

AN EXPERIMENTAL EXAMINATION OF BEHAVIOURAL ISOLATION BETWEEN
SOCKEYE SALMON AND KOKANEE,
THE ANADROMOUS AND NON-ANADROMOUS FORMS OF ONCORHYNCHUS NERKA

by

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ABSTRACT

The genetic relationship of anadromous (sockeye salmon) and non-anadromous (kokanee) Oncorhynchus nerka was examined in conjunction with the breeding behaviour of the two forms to determine: (1) if there is evidence of genetic divergence between the forms where they spawn sympatrically; (2) if such divergence is associated with significant premating isolation between the forms and; (3) if premating isolation results directly from the size difference between the forms (sockeye are much larger than kokanee at maturity).

Both sexes exhibit spawning territoriality; females establish and defend particular nest sites until death or displacement, males defend access to specific females from other males until the female has spawned out, they are displaced, or leave to compete for additional mates. Size and prior access to resources (mates and/or specific areas) are significant factors in intrasexual aggression in both sexes, with size the major factor in males and prior access the major factor in females.

Females accompanied by males larger than themselves lose weight at a faster rate than those accompanied by males smaller than themselves. Weight loss is related to egg loss, indicating females spawn at a faster rate when accompanied by large males.

Male mate preference depends on the size of the male. Males of various sizes prefer females of their own size or larger over females smaller than themselves. In contrast, all sizes of males tested demonstrated no preference between females of their own size and those larger. Large males, which have the widest range of potential mates (because of male intrasexual competition and female choice), are the most selective and small males, which have the narrowest range of potential mates, are the least selective.

There were significant differences in allele frequencies between sympatrically spawning sockeye and kokanee. However, there were no consistent differences between sockeye and kokanee at any of five polymorphic loci examined. The extent of genetic differentiation between sympatric forms appears to be less than that between neighbouring populations of the same form, judging from an examination of allele frequencies and/or allele compositions.

There was extensive assortative mating by form between sockeye and kokanee, which was not totally accounted for by the large size difference. In the two systems examined, males preferred to mate with females of their own form. In sockeye, such preferences are expected because of the size difference between forms. In kokanee, such preferences are not expected based on size alone, suggesting the evolution of premating

isolating mechanisms. The degree of premating isolation was positively correlated with the extent of genetic divergence between sympatric forms.

The results of this study are related to existing models of sympatric speciation to hypothesize that sockeye and kokanee have diverged in sympatry. The probable differences in selection between the marine and freshwater environments coupled with the assortative mating resulting from their size difference may have caused subsequent genetic divergence. This divergence appears to have been followed by the evolution of premating isolation.

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INTRODUCTION

Natural selection can be divided into two components, related to the ability to survive and the ability to reproduce. Sexual selection was described by Darwin (1871) as the evolutionary process arising from variability in the ability to reproduce. Animals possessing characters which by these means lead to the production of more offspring that contribute to the next generation are selected over others. The characters selected are those that confer an advantage in intrasexual competition and those that lead to the selection of high quality mates.

The factors involved in sexual selection within species and those involved in selection for reproductive isolation between species can be closely related. In both cases selection favours individuals which make the "correct" mate choice. Within species this means the highest quality mates; between species "correct" means selecting the right species. The reproductive success of individuals making the wrong choice in both situations may be similar, that is, close to zero.

The question arises: does a continuum exist between the two selective forces? That is, is it possible for the effects of sexual selection to result in selection for reproductive isolation? If so, the study of sexual selection may constitute an examination of the process of speciation.

Maynard Smith (1966) described situations in which the potential for this phenomenon exists. Stable polymorphisms (maintained by disruptive selection) between alleles that adapt individuals to different ecological niches are theoretically possible in heterogeneous environments. If a stable polymorphism arises this is likely to be followed by the evolution of reproductive isolation between the morphs. Both of these predictions have been verified in studies on Drosophila. Thoday and his colleagues demonstrated that disruptive selection can create and maintain polymorphisms in a population even in the face of massive gene flow (Thoday 1959; Thoday and Boam 1959; Millicent and Thoday 1961). In addition, disruptive selection was responsible for the evolution of complete reproductive isolation in one study (Thoday and Gibson 1962) and partial isolation in numerous others (e. g. Dobzhansky et al. 1976; Crossley 1974; Rice 1985; Koepfer 1987).

The requirements necessary for the evolution of a polymorphism via disruptive selection are severe. Maynard Smith (1966) presented two mandatory conditions: 1) the density dependent factors regulating population size must operate separately within the two niches and; 2) the selective advantages associated with being adapted to a particular niche must be large. The advantages necessary are greatly reduced if there is a an initial high degree of assortative mating by form.

Salmonids display characters necessary for the evolution of reproductive isolation in sympatry. There are strong selective forces acting on populations (e. g. Raleigh 1967; Brannon 1972; Bams 1976; Riddell and Legget 1981; Riddell et al. 1981). Homing to parental spawning grounds results in reduced gene flow among populations (e. g. Lindsey et al. 1959; Hartman and Raleigh 1964; McCleave 1967; Altukhov 1982). Behavioural and/or morphological polymorphisms exist in numerous stocks (e. g. Ricker 1938, 1940, 1972; Northcote 1962; Raleigh 1967; Hanson and Smith 1967; McCart 1970; Kelso et al. 1981). Finally, independent population regulation appears probable in many of the above examples.

The Pacific salmon Oncorhynchus nerka occurs in two forms, the anadromous sockeye salmon and the non-anadromous kokanee. Sockeye spend a year (and sometimes more) in lakes before migrating to the ocean, typically spending two to four years in the ocean before returning to population specific spawning grounds usually either in or tributary to lakes. Kokanee spend their whole life (typically 3 to 5 years) in lakes. At maturity, sockeye salmon are much larger than kokanee (two to three times as long), mainly because of the greater productivity of the marine environment. These forms occur together and separately. Where they occur together, spawning usually occurs in different localities at different times. In a few localities, sockeye and kokanee spawn in the same place at the same time.

Both anadromous and non-anadromous individuals can give rise to the opposite form (Foerster 1947; Ricker 1959, 1972; Scott 1984), presenting the possibility that one form may have given rise to the other in sympatry on numerous occasions. Where they spawn sympatrically there is a large degree of assortative mating by size and form; sockeye males mate almost exclusively with sockeye females and kokanee males attempt to mate with females of both forms (Hanson and Smith 1967; McCart 1970). Because of their small size, kokanee males are usually restricted to subordinate sneak positions in the male spawning hierarchy when in pursuit of sockeye females. This assortative mating by form, in association with the probable large selective differences between the marine and lacustrine environments (see Ricker 1940), creates the possibility for sympatric genetic divergence followed by the evolution of premating isolating mechanisms in the manner described in numerous theoretical models (e. g. Maynard Smith 1966; Rosenzweig 1978; Pimm 1979; Rice 1984).

The reproductive and genetic relationship of sockeye salmon and kokanee is examined in this thesis. Three major questions are addressed. First, what factors are involved in sexual selection within forms? To answer this, I experimentally examine the nature of the O. nerka mating system, paying special attention to the effects of size with forms. In chapter 1, the nature of spawning territoriality in kokanee is examined. In

chapters 2 and 3, female and male mate choice, respectively, are examined. Second, what is the genetic relationship between sockeye and kokanee in British Columbia? More specifically, is there evidence of sympatric genetic divergence between forms? To answer this, I electrophoretically compare sockeye and kokanee populations in British Columbia, from localities where they spawn either separately or sympatrically (Chapter 4). Finally, is there any evidence of the evolution of premating isolating mechanisms between sympatric sockeye salmon and kokanee? To answer this, the reproductive relationship of sockeye salmon and kokanee which spawn sympatrically in two systems are compared to: (1) that expected (Chapters 1 through 3) based on the size difference between the forms; (2) each other and; (3) to the degree of biochemical genetic divergence observed between sympatric forms in the two systems.

CHAPTER 1

EXPERIMENTAL EXAMINATION OF SPAWNING TERRITORIALITY IN SALMON

Introduction

The spawning behaviour of salmonids has been extensively studied (e. g. Needham and Taft 1934; Jones and King 1952; Fabricus and Gustafson 1954; Jones 1959; Hanson and Smith 1967; Hartman 1969; McCart 1970; Tautz and Groot 1975; Campbell 1977; Newcombe and Hartman 1980; Schroder 1981, 1982; van den Berghe 1984; Gross 1985; Sargent et al. 1986; Maekawa and Onozato 1986). Many of these studies have dealt with the description of pair formation and spawning behaviour, while others, notably Hanson and Smith (1967), Schroder (1981, 1982), van den Berghe (1984) and Maekawa and Onozato (1986) have attempted to document, and examine the factors contributing to variance in reproductive success of each of the sexes. For the most part, these later studies have concentrated on male behaviour, although there is growing interest in the factors contributing to variation in female reproductive success (Schroder 1981; van den Berghe 1984; van den Berghe and Gross 1984).

The salmonid mating system has been characterized as one in which females compete for territories (spawning sites) and males compete for direct access to females (Schroder 1981; Gross 1985; Sargent et al. 1986). This characterization is derived from numerous observations that only females participate in the

construction and defense of the nest site, while males move from female to female throughout their spawning lifetime. Some studies have pointed to the existence of male spawning territoriality, centered around females and/or high quality nest sites (Hanson and Smith 1967; Hartman 1969; McCart 1970; Jonsson and Hindar 1982).

Aggressive behaviour has been observed in both sexes, with the majority of aggressive acts directed intrasexually (Hanson and Smith 1967; McCart 1970; Schroder 1981, 1982). In males, outcome of intrasexual competition appears to be decided largely by the relative sizes of competing individuals; large males dominate small males in competition for access to females (e. g. Hanson and Smith 1967; McCart 1970; Campbell 1977; Schroder 1981). In females, the effects of size in intrasexual competition are largely unknown. Jonsson and Hindar (1982) suggested that size is an important factor in determining the spawning distribution of different sized morphs of Arctic charr, Salvelinus alpinus. Similarly, van den Berghe (1984) concluded that size was a factor in female intrasexual competition in coho salmon, O. kisutch. Little supporting evidence was presented in either study. In an experimental study on female intrasexual competition, Schroder (1981) found no evidence to suggest size was a factor in determining the outcome of female aggressive interactions, concluding that prior residence was the major factor. Prior residence has not been considered in male intrasexual competition.

In this chapter, I present experimental results pertaining to the existence and nature of spawning territoriality in male and female kokanee and the factors which influence the outcome of intrasexual competition in both sexes. I then compare and contrast the spawning behaviour of the sexes and relate these findings to the evolution of the salmonid mating system.

Brown's (1975) definition of territoriality is used: a territory is a fixed area from which intruders are excluded by some combination of advertisement, threat, or attack.

1. An experimental examination of the mating system in kokanee

Methods

In this first of three major sets of experiments, I examine the nature of spawning territoriality in kokanee. I first present a summary of the methods common to most of the experiments and then present the specific methods pertaining to the examination of the mating system in kokanee.

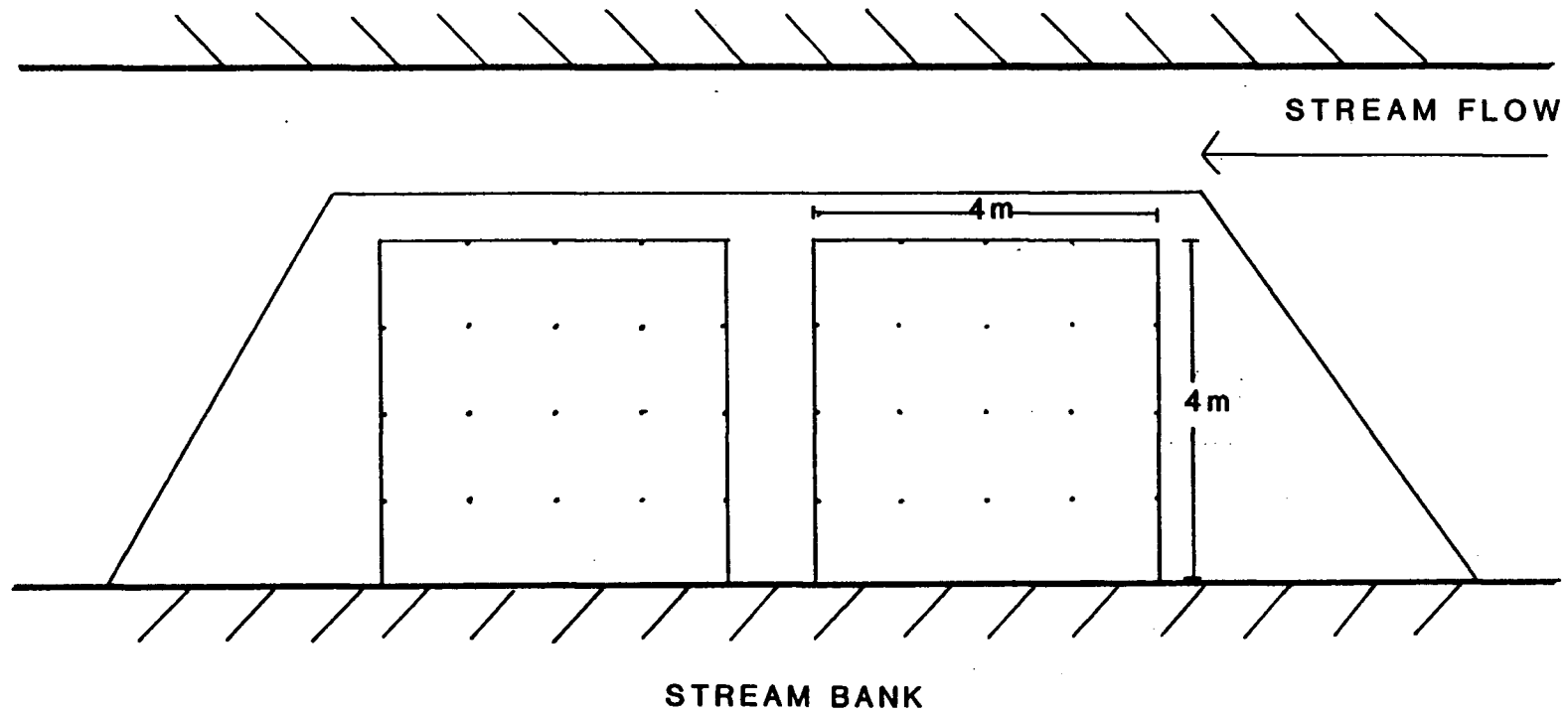
All experiments were undertaken in the Meadow Creek spawning channel, situated at the north end of Kootenay Lake, B. C. , during September 1982-1984 (see Vernon (1957) for a description of Kootenay Lake kokanee. Meadow Creek sustains the largest kokanee spawning run in Kootenay Lake and possibly the

world, with spawning populations often exceeding one million). Most experiments were carried out in enclosed arenas (Fig. 1), five by five, four by five, or four by four meters (depending on the experiment), constructed of 0.9 cm chicken wire fencing. Two arenas, separated from each other by 1 m, were enclosed within a larger fenced area to limit interaction of fish in an arena from those in the adjacent arena and those spawning naturally in the stream. Large white rocks were placed on the floor of each arena at one meter intervals. These were used to record the individual positions of fish over time.

