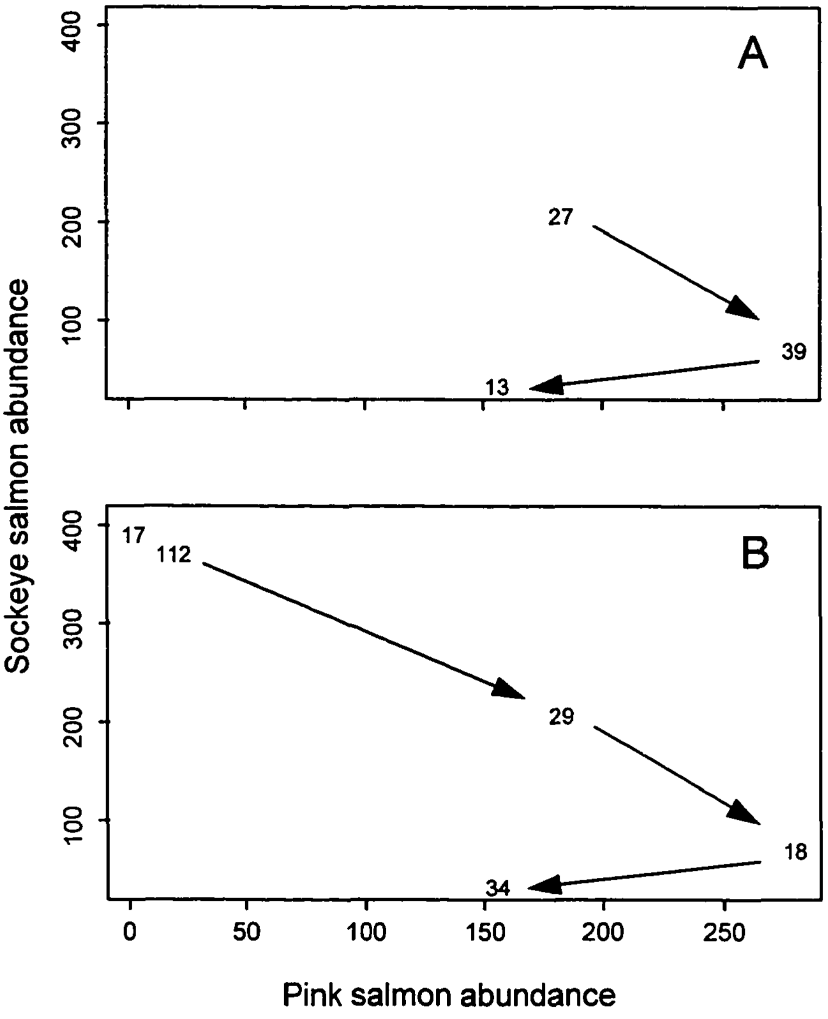

Figure 6.10. Niche breadths of pink (A) and sockeye (B) salmon plotted against abundance of each species in the study area in 1994. Numbers indicate 100 x determinant of variance-covariance matrices of multivariate data. Arrows indicate the order of measurement dates, i.e., August 31, September 4 and 8 for pink salmon and August 24, 26, 31, September 4 and 8 for sockeye salmon.

Discussion

Difference in habitat selection between the species

Pink salmon mainly concentrated in the lower sections of Lake Creek, whereas sockeye salmon ascended much farther upstream for egg deposition such as in 1993. It should be noted that despite a difference in absolute numbers of spawners entering Lake Creek each year the proportions of total spawners in each section of the creek were remarkably consistent during the three years of the study. In the whole system of Auke and Lake Creeks, however, probably more pink salmon, especially later spawners (Chapter 4), spawn in Auke Creek rather than in Lake Creek, but the historical ratios of spawners in these two creeks are not exactly known. Sockeye salmon, on the other hand, do not usually spawn in Auke Creek but spawn either in Auke Lake or Lake Creek. Bucaria (1968, cited in Taylor et al. 1992) observed that 52-55% of the adult sockeye salmon entering the Auke Lake system spawned in tributaries of the lake. I estimated that approximately 36 % of sockeye salmon spawned in Lake Creek in 1993 by tagging 741 spawners at the Auke Creek weir and recovering fish after spawning in Lake Creek (unpublished data).