All kokanee used in experiments were individually tagged. In the examination of territoriality tags were individually colour coded 0.5 by 2 cm plastic strips, sewn into the anterior base of the dorsal fin with surgical thread. For studies on intrasexual competition, colour coded 2 cm Floy dart tags were used, attached either to the anterior or posterior base of the dorsal fin.

The study of the kokanee mating system consisted of three experiments that examined which resources are necessary to evoke male and female intrasexual competition, and, possibly, territoriality. In the first, I monitored the chronology of arrival and settling of males and females into three 4 by 4 m marked areas. Second, the behaviour of males and females was compared in the experimental arenas, when the sexes were held separately and together. The third experiment compared the time

Figure 1. The design of experimental arenas used in the examination of spawning territoriality in kokanee. The exact dimensions of the arena varied slightly between experiments.



it took fish to establish spawning sites in the spawning channel where numerous fish were already present to the time it took fish to establish spawning sites in the arenas, where no additional fish were present.

A. Chronology of settlement on the spawning grounds

At 1700 hours on each day for a four week period, I recorded the number and sex of each fish holding position in each of three 4 by 4 m designated areas. Fish swimming through the marked areas were not recorded.

B. An experimental examination of territoriality in males and females

Twenty-five ripe (and in the case of females, unspawned) females and males were selected from schools of kokanee (in which fish are not aggressive or territorial), individually tagged and placed in an arena with (paired) or without an equal number of the opposite sex (unpaired). The behaviour of each fish was monitored over a three to five day period (depending on the weather; five days for the unpaired treatment performed in inclement weather and three days for the paired treatment). The position of each fish was recorded at approximately two hour intervals, six to seven times during daylight of each day (weather permitting). The individual behaviour of each fish was recorded during 15 two minute observation periods which were

spaced relatively evenly over the course of the three to five day treatment. All fish were observed within one hour of each other during each of the 15 observation periods, with the individual order of observation randomized between periods. Two observers were used. Within each observation period, each observer was restricted to recording the behaviour of one sex, with the sex observed switched between periods to control for possible differences between observers. The behaviours recorded were: chases, bites, lateral displays, T-displays, and digging. These behaviours were defined as follows:

- 1) Chases - any rapid direct approach towards another fish, often ending in contact of the two fishes.
- 2) Bites - open mouth attacks, always involving contact and usually preceded by a chase.
- 3) Lateral Displays - parallel body presentations in which the abdominal fins are lowered and the dorsal fin raised, with the body slightly inclined (head up, tail down). The display is usually performed in tandem by two individuals while swimming upstream and parallel to one another (separated by 5 cm to 1 m).
- 4) T-Displays - perpendicular body presentations in which the displaying fish holds its' body at an angle to the current (45-90) and the fish directly downstream from it. The displaying fish then drifts with the current, usually displacing the downstream fish. This is similar to "back-pedaling" described by Jones (1959) and Hanson and Smith (1967), and has been described by Hartman (1969) and named by Schroder (1981).
- 5) Digging - in females, consisting of a series of strong body

flexures while turned on one side. This digging creates a nest depression in the gravel in which eggs are eventually deposited (Tautz and Groot 1975). Some territorial females were observed to dig in the nests of other females while those females were involved in other aggressive interactions. The function of this digging is unclear.

Digging - in males, occurring in two forms. The aggressive dig consists of a dominant male (one courting a female) lowering its body to the substrate, rolling on its side, and making a series of body flexures which carry it upstream and push gravel downstream. This behaviour is only done when sneak males approach from the rear. The approach of the sneak males appears to be elicited by the dominant male lowering itself into the nest, as has been demonstrated in studies of rainbow trout, S. gairdneri, spawning behaviour (Newcombe and Hartman 1980). This suggests the kicking of gravel by the dominant male is an anti-sneak aggressive behaviour as approaching sneaks are faced with a shower of gravel in what otherwise would be a protected position from attack (*i. e.* behind the dominant male). However, it is not known if this behaviour affects the reproductive success of sneak males. The courtship dig is a short duration dig performed by males while courting females and occurs in the presence or absence of additional males. It involves repeated striking the caudal fin against the substrate while the male maintains its upright position. Little gravel is displaced, suggesting this behaviour is not associated with nest construction.

The activity patterns (behaviours and movement) of males and females in the two treatments (paired and unpaired) were compared with a two-way Anova model. A priori multiple comparisons were performed with the Least Significant Differences test. Two sets of data were analysed: the average distance between successive positions for each fish and the total number of aggressive behaviours per fish observed in 30 minutes of observation. The frequency of performance of behaviours was compared between the paired and unpaired treatments within each sex and then between sexes using the Chi squared contingency test. Intersexual aggressive activity between males and females in the paired treatment was compared using the students T-test. A $p < 0.05$ level of significance was used throughout the thesis.

To determine if the aggressive activities of males and females were associated with particular areas (unpaired) or mates and areas (paired) all fish were repeatedly displaced from their positions (by scrubbing the arena fence with hard bristle brushes). The positions each fish held 30, 60, 90, and 120 minutes after displacement were recorded, after which the whole process was repeated. In the unpaired treatment, males and females were displaced from their positions a total of nine times over the course of a day and a half, during which 30 position observations were recorded for each fish. Similarly, in the paired treatment, the fish were displaced five times over

the course of one day, during which 20 positions were recorded for each fish. If males and/or females do defend specific resources, they are expected to return to these resources after displacement. If they defend only a space around themselves and not a specific resource, they are not expected to return to their former positions following displacement.

C. The effect of competitors on the commencement of territoriality in kokanee

To test whether space was limiting on the spawning grounds, 25 males and 25 females were collected from schools of kokanee, tagged to identify their sex and released back into the stream. At the same time, an equal number of individuals in similar physical condition were captured, tagged, and placed in an empty experimental arena (see Experiment B). Each day an observer walked the spawning channel and recorded whether tagged individuals were holding position on the spawning grounds or whether they were moving about or in schools. The total number of males and females which had established spawning sites after three days in each treatment were compared.

Results

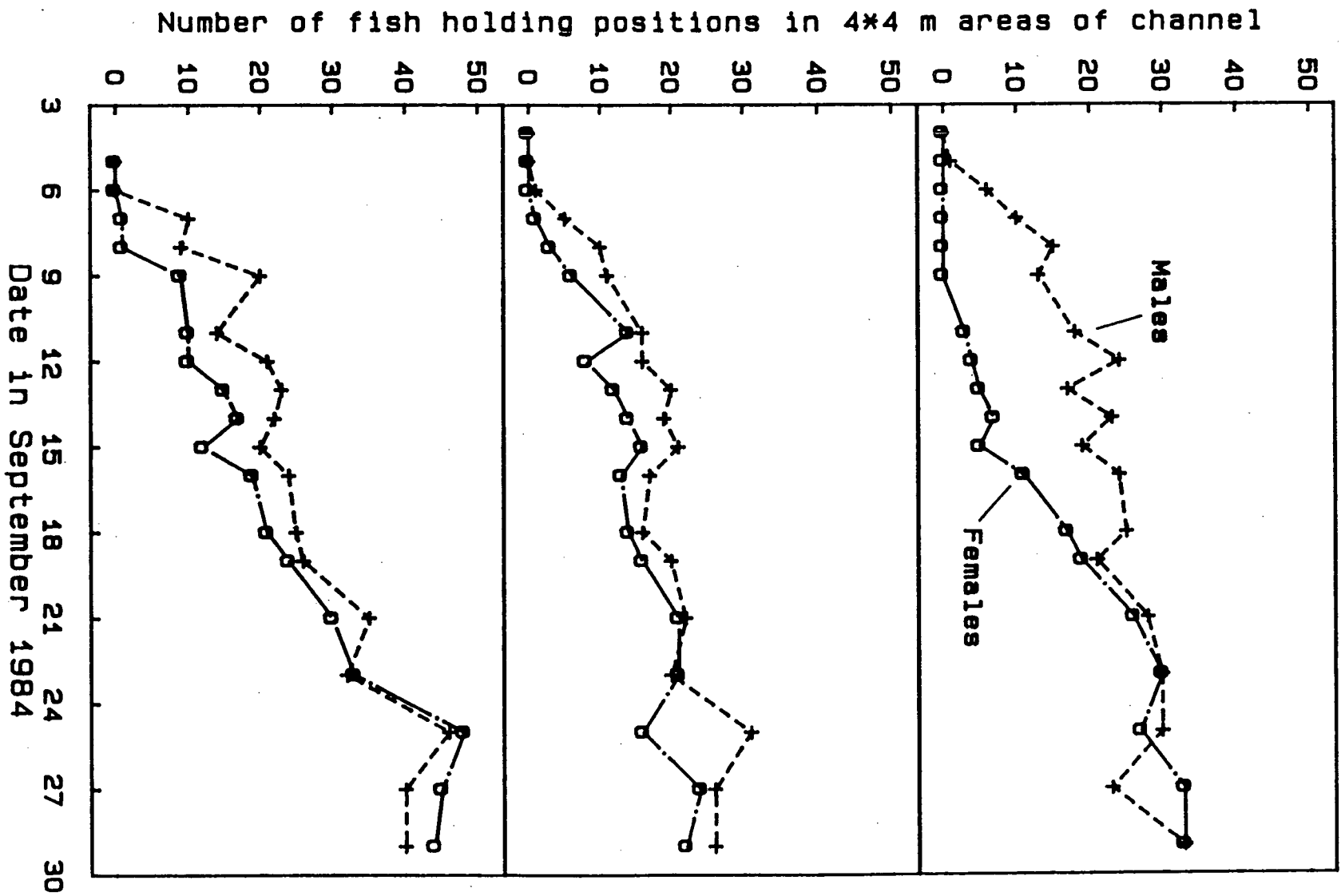
A. Chronology of settlement on the spawning grounds

Kokanee began establishing positions during the first week of September in each of the three areas monitored in the spawning channel (Fig. 2). The number of kokanee maintaining position in all areas increased over the month, leveling off at the end of the spawning run in late September. The sex ratio of kokanee which held positions within these areas was skewed toward males early in September but converged toward equality over the three and one half weeks of observation. During the time in which males were more numerous than females, males were aggressive toward each other, and fairly evenly spaced across the areas. They did not cluster around the few spawning females present.

B. An experimental examination of territoriality in males and females

The behaviour of males and females was examined in experimental arenas, with the sexes held separately (unpaired) and together (paired). If males and/or females are solely territorial of nest site resources, then they are expected to compete amongst themselves for these resources both in the presence and absence of the opposite sex. Site specific intrasexual aggression would be evidence of such territoriality. In contrast, if males and/or females are solely territorial of mates, then they would be expected to compete among themselves

Figure 2. The number of males and females holding positions in three 4 by 4 m designated areas of the Meadow Creek spawning channel, over the course of the run in September, 1984.



only in the presence of the opposite sex and exhibitions of intrasexual competition would be expected to be site and/or mate specific and persistent over time.

The size range of fishes (fork lengths) used in each treatment are given in Table 1. The mean distance between successive positions held by individual fish (MDP) was significantly different between the sexes and between treatments (paired or unpaired) (Table 2; $p < 0.001$). On average, females moved about less than males in both treatments and males and females which were paired with the opposite sex tended to move about less than those which were kept separate from the opposite sex (Fig. 3). Females moved about significantly less than males when the sexes were held separately ($p < 0.001$), but there was no significant difference in the movement of the sexes when they were held together ($p > 0.6$). Within sex, males which were held together with females moved about significantly less than males which were held in the absence of females ($p < 0.001$). Although paired females tended to move about less than unpaired females, the difference was not significant ($p < 0.07$).

The total aggressive activity of fishes differed significantly between the sexes ($p < 0.001$) but not between treatments (paired and unpaired) ($p > 0.15$; Fig. 4). The interaction of sex and pairing was significant ($p < 0.05$). Females displayed fewer aggressive behaviours than males in both treatments ($p < 0.05$). Within sexes, females in the presence of

Table 1. Mean fork lengths, weights and size ranges (+SE) of males and females used. Letter designations are: m,f=sex; U=unpaired test group (i. e. sexes separated); PA=paired test group; S=small size; L=large size; P=prior access; NP= without prior access; WF=males which were recently with females; WOF=males not recently with females; WA=males previously in area and; WOA=males not previously with females or in area.