In sympatric populations of salmonids, it is commonly observed that they segregate spawning areas by spawning lower and upper portions of a stream; for example masu salmon and Asian char (Maruyama 1981), brook trout and brown trout (Witzel and MacCrimmon 1983), and Atlantic salmon and brown trout (Baglinière et al. 1994). Hoopes (1972) observed that the spawner distributions of sockeye salmon in the tributaries of Brooks Lake, Alaska, were quite similar during three years of stream survey. A similar finding was made for Sakhalin taimen (*Hucho perryi*) spawners in northern Hokkaido (Fukushima 1994).

Pink salmon preferred to spawn at the areas with shallower water depth, faster current velocity and the larger gravel than sockeye did in those sections where both species coexisted in large numbers. The selection of water depth by sockeye salmon was twice more variable than that by pink salmon. This observation agrees with Burgner's (1991) finding that water depth does not seem to be a critical factor to female sockeye salmon in selecting a spawning site. Although the difference in microhabitat selection between the species was statistically significant ($p < .0001$), it is probably not feasible to classify or separate their microhabitat preference with only the habitat variables used in the present study.

Seasonal variation of microhabitat selection

Actual measurements of water depth at sockeye salmon redds were nearly constant through the spawning season despite a considerable fluctuation of available stream depth. As a result, sockeye salmon must have selected relatively deep areas or pools when the water level was low, especially later in the season. Such a shift toward pools can be inferred also from the reduced measurements of channel gradient during the same period. This may simply be a physical consequence of the inability of sockeye salmon to spawn, during low flow, at places where they would otherwise spawn when there was sufficient water flow. The spawning habitat of sockeye salmon is often associated with upwelling water (Olsen 1968; Lorenz and Eiler 1989) that provides relatively constant incubation temperature during winter. Because pool areas with negative channel gradient are more likely to provide such upwelling water (Stuart 1953; Vaux 1962), eggs deposited by later spawners should have benefited from incubating in constant and probably warmer temperatures than eggs deposited in riffle areas by earlier spawners at least during the 1994 season. Unlike sockeye salmon, the seasonal variation of microhabitat selection in pink salmon was small.

Intra- and interspecific interaction during spawning

Interactions between and within species were implied from the analyses of their microhabitats. The variation of niche breadth represented by the determinants of variance-covariance matrices suggests that pink salmon spawners were forced to exploit less preferred habitat for egg deposition when their abundance was around 300 fish in the 150-m study area, which resulted in the widest niche breadth on September 4 among the three dates. The effect of sockeye salmon spawners on pink salmon is unknown because of the small number of observed niche breadths for pink salmon and a relatively small range of abundance variation in sockeye salmon.

Habitat selection by sockeye salmon appeared to be quite specialized on the first date of measurement (August 24) with the niche breadth being the narrowest among the five dates, despite an extremely high spawner abundance (400 fish). This was because the spawners observed on August 24 probably originated from the same cohort, inherently having relatively equal habitat preferences, and because the study area (sections 7-9) can accommodate much more sockeye salmon spawners than pink salmon spawners (Figure 6.3) so that the 400 sockeye spawners were probably below its carrying capacity at which the niche breadth starts to increase. Two days later (August 26), however, there was a dramatic increase in the niche breadth to a six times larger value. This may be due to a combination of a remarkable change in the habitat availability between the two dates (Table 6.2) and the fact that the redds were sampled both from the old cohorts who had been digging the same spots since before the availability changed and from new cohorts who would have selected the best available habitat under a new environmental regime.

The niche breadth of sockeye salmon subsequently decreased with the decreasing abundance of spawners, but it might have decreased beyond its optimum size of niche breadth or "virtual niche breadth" (sensu Colwell and Futuyma 1971) on September 4 because of competitive interaction with increased pink salmon spawners. This may explain why the niche breadth increased again on September 8, although the sample size (17) is somewhat small for a multivariate analysis to obtain a reliable statistic such as niche breadth.

Microhabitat preferences between pink and sockeye salmon were largely overlapping. Even though the difference measured in four dimensional space was statistically significant, discrimination of their habitat was almost impossible. It is not known whether the number of habitat variables in this study was large enough to characterize the microhabitat selection of pink and sockeye salmon. Inclusion of other variables such as intragravel water temperature and depth of egg deposition might have better separated the habitat selection by the species.