Exp.	Test Sex	Group	Mean Fork Length	Range	N	Mean Weight	Range	N
1b	m	U	21.3 (0.2)	19.3-23.2	25			
	m	PA	21.3 (0.2)	19.6-24.5	25			
	f	U	21.0 (0.2)	18.9-22.6	25			
	f	PA	20.8 (0.2)	19.2-23.7	24			
2b	f	S	19.7 (0.1)	17.7-20.9	165	78.6 (0.8)	56.1-97.5	158
		L	22.5 (0.1)	21.5-29.4	165	112.3 (1.8)	84.7-250.0	165
2c	f	SP	19.6 (0.1)	18.3-20.6	60	76.8 (1.3)	58.2-95.9	54
		LP	22.2 (0.1)	21.5-28.7	60	108.0 (2.2)	84.7-221.3	60
		SNP	19.4 (0.1)	17.7-20.5	60	76.9 (1.2)	57.2-94.4	59
		LNP	22.4 (0.1)	21.5-27.8	60	112.2 (2.5)	90.9-216.6	60
3a	m	S	20.1 (0.1)	18.5-20.7	70	76.3 (0.9)	58.5-88.8	56
		L	22.1 (0.1)	21.5-24.6	70	102.2 (1.3)	81.9-138.9	56
3b	m	P	20.3 (0.0)	20.0-20.5	70	80.6 (0.6)	69.6-93.7	70
		NP	20.3 (0.0)	20.1-20.5	70	80.5 (0.6)	71.4-93.2	70
3c	m	SP	20.1 (0.1)	18.1-20.8	70	76.7 (0.8)	57.8-92.0	56
		LNP	22.1 (0.1)	21.5-24.0	70	104.1 (1.4)	83.1-138.0	56
3d	m	WF	20.3 (0.0)	20.1-20.5	56	82.6 (0.5)	76.2-92.3	56
		WOF	20.3 (0.0)	20.1-20.4	56	82.3 (0.7)	73.3-94.5	56
3e	m	WA	20.3 (0.0)	20.1-20.4	56	86.1 (0.6)	75.2-96.2	56
		WOA	20.3 (0.0)	20.1-20.4	56	83.3 (0.5)	74.9-91.0	56

Table 2. The mean number of digs and aggressive behaviours displayed by 25 males and 25 females over 30 minutes of observation when held together with an equal number of the opposite sex (T) and when held separate from the opposite sex (S), over three to five days in an experimental arena. The means of the mean distance between successive positions (MDP) (+SE) held by each fish over three to five days are also presented.

		Dig	Chase	Bite	Lateral Display	T Display	Total (SE)	MDP (SE)
Males	S	0.4	18.4	2.4	18.4	6.0	45.7 (4.5)	1.78 (.01)
	T	1.3	22.8	4.6	15.4	6.6	50.6 (5.0)	0.93 (.01)
Females	S	2.3	22.9	2.8	4.2	2.9	35.1 (4.3)	1.10 (.01)
	T	8.0	13.4	3.6	1.0	0.9	26.5 (3.1)	0.86 (.01)

Figure 3. Mean distance between successive positions held by 25 males and 25 females that were held (A) separate from the opposite sex over five days and (B) together with the opposite sex over three days of observation in an experimental arena.

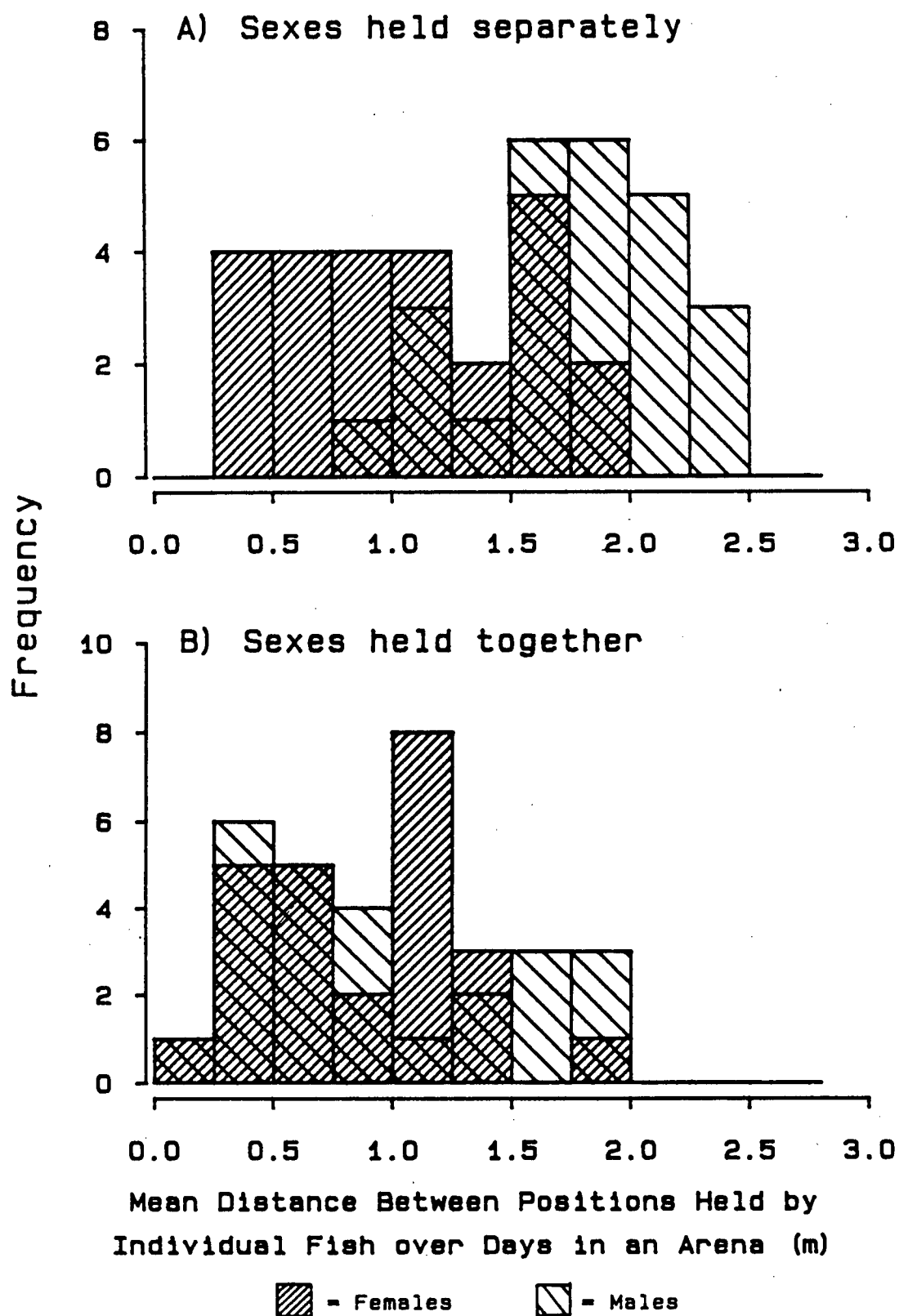
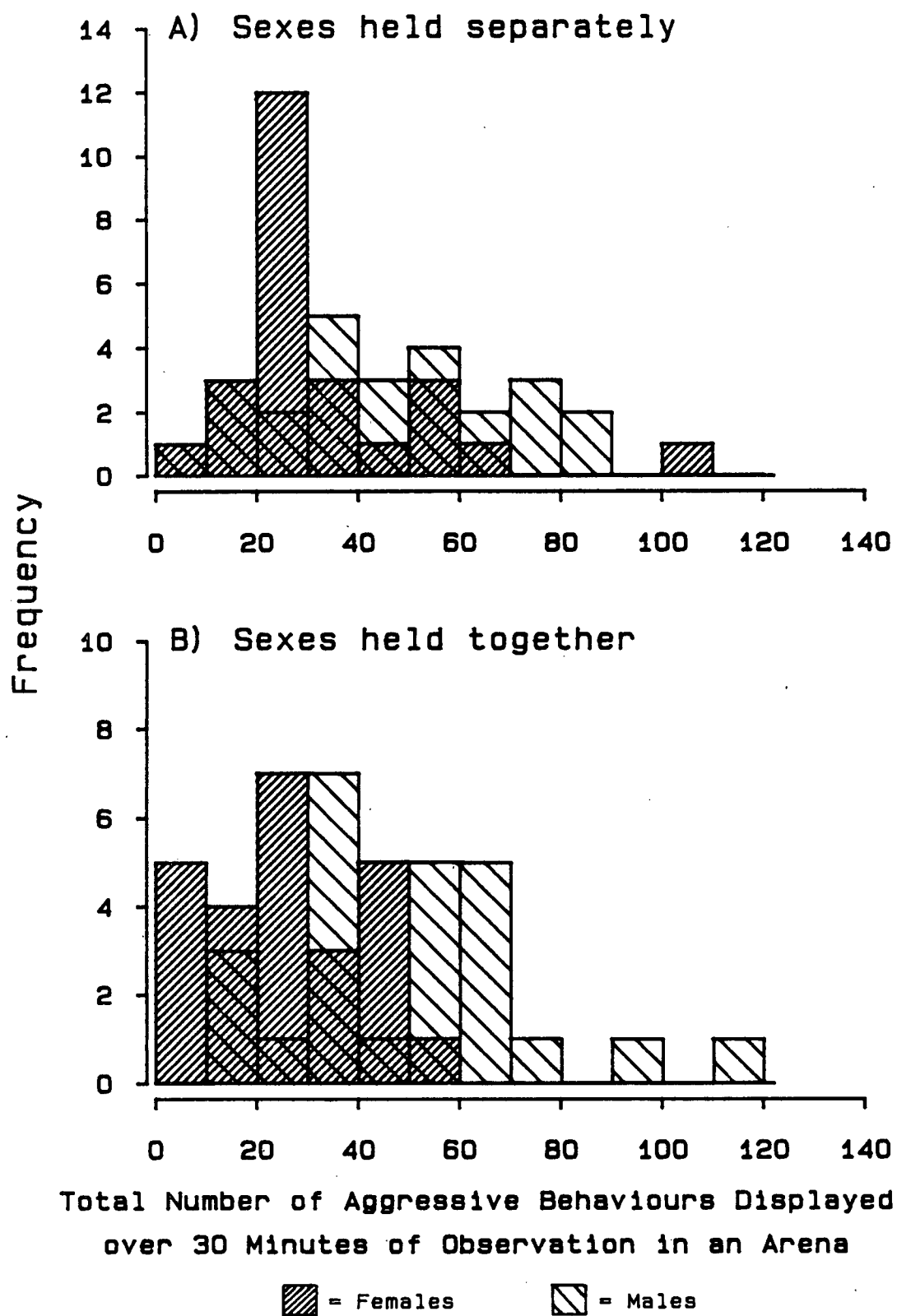


Figure 4. Total aggressive activity over 30 minutes of observation by 25 males and 25 females that were held (A) separate from the opposite sex for five days and (B) together with the opposite sex for three days in an experimental arena.



males displayed fewer aggressive behaviours than females held separately from males ($p < 0.05$). The decrease in aggressive activity in the presence of males was associated with a significant increase in the amount of nest construction (digging) observed ($p < 0.001$), such that the total female activity levels (sum of digging and aggressive behaviours) did not differ significantly between treatments ($p > 0.15$). There was no significant difference in the aggressive activity of males between treatments ($p > 0.4$).

To further compare male and female behaviour, aggressive behaviours were divided into two categories: "Direct Actions", those which involved direct assaults on other individuals (chases and bites) and "Displays", behaviours which involved lateral or perpendicular body presentations which in themselves did not involve direct physical contact with the receiver (lateral displays and T-displays).

There were no significant differences within sexes between treatments in the relative frequency of performance of either Direct Actions or Displays ($p > 0.3$; Table 2), but there were great differences between the sexes in the relative frequency of Direct Actions and Displays ($p < 0.005$). Male activity was divided nearly equally between Direct Actions and Displays but female activity involved mainly (83%) Direct Actions. Females were more aggressive towards males than males toward females (T-test, $p < 0.001$; Table 3). Direct Actions composed the majority

Table 3. Comparison of the mean intersexual aggressive behaviour of 25 male and 25 female female kokanee observed for 30 minutes each over three days in an experimental arena.

	Chase	Bite	Lateral Display	T Display	Total	(SE)	% Total Aggression
Males	3.6	0.7	0.8	0.9	5.9	(0.8)	11.1%
Females	8.2	1.9	1.0	0.9	12.4	(1.1)	31.9%

of intersexual interactions of both sexes.

There were significant differences in movement (MDP) among females in both the paired and unpaired treatment (One-way anova, $p < 0.001$). The MDP for paired females, averaged over 21 observations taken over three days, ranged between 0.12 and 1.77 m. The MDP for unpaired females, averaged over 31 observations taken over 5 days, ranged between 0.39 and 1.91 m. In both treatments, the majority of females held to particular areas, which they aggressively defended (Figs. 5a and 6a). Some females failed to establish fixed positions. The degree to which females held to specific positions depended on whether males were present or absent. In the absence of males, females moved around more within given areas, and returned less specifically when displaced. In the presence of males, the majority of females held to specific locations and returned precisely to those positions when displaced (Figs. 5b and 6b).