CHAPTER 7. CONCLUSION

Historical fry and smolt productions of pink and sockeye salmon were well expressed by the Ricker spawner-recruit model in the Auke Lake system over 14 years. Average fry and smolt production per spawner was twelve fry for pink salmon and nine smolts for sockeye salmon. Time series of recruit-per-spawner were positively correlated between pink and sockeye salmon ($r = .650, p < .05$), suggesting the existence of common environmental variables influencing the production of these species. Residuals of the Ricker model for pink salmon were negatively correlated with sockeye spawning stock ($p < .05$), but it is unlikely that early spawning sockeye salmon can adversely affect the fry production of late spawning pink salmon in the Auke Lake system. Since the Ricker residuals of sockeye salmon were not correlated with pink salmon spawning stock, species interaction between the species, if it exists, is probably not influential enough to adversely affect fry or smolt production of the Pacific salmon. The Ricker residuals of sockeye salmon were positively correlated with precipitation during September and May in the following spring; i.e., the stages of early incubation and the first feeding ($p < .05$). Because sockeye salmon migrate into Auke Lake and Lake Creek when the spawning grounds are relatively dry, higher-than-average precipitation is probably essential for the survival of early developing embryos. For pink salmon embryos that normally start development when the spawning grounds receive higher precipitation, the importance of precipitation lessens.

Estimated spawner capacity of pink salmon that maximizes fry production from the Auke Lake system was 21,446 adults (95 % C.I. = 14,031-42,131) and was approximately 15 times greater than the spawner capacity of sockeye salmon (1,724 fish; 95 % C.I. = 1,237-2,858). The compensatory mortality observed in sockeye salmon smolt production may be coincidence; the strong compensation in two broods (1979 and 1980) of the species could be largely due to different environmental conditions in the late 1970's. Increasing trends for the Ricker residuals of pink and sockeye salmon since the late 1970's ($r = .728, p < .01$ for pink salmon, and $r = .628, p < .05$ for sockeye salmon) suggest that the Pacific salmon during the late 1970's and the early 80's presented a relatively unfavorable environment for either spawning or egg incubation in the Auke Lake system. Responsible variables for this trend or nonstationarity (sensu Hilborn and Walters 1992) could not be detected among available variables of climatology and hydrology data. Sockeye smolt production in the Auke Lake system is strongly influenced by environment including both detected variables such as precipitation and undetected variables, and sockeye probably had a different spawner-recruit relationship during the early 1980's. It should be noted that sockeye escapements were consistently greater (around 8,000) before the 1980's.

Female spawners of pink salmon varied in stream life (5-11 days), spawning efficiency (30-70 % of females in daily entry cohorts retained less than 500 eggs at death), and habitat selection (30-70 % spawned in the lake outlet stream rather than the lake inlet stream). The variation of stream life, spawning efficiency, and habitat selection was best explained by stream discharge, stream temperature, and a combination of immigration date and discharge, respectively. Observed spawning efficiency of pink salmon was considerably low, but the pattern of this efficiency was not related to spawner density. Extremely high stream temperature of Auke Creek during early spawning season apparently prohibited normal egg deposition. Egg retention of sockeye salmon in Auke Creek was also abnormally high during 1993.

If the observed habitat shift (proportionately more use of the cooler inlet stream early in the spawning season when stream temperatures in the outlet stream are warm) had been common to other cohorts of pink salmon populations in the Auke Lake system, this shift would contribute to synchronicity of fry emigration and would explain the relatively similar time spans between upstream and downstream migrations of pink salmon observed for different cohorts. Synchronicity of fry emergence and emigration from the system may also occur among sockeye salmon. Adult upstream migration of sockeye salmon in 1993 lasted almost a month and half, but their actual spawning duration was much shorter because the early spawning cohorts waited in Auke Lake for about 20-25 days before they ascended the spawning stream Lake Creek. Furthermore, observed variation of microhabitat selection in which sockeye spawners shifted from riffles to pools as the spawning season progressed suggests that the eggs spawned later in the season probably incubated under a warmer temperature regime than the eggs spawned earlier, because pools are more likely to provide upwelling ground water that is relatively constant in temperature and warmer than surface water during winter. Synchronicity of fry emergence and outmigration to the first feeding areas (i.e., Auke Bay for pink salmon and Auke Lake for sockeye salmon) are known to be positively correlated with their survival (Brannon 1987; Randall et al. 1987; Taylor et al. *in press*).