There were significant differences in movement (MDP) among males in both paired and unpaired treatments (One-way anova, $p < 0.001$). In the unpaired treatment, the MDP ranged between 0.85 and 2.35 m. In the paired treatment, the mean distances between positions were substantially smaller, ranging from 0.18 to 1.81 m. Male movement was localized in both cases, although much more so in the presence of females. Some males, in the absence of females, aggressively maintained positions within given areas over days. The general areas occupied by five of

Figure 5. Areas in which individual females, kept apart from males, spent most of their time over (A) five days of undisturbed observation and (B), later, over one and one half days of repeated disturbances (and displacements from their positions) in an experimental arena. Each fish is identified by letter. Greater density of the shading of areas indicates higher rank of the female in total activity (sum of digging and aggressive activities). The parenthesized number beside each letter indicates the percentage of total observations in which the female was observed within the designated area.

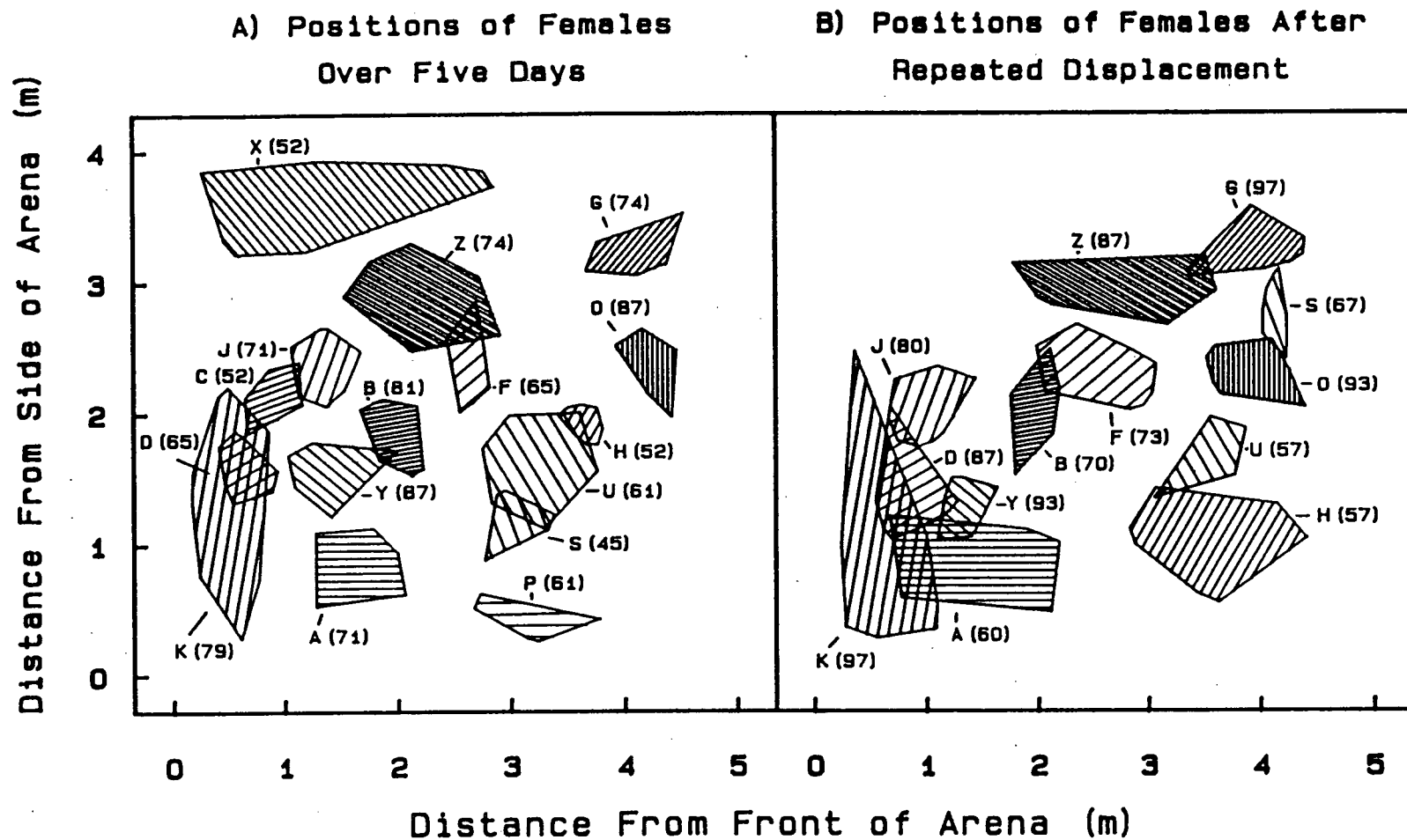
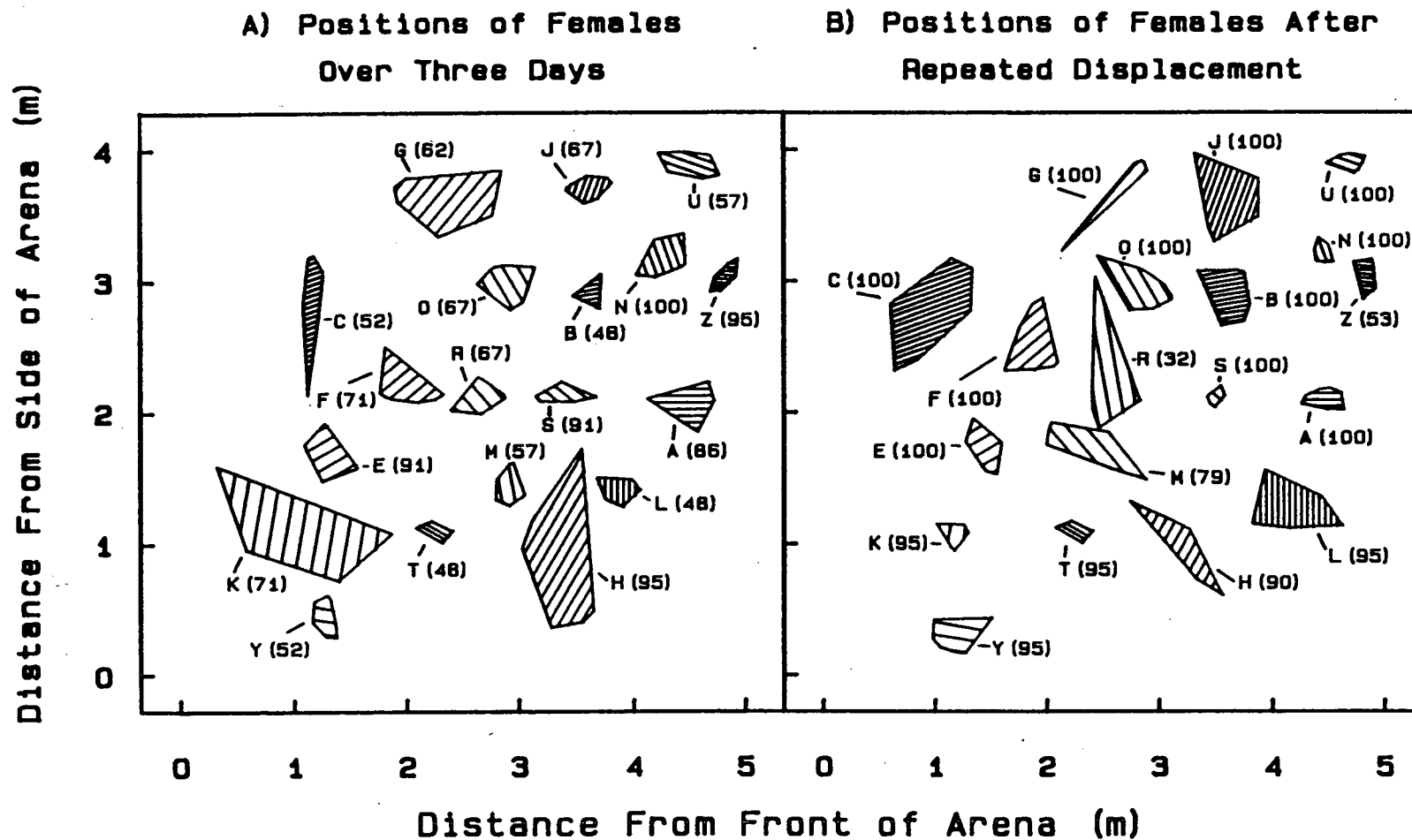


Figure 6. Areas in which individual females, in the presence of males, spent most of their time over (A) three days of undisturbed observation and (B) later, over one day repeated disturbance (and displacement from their positions) in an experimental arena. See legend to Fig. 5 for further details.



the six most aggressive males in the unpaired treatment are shown in Fig. 7. These males ranged within small but often overlapping areas during the majority of the observation periods and returned, fairly precisely to these areas when repeatedly displaced. In the presence of females, males courting females largely excluded other males from their direct vicinity, and returned to their positions, attending the same female, after repeated displacement (Fig. 8). Some males adopted sneak positions behind pairs and usually returned to their sneak positions behind the same female after displacement.

C. The effect of competitors on the commencement of territoriality

Kokanee released back into the crowded spawning channel established positions at a much slower rate than those placed into an experimental arena (38 of 50 defended positions in the arena as compared to 3 of 19 observed in the channel after the same three day period; Chi-squared test, $p < 0.001$). Most of the 16 tagged kokanee which did not establish spawning positions in the channel over three days were observed in schools of kokanee, upstream from their release point. The position of schools (sometimes consisting of over 10,000 fish) in the stream remained constant over days, usually in pools or back eddies, even though the individual fish making up the schools moved. This suggests that the schools did not move as a unit, but rather that individual fish or small groups of fish moved

Figure 7. Areas in which individual males, kept separate from females, spent most of their time over (A) five days of undisturbed observation and (B) later, over one and one half days repeated disturbances (and displacements from positions) in an experimental arena. The positions of only five of the most aggressive males are shown. See legend to Fig. 5 for further details.

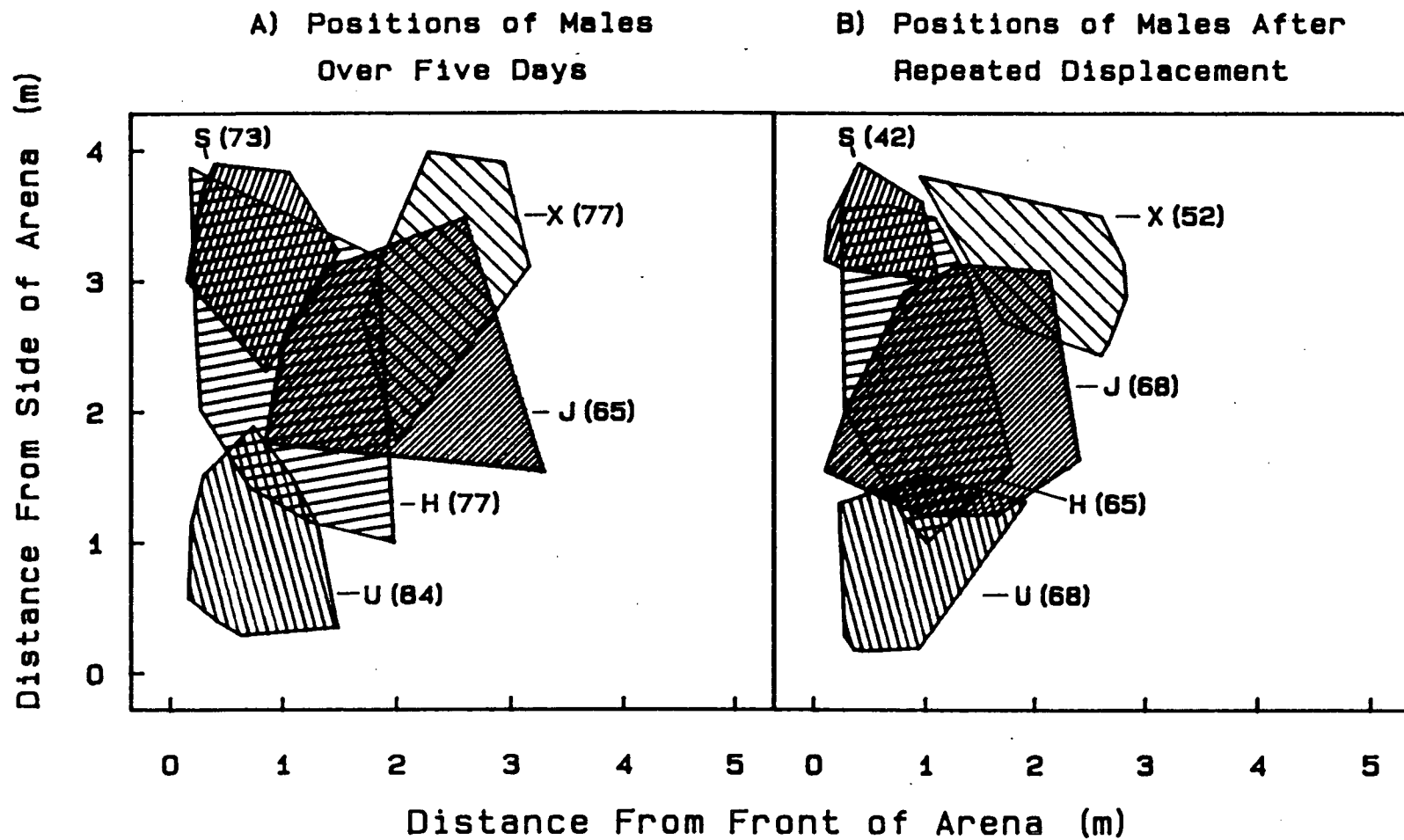
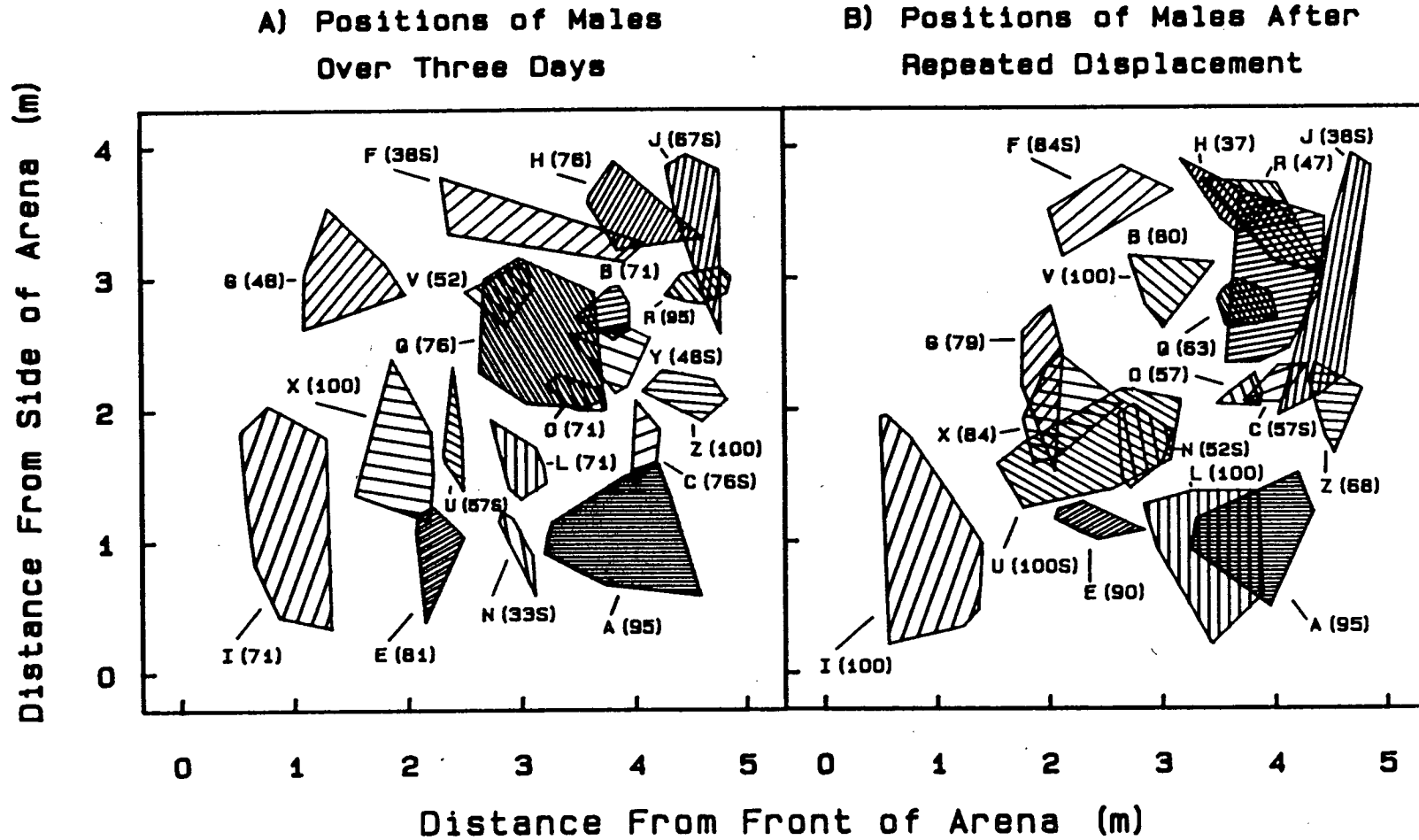


Figure 8. Areas in which individual males, in the presence of females, spent most of their time over (A) three days of undisturbed observation and (B) later, over one day of repeated disturbance (and displacement from their positions) in an experimental arena. The letter "S" beside particular males indicates that they spent the majority of their time attempting to sneak fertilizations from females attended by other males. See legend to Fig. 5 for further details.



upstream from school to school.

2. The effects of size and prior access in female intrasexual competition

Methods

A. Preferred spawning sites

The effects of size and prior access in female intrasexual competition were tested in two 5 by 5 m experimental arenas in Meadow Creek spawning channel in September, 1983. It was first necessary to determine which areas of the arenas were preferred by females and whether the preferred areas differed between "small" and "large" individuals (The size ranges of females used are given in Table 1). 'Preferred areas' were determined by allowing different numbers of females of each size class (5, 10, 15, 20; repeated twice for each size group, 200 females in total), accompanied by an equal number of males, to establish positions (nest sites) in each experimental arena over an 8 to 14 hour period. At the end of a period, the position of each female, along with data on whether it was (1) accompanied by a male, (2) holding position and (3) constructing a nest (digging), were recorded. 'Preferred areas' were considered to be those inhabited by females attended by males.

B. The effects of size in female intrasexual competition

In each of 11 trials, 15 large and 15 small ripe unspawned and individually tagged females were introduced simultaneously into Arena 2 (downstream) at 1800 hours and allowed to compete for positions over a 24 hour period. The position of each female (and whether it was holding position) was recorded twice, at 0800 hours on the following morning and again at 1730 hours. 'Winners' of female competition trials were judged to be those females that held positions within the 'preferred area' during both the dawn and dusk observation periods. To derive an independent score for each trial, the number of small females that held positions in the preferred area was subtracted from the number of large females which did so.

C. The effect of prior access in female intrasexual competition

In each of four trials, 30 females (15 large and 15 small; those from trials 4, 6, 8 and 10 of the size experiment), were taken from arena 2 at 1800 hours, introduced into arena 1, and allowed to establish nest sites over a 24 hour period. The position of each of these females was recorded twice during this 24 hour period. At the end of the 24 hour period, 30 females (15 large and 15 small; those from trials 5, 7, 9 and 11) were taken from arena 2, placed in arena 1, and allowed to compete with the incumbent females over a 24 hour period. The success of the immigrant females in establishing territories was

measured by subtracting the number of immigrant females (no prior access) holding positions in the preferred area from the number of incumbent (those with prior access) females doing so.

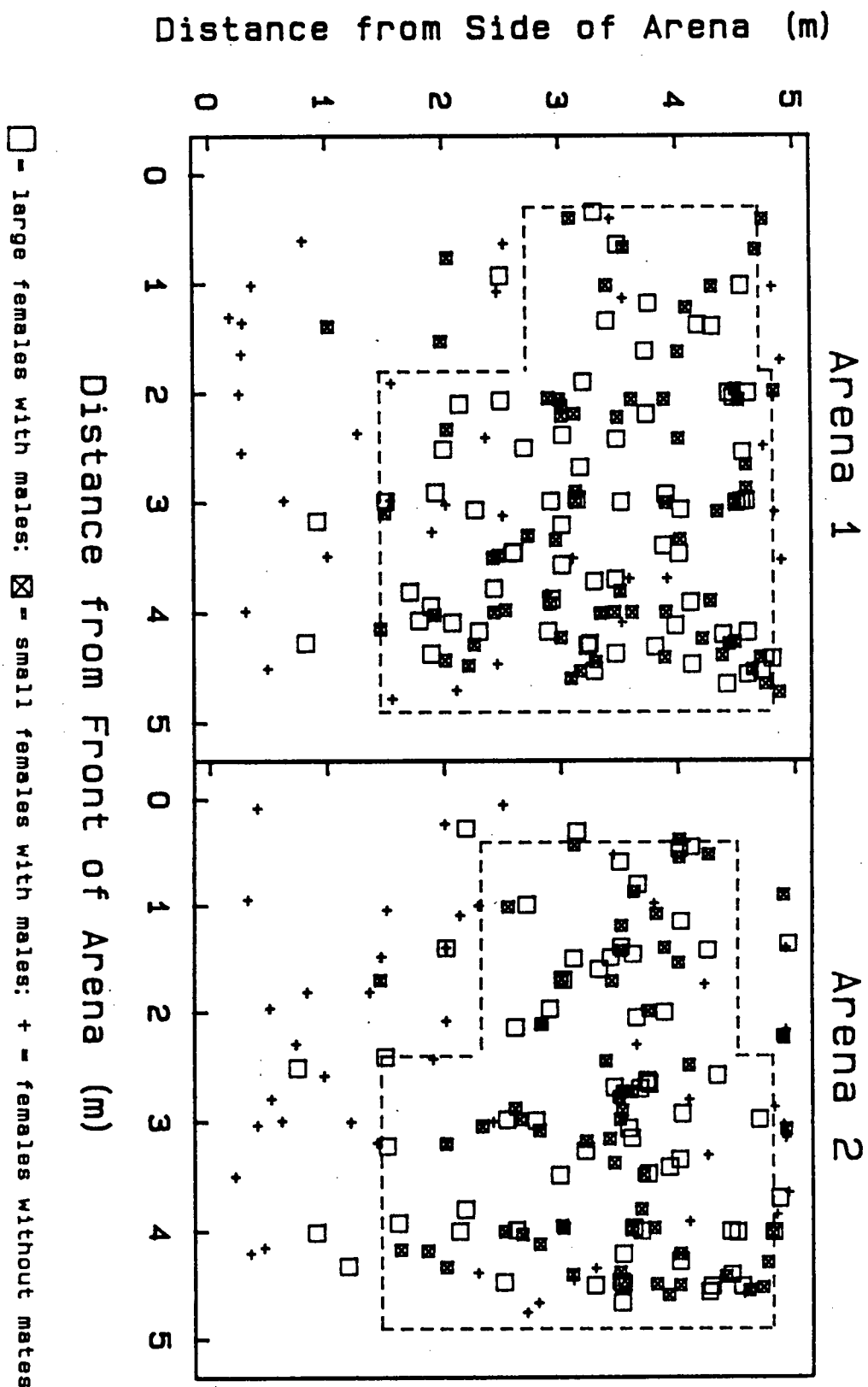
The data from each experiment were analysed using the Wilcoxon matched pairs signed rank test (one tailed). The matched pairs in this experiment are the non-independent outcomes of each trial (that is, whether or not a fish held position within the preferred spawning area of the arena).

Results

A. Preferred spawning sites

Large and small kokanee females attended by males established nest sites in the same general vicinity in both experimental arenas. Positions in the downstream, offshore portions of each arena were always occupied (Fig. 9), independent of the number of females present. As female density increased, females established positions slightly upstream of this preferred area. The offshore portions of each arena were the areas of maximal water velocity. Water left each arena through both the rear fence and the lower reaches of the outer fence. This resulted in a distinct deviation of the current towards the offshore fence in the downstream offshore portion of each arena (as demonstrated by plotting the course of released dye).

Figure 9. Positions held by 'large' and 'small' kokanee females which were accompanied by males in arenas 1 and 2. The positions of females that were not accompanied by males are shown. The dotted lines enclose an area where over 85% of females of both size groups established nest sites.



To broadly delineate the areas preferred as spawning sites by females, a section of each arena in which the majority of females established nest sites was visually identified (Fig. 9). The subjective boundaries of these "preferred areas" were supported by nearest neighbour analyses of the positions of all attended females. The "preferred area" took up just over one half the total possible spawning area in each arena (13.5 and 12.8 square meters of arena 1 and 2, respectively). In arena 1, 63 of the 66 large females (95%) and 58 of 64 small females (91%) attended by males established nest sites within the "preferred area". In arena 2, 54 of 60 large females (90%) and 56 of 64 small females (88%) attended by males established nest sites within the "preferred area". The majority of female nest construction (digging) was observed within the "preferred areas". In arena 1, all 19 large females and 20 of 22 small females observed constructing nests (digging), did so within the "preferred area". In arena 2, 24 of 26 large females and 21 of 24 small females observed digging, did so within the "preferred area".

To verify that the "preferred area" of each arena was preferred, and competed for, by females, I twice (with separate groups of females, no males present) removed females from the "preferred area" of arena 1 and recorded the positions of the remaining females five hours later (the "preferred area" referred to here is smaller than that described above, as it was

roughly estimated in the field without the aid of the data on female positioning that were then being collected). I also removed females that held positions outside the "preferred area" on one occasion and similarly recorded the positions of the remaining females.

After the females holding territories within the "preferred area" were removed, the area was always re-occupied by females emigrating from the non-preferred area (Fig. 10). Over the two trials, 21 females were removed from the "preferred area" and 22 other females moved into and established positions within this area over the course of five hours. Five of the immigrant females were observed constructing nests (digging). In contrast, few females emigrated from the "preferred area" to the outlying areas after females were removed from these 'non-preferred' areas (Fig. 11). Of the five females that left the "preferred area", three moved to positions just beyond the boundaries, and two left the area completely.

The examination of positions established by spawning pairs, supported by data from the removal experiment, demonstrates that females preferred to establish nest sites in the outer, downstream portions of the experimental arenas and that female interactions limited the number of females which could do so. In the following experiments, "winners" of female intrasexual competition for nests sites were judged as those individuals which maintained positions within the "preferred area" over the

Figure 10. Positions occupied by females in arena 1 (A) before females were removed from the preferred area and five hours after (B) females were removed from the preferred area.