Estimates of daily egg loss from pink salmon spawning ground in Auke Creek were roughly proportional to the number of spawners on the spawning ground. The maximum daily egg loss was estimated to be 300,353 ± 23,741 (±1 SE) eggs by Model 1 (i.e., variable catchability model) and 398,422 ± 26,025 (±1 SE) eggs by Model 3 (i.e., constant catchability model). These estimates of egg loss are equivalent to a mortality of 210-280 female pink salmon per day. Two freshets after the spawning season did not trigger any egg loss, so that egg mortality due to scouring of the streambed was negligible. This agrees with the analysis of historical spawner-recruit data in which residuals of the Ricker model for pink salmon were not correlated with stream discharge during spawning season (negative correlation with November discharge is spurious, see Chapter 3). Eggs caught by sampling nets were more advanced in development as the season progressed, and most of the eggs from later samples were alive when sampled. These observations demonstrate that the eggs were actually washed out from the streambed due to redd superimposition by later spawners of pink salmon and that the redd superimposition caused higher mortality for the eggs spawned by the early run spawners than for the eggs by the later run spawners.

I believe that the observed density-dependent fry production curve is largely due to the mortality from redd superimposition because high egg retention, another important source of mortality, was not density-dependent and because, if the density-dependence was caused by physiological mechanisms such as a lack of intragravel oxygen for developing embryos, the fry production curve could have exhibited more dome-shaped appearance rather than asymptote. However, it should be recalled that pink salmon in the Auke Lake system underwent an environmental shift after the 1970's. Data points that caused the production curve to exhibit density-dependence are mostly from the late 1970's and early 1980's during which the environment was relatively unfavorable for Pacific salmon in the Auke Lake system.

Spatiotemporal distributions of spawning adults were consistently different between pink and sockeye salmon in Lake Creek regardless of relative and absolute difference in spawner abundance each year. The peak sockeye spawning preceded the peak pink spawning by approximately one week, and the stream sections most preferred by sockeye salmon were always located about 250-350 m above the most preferred sections by pink salmon. Microhabitat selection in terms of four habitat variables (water depth, current velocity, channel gradient and gravel size) were significantly different between these species ($p < .0005$), but the difference was not large enough to allow discrimination or classification of their microhabitat selection due to a large overlap in the four dimensional niche space. Sample variation of the multivariate microhabitat data was explained primarily by water depth and current velocity for pink salmon, while that variation was more importantly explained by channel gradient for sockeye salmon. The large variation of channel gradient for sockeye salmon probably reflects their habitat shift from riffles to pools. Throughout the spawning season, spawning habitat selection of sockeye salmon was variable among different spawning timings, but that of pink salmon was relatively consistent. This may indicate that sockeye salmon have a broader tolerance range of habitat variables than do pink salmon.

Effects of interspecific interaction (e.g., competition) between pink and sockeye salmon on their fry and smolt production is probably negligible compared to density-dependent and environmental effects, although some pink salmon spawners, due to their later spawning each year in Lake Creek, may superimpose their redds on sockeye salmon redds. The large overlaps observed between microhabitats of pink and sockeye salmon in this study do not necessarily indicate competition between the species. Competition can be demonstrated only when a species reduces its niche breadth because of the existence of other species. Should resources not be in short supply, two species can share them without detriment to each other (Pianka 1994). The field study conducted in Lake Creek lacks enough data to detect the existence of competitive interaction between pink and sockeye salmon.

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APPENDICES

Appendix I. Reconstruction of stream discharges in Auke Creek

Auke Creek discharges during the study period (1979-94) were reconstructed using a multiple linear regression model based on the discharge and precipitation data during 1962-1975. Only the discharges between July 1 and October 31 were reconstructed because spring discharges are influenced not only by precipitation but also by snowmelt that may be a complex function of snowfall, rainfall, air temperature, wind, etc.

The daily Auke Creek discharge D was found a function of daily precipitation of preceding eight days, X_1 through X_8, including the day the discharge was measured such that

$$W = 2.08 + 0.46X_1 + 1.14X_2 + 0.92X_3 + 0.68X_4 + 0.52X_5 + 0.44X_6 + 0.35X_7 + 0.31X_8$$

where $W = \frac{D^{0.3} - 1}{0.3}$. The power of .3 (= λ) was chosen such that a likelihood function below is maximized (Box and Cox 1964)

$$\boldsymbol{L} = -\frac{n}{2}\ln\frac{RSS}{n} + (\lambda - 1)\sum_{i=1}^{n}\ln D_i$$

where RSS is the residual sum of squares. The nine coefficients in the linear model above were all significant ($p < .00001$). Note that the largest coefficient (excluding the y-intercept) was for precipitation of a previous day X_2, and that subsequent coefficients decreased as a time lag became larger. Precipitation on the first day X_1 apparently does not have full effect on discharge until the next day.