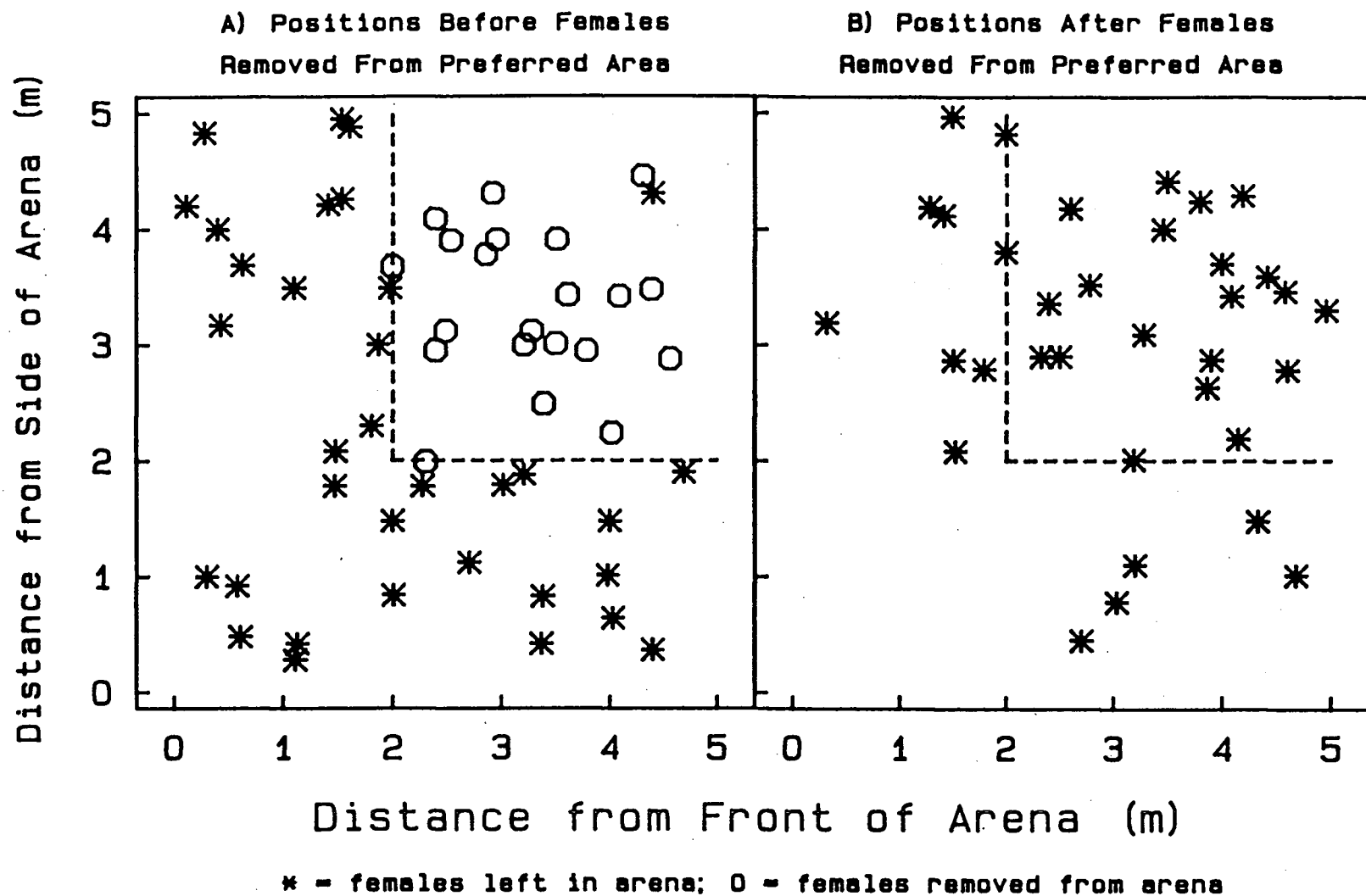
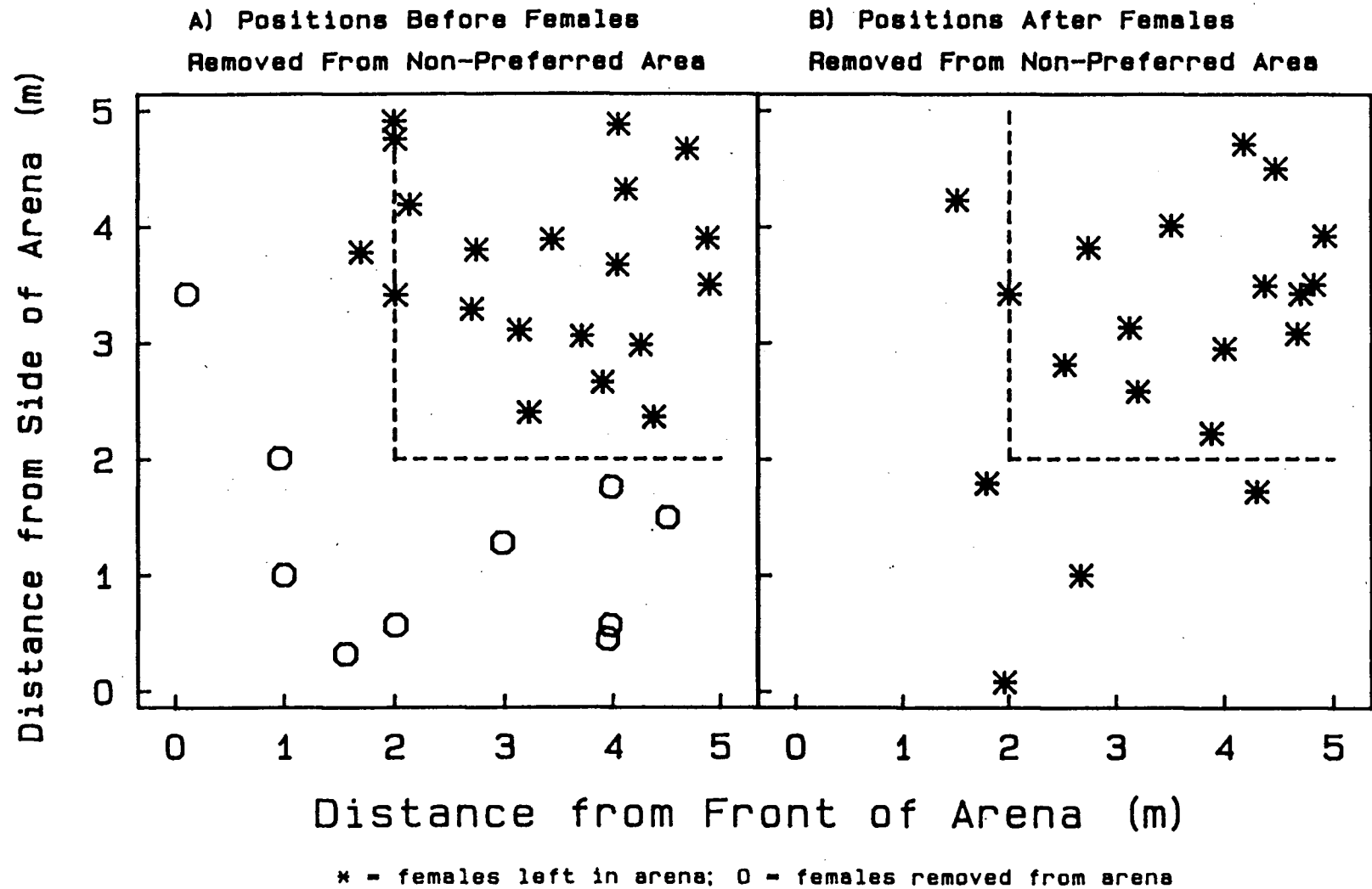


Figure 11. Positions occupied by females in arena 1 (A) before females were removed from the non-preferred area (B) five hours after females were removed from the non-preferred area.



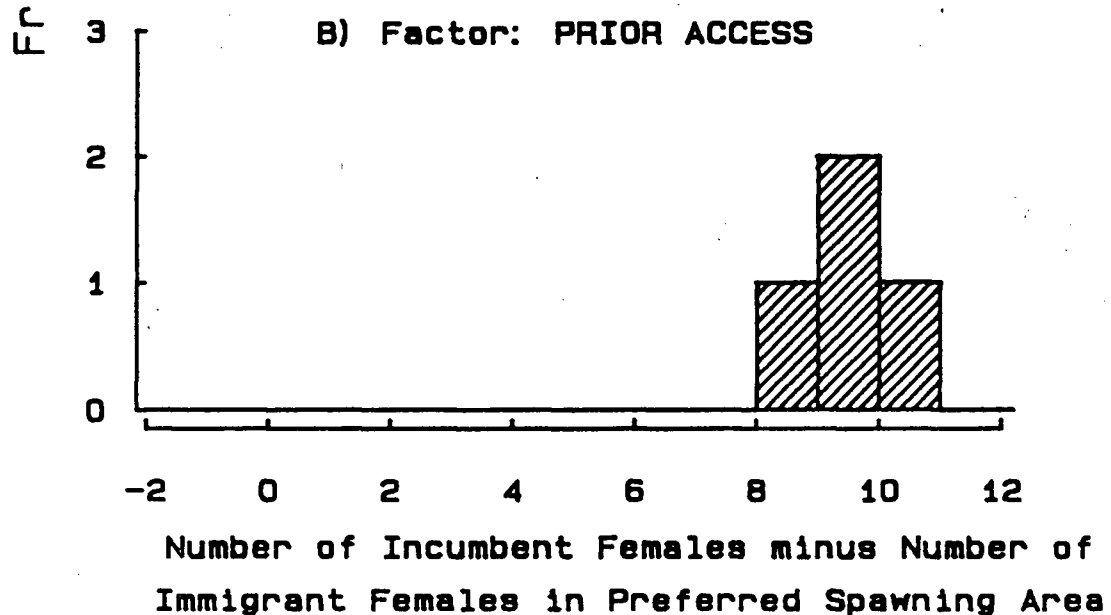
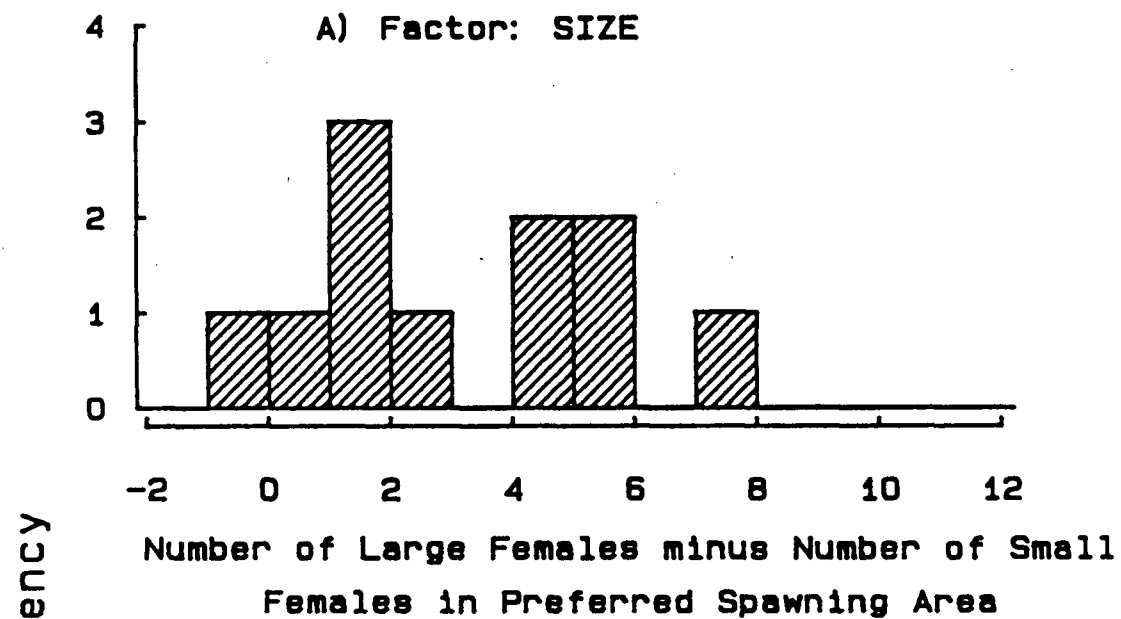
course of 24 hour trials.

B. Size in female intrasexual competition

Large females (14% longer, 43% heavier; Table 1) dominated small females in competition for preferred sites in 9 of 11 trials in arena 2 ($p < 0.05$; Fig. 12a). In only one trial was the number of small females holding position within the preferred area greater than the number of large females in the same area. In one other trial, the numbers of large and small females in the preferred area were equal. On average, 64% ($6.6 \pm 0.5\text{SE}$ per trial) of females that maintained positions within the preferred area were of the large group and 36% (3.7 ± 0.6) were of the small group.

The effect of size was maintained when females were transferred to arena 1 and allowed to re-compete for positions over 24 hours (number of large females holding position in preferred area minus the number of small females holding position; in the four trials = 8, 2, 5, 7; $p = 0.05$). On average, 9.8 (0.8SE) large and 4.3 (0.6) small females maintained position in the preferred area. The majority (71%) of large (26 of 39) and small (13 of 16) females which held preferred territories in arena 1 previously held preferred territories in arena 2. Of the remaining 16 females, 11 had previously held position in the preferred area of arena 2 during one of the two observation periods. The repeatability of the results at the

Figure 12. The difference between the number of females from two test groups which were able to hold positions within the preferred spawning area. (A) In 11 trials, groups of 15 'large' and 15 'small' females competed for access to preferred positions over 24 hours. (B) In four trials, groups of 30 females (15 'large' and 15 'small') which had previous access to the preferred positions competed against a similar number and size range of females for access to preferred positions over 24 hours.



individual level demonstrates that there is significant variation among individuals in the ability to acquire territories that is not accounted for by size differences alone.