Appendix II. Calculation of daily spawner abundance in Auke Creek

Let

N_i = pink salmon escapement on day i,

M_i = the number of pink salmon tagged on day i,

m_{ij} = the number of tags originated from M_i and recovered on day j, and

$m_{i\cdot}$ = $\sum_{j=i}^{\infty} m_{ij}$, the total number of tag recoveries from M_i.

The estimated number of pink salmon that entered on day i and spawned in Auke Creek (as opposed to Lake Creek) becomes

$$\hat{N}_{Ai} = \frac{m_{i.}}{M_i} N_i .$$

The estimate of survival rate of Auke Creek spawners from day i to day t is

$$\hat{\phi}_{it} = \frac{m_{i.} - \sum_{j=i}^{t} m_{ij}}{m_{i.}} .$$

Thus the estimated number of Auke Creek spawners that entered on day i and were still alive on day t is

$$\hat{S}_{it} = \hat{N}_{Ai} \cdot \hat{\phi}_{it} = \frac{m_{i.}}{M_i} N_i \cdot \frac{m_{i.} - \sum_{j=i}^{t} m_{ij}}{m_{i.}}$$

$$= \frac{N_i}{M_i}\left(m_{i.} - \sum_{j=i}^{t} m_{ij} \right) .$$

Therefore, the estimate of Auke Creek spawner abundance on day *t* is obtained as

$$\hat{S}_t = \sum_{i=1}^{t} \hat{S}_{it} = \sum_{i=1}^{t} \frac{N_i}{M_i} \left(m_{i.} - \sum_{j=i}^{t} m_{ij} \right).$$

Appendix III. Estimated remaining rates and capture probabilities of pink salmon eggs during egg loss estimation

Table A.1. Estimated remaining rates of marked eggs for Models 1, 2 and 3.

	Model 1			Model 2			Model 3		
	$l_{i,1,k}$	$l_{i,2,k}$	$l_{i,3,k}$	$l_{i,1,k}$	$l_{i,2,k}$	$l_{i,3,k}$	$l_{i,1,k}$	$l_{i,2,k}$	$l_{i,3,k}$
Exp. 1	7.71E-02	1.73E-01	4.46E-05	8.61E-02	1.18E-01	1.87E-01	7.44E-02	1.66E-01	4.46E-05
	-	1.06E-01	2.73E-01	-	1.18E-01	1.87E-01	-	1.02E-01	2.62E-01
	-	-	1.67E-01	-	-	1.87E-01	-	-	1.61E-01
Exp. 2	3.75E-01	5.43E-01	8.13E-05	4.18E-01	3.71E-01	3.40E-01	3.61E-01	5.21E-01	8.13E-05
	-	3.32E-01	4.97E-01	-	3.71E-01	3.40E-01	-	3.21E-01	4.77E-01
	-	-	3.04E-01	-	-	3.40E-01	-	-	2.94E-01
Exp. 3	2.56E-01	4.83E-01	9.14E-05	2.86E-01	3.30E-01	3.82E-01	2.47E-01	4.64E-01	9.14E-05
	-	2.96E-01	5.59E-01	-	3.30E-01	3.82E-01	-	2.85E-01	5.37E-01
	-	-	3.42E-01	-	-	3.82E-01	-	-	3.30E-01
Exp. 4	2.56E-01	8.87E-02	1.53E-05	2.86E-01	6.06E-02	6.38E-02	2.47E-01	8.51E-02	1.53E-05
	-	5.43E-02	9.34E-02	-	6.06E-02	6.38E-02	-	5.24E-02	8.96E-02
	-	-	5.72E-02	-	-	6.38E-02	-	-	5.52E-02
Exp. 5	6.25E-02	1.28E-01	2.28E-05	6.98E-02	8.79E-02	9.54E-02	6.03E-02	1.23E-01	2.28E-05
	-	7.87E-02	1.39E-01	-	8.79E-02	9.54E-02	-	7.59E-02	1.34E-01
	-	-	8.54E-02	-	-	9.54E-02	-	-	8.24E-02
Exp. 6	6.60E-02	1.42E-01	7.42E-06	7.38E-02	9.74E-02	3.11E-02	6.37E-02	1.37E-01	7.42E-06
	-	8.72E-02	4.54E-02	-	9.74E-02	3.11E-02	-	8.41E-02	4.36E-02
	-	-	2.78E-02	-	-	3.11E-02	-	-	2.68E-02

Table A.1. (Continued)