C. The effect of prior access in female intrasexual competition

Incumbent females (those with 24 hour prior access) dominated immigrants in intense competition for preferred nesting sites in all four trials ($p=0.05$; Fig. 12b). Of the 62 females maintaining position within the preferred area, 49 (79%) had been in the arena 24 hours prior to the addition of the immigrant females. Relative size was not a factor in determining which incumbent females were able to maintain their territories. The number of small incumbent females holding preferred positions increased from 16 to 19 after the addition of the second group of females and the number of large incumbent females decreased from 39 to 30. There was no significant difference between the number of preferred positions attained by large and small immigrant females. The sample sizes were small and it is possible that large females possess an advantage on the average over small females in establishing positions within an already inhabited area. Large immigrant females held 8 preferred positions compared to the 5 held by small immigrant females.

Of the 49 females with prior access which held positions within the preferred area, 42 (85.7%; 27 of 30 large, 15 of 19

small) held positions in the preferred area during the day prior to the introduction of the immigrant females. Of the remaining seven females, five (10.2%) held positions in the preferred area during only the previous evening observation period and two were never observed holding positions within the preferred area. These results demonstrate that the advantage of prior access is accrued from holding specific positions (prior residence) and not simply from an association with arena surroundings.

The effects of prior access were also apparent in the comparison of the number of incumbent and immigrant females observed within 1.25 m of the stream bank (usually schooling) during both the AM and PM observation periods. In all four trials, immigrant females were the majority of the schooling fishes (number of females without priority minus number of females with priority schooling near bank in the four trials = 11, 9, 5, 2; one-tailed Wilcoxon test, $p=0.05$). Of the 51 females (from a total of 240) which consistently held to the stream edge (where they would be unlikely to attract males), 38 (74%) were immigrants (17 large, 21 small); whereas only 13 (26%) were residents (3 large, 10 small). The number of resident females schooling near the stream bank was little affected by the doubling in number of females present. Summed over the four trials, 10 incumbent females (1 large, 9 small) maintained position near the stream bank before the addition of the immigrant females; only 13 (3 large, 10 small) held to the stream bank after their addition.

The slight decrease in the number of preferred territories (56 to 49) held by resident females, coupled with the marginal increase in the number of resident females schooling near the stream bank (10 to 13) after the number of females in the arena was doubled demonstrates that prior access to preferred spawning areas greatly increases the chances that females will be able to win future competitions for positions within those areas.

3. Effects of size and prior residence in male intrasexual competition

Methods

Size, prior access and the interaction of these two factors in male intrasexual competition were examined in three experiments during September, 1984. For each of 10 trials, seven territorial unspawned females were established in a 4 by 4 m experimental arena. The females were selected in the morning from twelve females which had been placed in the arena on the previous evening and allowed to compete for territories. Only females which held defended positions were selected (females without nest sites are unattractive to males (Schroder 1982; Fig. 9), thus minimizing differences in female territoriality within and between trials.

Males were selected, measured (fork length), weighed and

tagged on the eve of a competition trial and held overnight in 1.5 m fine screen cages in the creek. The mean lengths and weights of all male size groups for each experiment are presented in Table 1. All males selected were sexually ripe and in excellent physical condition.

One hour after the removal of the excess females in the morning, males were introduced into the arena containing the seven territorial females. In the "size" experiment, 14 males, seven 'large' and seven 'small' were introduced simultaneously. In the "prior access" experiment, seven small males were initially introduced and four hours later seven additional small males were added. In the "interaction" experiment (size x prior access) seven small males were introduced, and four hours later seven large males were introduced.

The position of each male (with respect to females) was recorded four hours after all fish were first in the arena together. The four male positions scored were: (1) 'dominant' (male closest to the female); (2) 'competitor' (where two males were competing for access to a female with no clear dominant); (3) 'sneak' (males which held position behind a mating pair) and; (4) 'loner' (males not involved with any female). All fish were released at the end of each trial and were not used in subsequent trials or experiments.

An independent score was generated for each trial to

quantify the outcome of intrasexual competition. This was done by subtracting the number of males of one group (small, no prior access) which held dominant positions from the number of those of the other group (large, prior access) which held dominant positions. Males which were classified as 'competitors' were given half scores, reflecting the fact that two males were evenly matched in competition for access to a female. Less than five percent of all males observed were classified as 'competitors'. The Wilcoxon matched pairs signed rank test was used to analyse the data within experiments and the Mann Whitney U test was used in comparisons between experiments.

It became apparent that prior access to females afforded males an advantage in subsequent competition for access to females. Males may gain an advantage in competition simply by having been previously associated with females. Alternatively, an association with a physical territory while with females may give males an advantage in future competition for access to new females arriving in the area. Two experiments were designed to test these possibilities. The methodologies were similar to the previous three experiments.

In the first experiment, seven males were given access to one group of territorial females for four hours. The males were then seined from the arena, and placed in a large water filled can along with seven males of the same size, which had not recently been with females. After a few minutes, all were

released simultaneously into another arena with seven novel territorial females, and allowed to compete for four hours.

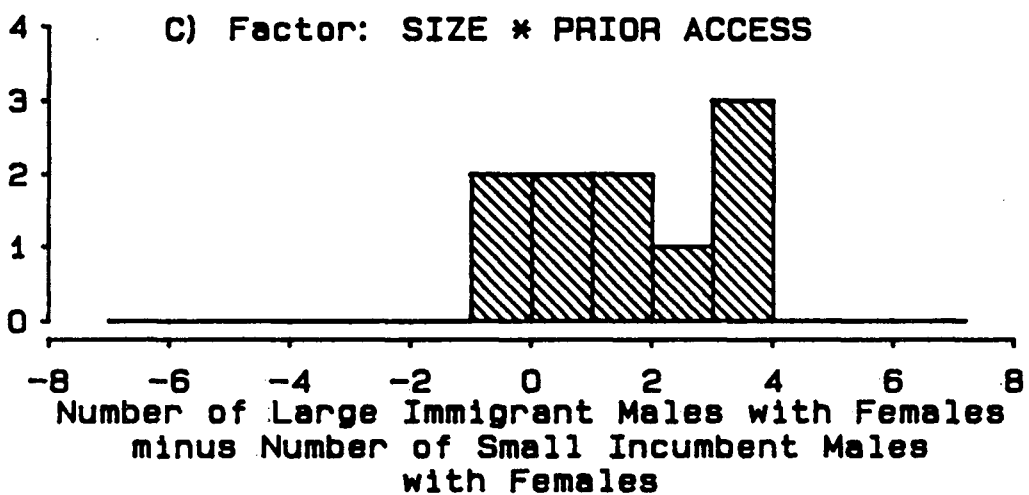
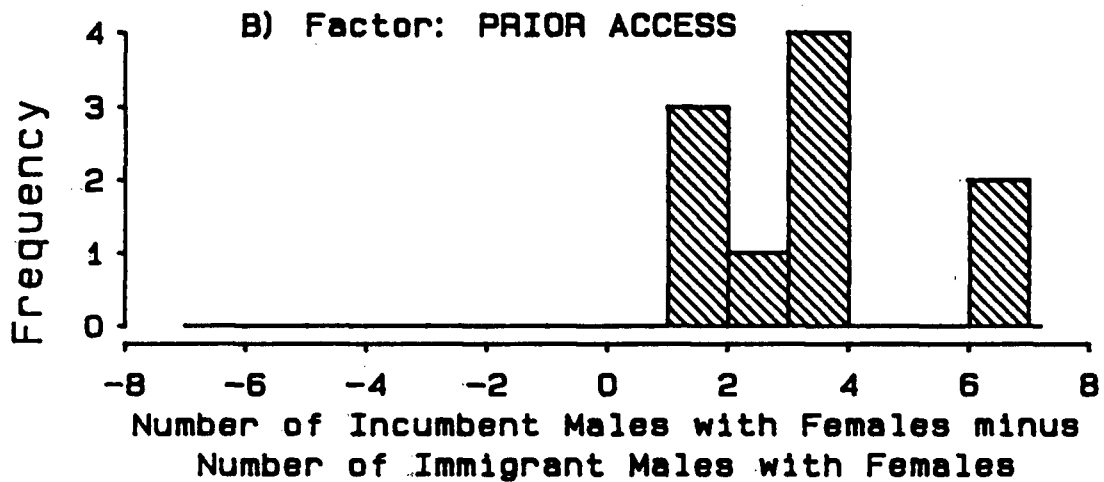
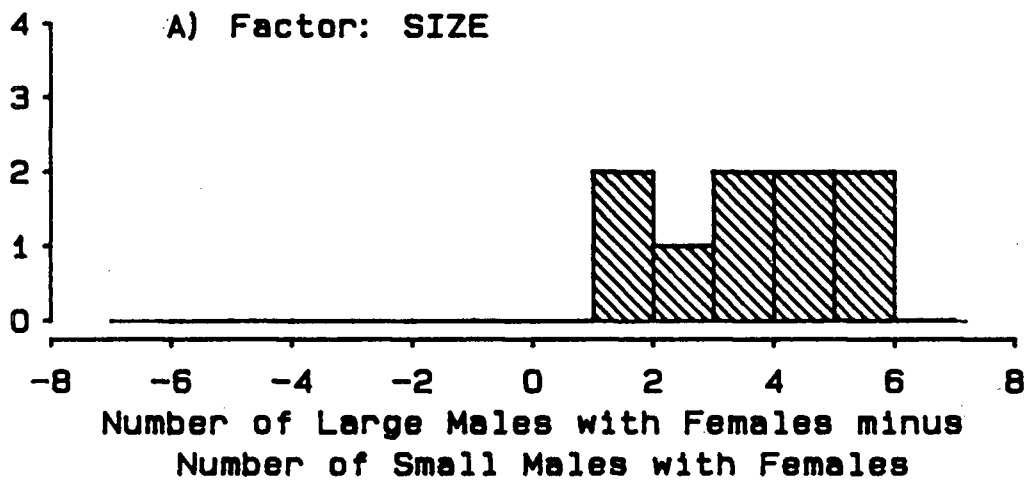
In the second experiment, in each of two arenas seven males were given four hours prior access to seven females and then both the males and females were seined from the two arenas. Seven females from each arena were introduced into the other arena. The males taken from each arena were supplemented by seven novel males of similar size and introduced into the arena they had previously occupied. Thus, in each of eight trials, seven males were faced with seven new females and seven new males in an arena they had previously occupied with seven other females for four hours.

Results

A. Size in male intrasexual competition

Large males (10% longer, 35% heavier; Table 1) dominated small males in competition for access to females in all ten trials in which males of both size groups were introduced simultaneously into the arena ($p < 0.005$; Fig. 13a). Of the 66 (of a possible 70) females attended by males at the end of all trials, 50.5 (76.5%; half scores were given to males classified as 'competitors') were accompanied by large males and 15.5 (23.5%) were accompanied by small males. Most males attended only a single female (62), although two large males defended

Figure 13. Difference between test groups in the number of males which held dominant positions beside females, for each of three separate experiments consisting of 10 four hour trials. (A) 'Large' males competed against 'small' males for access to females. (B) Males with four hours prior access to females competed against similar sized immigrant males for access to females. (C) 'Small' males with four hours prior access to females competed against 'large' immigrant males.



access to two adjacent females simultaneously. Small males were fifteen times more likely to adopt sneak positions than large males (15 of 70 versus 1 of 70).

Males tended to stay with particular females. Thirty-four of the 45 large males (76%) that were observed with females after both four and eight hours, remained with the same female. Similarly, 11 of the 13 small males (85%) that were observed with females on both occasions remained with the same female. Of the 9 males which assumed sneak positions after both 4 and 8 hours, 5 (56%) maintained their position behind the same female.

B. Prior access in male intrasexual competition

Males with four hours prior access to females dominated introduced males of the same size in competition for access to females in all ten trials ($p < 0.01$; Fig. 13b). Of the 66 attended females, 47.5 (72%) were accompanied by males with prior access. All males with females defended access to single females only. There was no difference between groups in the number of males which adopted sneak positions behind females. In total, seven males with prior access (10%) and 11 males without prior access (15.7%) adopted sneak positions.

Fifty three of the 70 females were attended by males immediately before the addition of those with no prior access. Four hours later, males with prior access still attended 48.5

females. Thus, the addition of more males had little effect on the number of male with prior access that attended females.

Thirty five of 47 males with prior access (75%) that were observed with females in a dominant role immediately before the addition of the other males and that courted females four hours later (in any role) remained with the same female. The majority (34) retained their dominant position. Similarly, males which adopted sneak positions tended to stay with the same female after the addition of the other males (2 of 3).

C. The interaction of size and prior access

There was no significant difference between the advantage associated with size and that associated with prior access when the factors were examined separately (comparison of the results of the two previous experiments; $p > 0.4$). The effects of size approached significance over prior access when small males were given four hours prior access to females before the addition of large males ($p < .1$; Fig. 13c). Thirty-eight of the 65 attended females were accompanied by large males with no prior access whereas only 27 were accompanied by small males with four hours prior access.

The effects of size were strongly evident when the positioning of small males relative to females was compared immediately before the addition of large males and four hours

later. The number of small males holding dominant positions was nearly halved (53 to 27), whereas the number of small sneak males nearly tripled (6 to 17) and the number of small males alone more than doubled (12 to 26)($p < 0.05$).