	Model 1			Model 2			Model 3		
	$l_{i,1,k}$	$l_{i,2,k}$	$l_{i,3,k}$	$l_{i,1,k}$	$l_{i,2,k}$	$l_{i,3,k}$	$l_{i,1,k}$	$l_{i,2,k}$	$l_{i,3,k}$
Exp. 7	4.29E-02	6.91E-02	1.22E-05	4.79E-02	4.72E-02	5.08E-02	4.14E-02	6.63E-02	1.22E-05
	-	4.23E-02	7.44E-02	-	4.72E-02	5.08E-02	-	4.08E-02	7.14E-02
	-	-	4.55E-02	-	-	5.08E-02	-	-	4.39E-02
Exp. 8	5.92E-02	1.45E-01	2.83E-05	6.61E-02	9.94E-02	1.18E-01	5.71E-02	1.40E-01	2.83E-05
	-	8.90E-02	1.73E-01	-	9.94E-02	1.18E-01	-	8.59E-02	1.66E-01
	-	-	1.06E-01	-	-	1.18E-01	-	-	1.02E-01
Exp. 9	2.23E-01	4.43E-01	1.55E-05	2.49E-01	3.03E-01	6.50E-02	2.15E-01	4.26E-01	1.55E-05
	-	2.71E-01	9.50E-02	-	3.03E-01	6.50E-02	-	2.62E-01	9.12E-02
	-	-	5.82E-02	-	-	6.50E-02	-	-	5.61E-02
Exp. 10	2.50E-02	5.74E-02	1.08E-05	2.79E-02	3.93E-02	4.53E-02	2.41E-02	5.51E-02	1.08E-05
	-	3.52E-02	6.62E-02	-	3.93E-02	4.53E-02	-	3.39E-02	6.36E-02
	-	-	4.05E-02	-	-	4.53E-02	-	-	3.91E-02
Exp. 11	9.09E-02	2.03E-01	4.35E-05	1.02E-01	1.39E-01	1.82E-01	8.78E-02	1.95E-01	4.35E-05
	-	1.24E-01	2.66E-01	-	1.39E-01	1.82E-01	-	1.20E-01	2.55E-01
	-	-	1.63E-01	-	-	1.82E-01	-	-	1.57E-01

Table A.2. Estimated probabilities of capture for Models 1, 2 and 3.

	Model 1			Model 2			Model 3		
	$P_{1,k}$	$P_{2,k}$	$P_{3,k}$	$P_{1,k}$	$P_{2,k}$	$P_{3,k}$	$P_{1,k}$	$P_{2,k}$	$P_{3,k}$
Exp. 1	2.22E-02	2.72E-02	2.17E-02	2.23E-02	2.73E-02	2.19E-02	2.20E-02	2.70E-02	2.16E-02
Exp. 2	8.14E-03	1.51E-02	1.66E-02	8.26E-03	1.53E-02	1.68E-02	6.07E-03	1.12E-02	1.24E-02
Exp. 3	1.25E-02	7.46E-03	2.75E-02	1.29E-02	7.66E-03	2.82E-02	9.45E-03	5.62E-03	2.07E-02
Exp. 4	2.82E-02	2.35E-02	1.63E-02	2.83E-02	2.36E-02	1.63E-02	2.81E-02	2.34E-02	1.62E-02
Exp. 5	3.21E-02	1.86E-02	2.44E-02	3.22E-02	1.87E-02	2.45E-02	3.22E-02	1.87E-02	2.45E-02
Exp. 6	2.60E-02	8.08E-03	1.42E-02	2.60E-02	8.10E-03	1.42E-02	2.68E-02	8.32E-03	1.46E-02
Exp. 7	2.36E-02	4.04E-02	4.16E-02	2.37E-02	4.04E-02	4.17E-02	2.54E-02	4.34E-02	4.48E-02
Exp. 8	4.47E-02	2.36E-02	1.33E-02	4.49E-02	2.38E-02	1.34E-02	4.68E-02	2.47E-02	1.39E-02
Exp. 9	1.31E-02	1.33E-02	1.47E-02	1.31E-02	1.34E-02	1.47E-02	1.12E-02	1.15E-02	1.26E-02
Exp. 10	2.07E-02	3.46E-02	5.06E-02	2.07E-02	3.46E-02	5.06E-02	2.27E-02	3.80E-02	5.56E-02
Exp. 11	4.56E-02	2.73E-02	2.30E-02	4.59E-02	2.75E-02	2.32E-02	4.59E-02	2.74E-02	2.32E-02