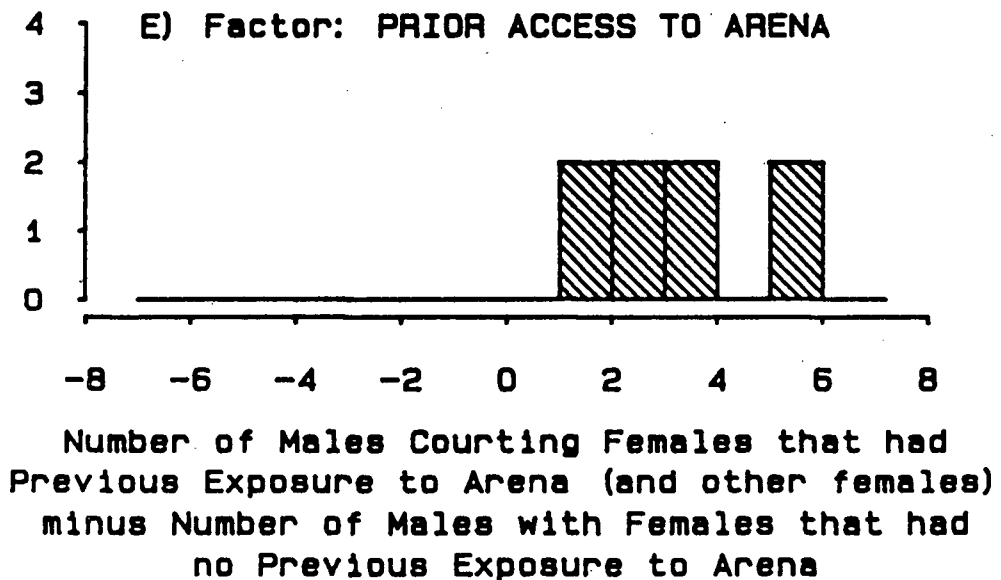
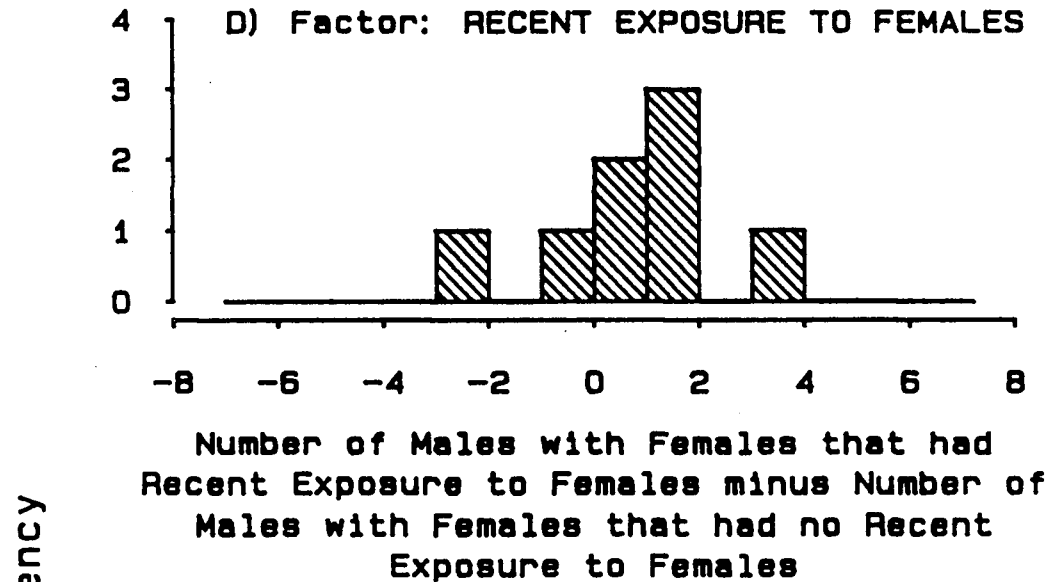
Thirty-one of 35 small males (79%) that were associated with females in dominant roles before the addition of the large males and which were observed with females four hours later (in any role) remained with the same female. Eight of the formerly dominant small males were forced into sneak roles with the females they previously courted. Similarly, 75% (3 of 4) of males that adopted subordinate sneak positions before the addition of the large males remained with the same female.

D. Factors involved in the advantage associated with prior access

Males that were in the presence of females for four hours fared no better than males with no recent experience with females in contests for access to novel females in novel localities ($p > 0.6$; Fig. 14a). Only 28 of the 54 attended females (52%) were accompanied by males which had recently been with other females. Therefore, simply being with females did not noticeably increase the chances of a male in future competitions for access to novel females.

Males that were returned to the arena they had previously

Figure 14. Difference between test groups in the number of males which held dominant positions beside females, for each of two experiments consisting of eight four hour trials. (D) Males which had immediately previously been with females competed against males which had not recently been with females for access to novel females in novel surroundings. (E) Males which had previously been with females competed against males which had not recently been with females for access to novel females in surroundings familiar to the first group of males.



occupied with one set of females dominated inexperienced males in competition for access to novel females (36 to 14 overall; $p < .02$; Fig. 14b). After their temporary removal, males with prior access tended to return to their previous positions. The mean distance between positions of males with prior access that held dominant positions both before and after the removal of the females they were courting and the introduction of novel females and males was only 0.59 m (0.08SE, $n=30$), a mean distance comparable to that of males which were left undisturbed with females (Table 2).

The effect of prior access to an area was significantly different from the effect of immediate previous experience with females ($p < 0.02$). These results demonstrate that at least part, if not all, of the advantages associated with prior access in males are accrued from a site specific association with the physical environment.

Discussion

Female territoriality

Females aggressively attempt to exclude other females from their near vicinity both in the presence and absence of males. The locations defended are specific. Females remained in the same place for several days and returned to their positions after repeated displacements. The selection and territorial

defense of spawning sites both in the the presence and absence of males (i. e. before any egg deposition) suggests that females initially defend positions as sites for future egg deposition and, later, defend them to protect their developing progeny.

Females are selective in their choice of spawning sites, usually preferring areas of particular current velocity and gravel composition (both dependent on size of female), and upwelling or bending currents (Fabricus and Gustafson 1954; Hartman 1969; McCart 1970; Tautz and Groot 1975; Jonsson and Hindar 1982; Schroder 1982). Such selectivity helps ensure that the embryos will receive sufficient oxygen during development (Brannon 1972; Koski 1975; Tautz and Groot 1975; Tappel and Bjornn 1983). Substantial and repeatable nest site selectivity was evident in this study. The preferred sites in arenas near the stream bank were in the quadrants that were furthest downstream and away from the stream bank, areas typified by the higher water velocities and the greater bending and upwelling of currents. Hence, kokanee female territory preferences within the arenas were seemingly related to the incubation qualities of the areas selected.

Territorial behaviour in females can be related to the necessity to establish and defend nest sites if they are to achieve a significant measure of reproductive success. It takes between 80 and 140 days for O. nerka eggs to hatch and the young spend several more months before emerging from the gravel

(Foerster 1968). Eggs which are not buried beneath the gravel are vulnerable to mechanical shock (Smirnov 1955), egg predation (Jones and King 1952; van den Berghe 1984; Maekawa and Onozato 1986) and climatic disturbances (Holtby and Healey 1986) and are unlikely to survive.

Territorial behaviour in females is further promoted by the variability in incubation quality among areas in the stream (Koski 1975), and the often limited number of nesting sites available (e. g. McNeil 1964; van den Berghe 1984; see Exp. 1c and 3b). Females that successfully compete for, establish, spawn in, and defend high quality nest sites will have greater reproductive success.

Aggressive female intrasexual interactions have been observed previously in Pacific salmon (Hanson and Smith 1967; McCart 1970; Tautz 1977; Schroder 1981, 1982; van den Berghe 1984). Tautz (1977) concluded that female aggressive interactions limit the number of females which can establish spawning sites at any one time. In my experiments, female interactions limited the number of females which could establish positions both in experimental enclosures and in the wild. Non-territorial females taken from the wild quickly established territories when placed in arenas in which no other females were present. In contrast, non-territorial females released back into the wild, or into arenas containing territorial females, usually remained non-territorial (schooling). When females were

removed from preferred spawning areas, their localities were almost immediately filled by other females. Female size is also a factor in determining the rate at which females establish territories. Large females accounted for 64% of the females holding territories within preferred areas of the experimental arenas, when in competition with an equal number of small females. However, once a female has established a territory, she is unlikely to be displaced until near death, independent of size (Fig. 12b). The strong effect of prior residence has previously been noted in Atlantic salmon (Salmo salar) (Jones 1959), coho salmon (O. kisutch) (van den Berghe 1984), and documented in chum salmon (O. keta) (Schroder 1981, 1982).

Male territorial behaviour

Kokanee male behaviour differs markedly in the presence and absence of females. In the presence of females, males often stayed with particular females for several days, aggressively preventing access to these females by other males, a behaviour which has been reported in the wild (Needham and Taft 1934; Hanson and Smith 1967). Males consistently returned to the females they courted after they were displaced from their position, demonstrating that specific resources and perhaps particular females are defended. Males returned to previous positions even after the females they were courting were removed.

In the absence of any females, males aggressively hold to general areas and return to them when displaced but they do not tend to successfully exclude other males from their vicinity, as they do when females are present. Males do not compete amongst themselves solely for direct access to females, as is sometimes suggested (Schroder 1981, 1982; Gross 1985; Sargent et al. 1986). While male intrasexual competition in the absence of females does not result in the exclusion of other males, the association with an area appears to increase the chances that incumbent males will win competitions for access to females moving into that area. Males with prior access to an arena (and a set of females) dominated immigrant males in competition for access to immigrant females. This may explain why males often outnumber females early in salmon spawning runs (e. g. Lorz and Northcote 1965; Johnson 1980), and why many males establish positions on the spawning grounds prior to the arrival of females (Fig. 2).

The absence of definitive male territorial behaviour in the absence of females can be related to intense levels of male competition and the long period (weeks) over which sexually active females are available. Territorial defense by males of resources necessary to females is common in polygamous mating systems (e. g. Howard 1978; Wells 1977; Searcy 1979; Fricke 1980), but is not economically feasible in mating systems in which the distribution of resources necessary to females is extremely clumped (Emlen and Oring 1977). Clumping of females

leads to a clumping of males, which can prohibitively increase the costs for males of maintaining resource territories, while waiting for females. When the costs of maintaining resource territories are too large, males often gather around the resources necessary for females, and compete amongst themselves for direct access to arriving females (e. g. Davies and Halliday 1979). This appears to be the case in Pacific salmon, where the clumping of females in population specific spawning locations is extreme and male intrasexual competition is intense.

Two factors promote intense male intrasexual competition in salmon. First, females are a limiting resource to males. While sex ratios are usually fairly even in salmon spawning populations (e. g. Hanson and Smith 1967; Foerster 1968; Sargent et al. 1986), the operational sex ratio is strongly skewed towards males (Schroder 1981), because males are sexually active throughout their whole spawning lifetime, whereas females are only sexually active until they have laid all of their eggs. Males must compete with other males to gain and maintain close access to females. The intensity of this competition is likely exaggerated because the total lifetime reproductive effort of Pacific salmon males occurs over a single short period of time. Selection has probably favoured high aggression levels and decreased the probability that males will abandon all competitions for access to females.

The strong territorial behaviour exhibited by males that

are courting females can be related to the necessity for males to gain close access to individual females prior to spawning. Fertilization is external and female nest sites are usually in open areas, creating an opportunity for numerous males to participate in the spawning act (e. g. Jones and King 1952; Hanson and Smith 1967; Campbell 1977; Jonsson and Hindar 1982; Gross 1985; Jonsson 1985). Males which hold the position closest to the female (dominant position) immediately prior to spawning usually fertilize the large majority of eggs laid (Schroder 1982; Chebanov et al. 1983; Maekawa and Onozato 1986). The benefits to males of winning competitions for close access to females are clear. The benefits of maintaining this position for some time (territoriality), appear to be derived from the spawning behaviour of females. Salmon females lay their eggs in a series of closely situated nests (usually three in kokanee). Spawning events are brief (seconds), and may be separated by hours to days. To ensure they are present at the time of spawning, males must defend their dominant positions for a protracted period.

Numerous field studies have documented size as a factor in male intrasexual competition (Hanson and Smith 1967; Hartman 1969; McCart 1970; Campbell 1977). In the experiments here reported, on average, a 10% difference in length more than tripled the chances that large males would prevail over small males when vying for access to females. Small males attempt to reduce their losses by becoming sneaks to spawning pairs. By

contrast with females, prior access did not override the effects of size in males. While as little as four hours previous residence conferred a large advantage to equal sized competitors, the effect was largely negated when immigrant males were larger. However, because female attractiveness to males increases as they near spawning (Schroder 1982; Hutching and Myers 1985; pers. obs.), prior access probably allows males to maintain their position relative to the female during brief pulses of exaggerated female attractiveness.

Comparison of spawning territoriality in males and females

The expression of territoriality differs markedly between the sexes. Males temporarily defend (hours to days) access to particular females and the areas they occupy whereas females attempt to defend their territories (nest sites) until death. The difference in behaviour can be related to the potential for males to fertilize many more eggs than a single female can produce. Having spawned with a female, a male has the option of remaining with the female and defending the developing embryos or of leaving to search for additional mates. The cost to males of leaving their already protected embryos are small in comparison to the potential gains of mating with additional females. The presence over a period of time of numerous sexually active females makes it likely that departing males will encounter other sexually active females. In addition, males which dominate the competition for access to one female

are likely to possess physical and/or behavioural characteristics (size, aggression) which enhance their chances of gaining access to other females.

The different weighting of the effects of size and prior residence in intrasexual competition in males and females can also be related to the different reproductive strategies of the sexes. Females invest a large amount of energy in relatively few eggs, which they deposit in closely situated nests and subsequently defend until they are displaced or die. Loss of a territory by a female that is as yet unspawned means, at the least, searching and competing for a new nest site, further limiting the energy available for nest construction and protection; at the most, it means leaving developing progeny undefended, and at risk of nest superimposition by other females (Jones 1959; McNeil 1964; van den Berghe 1984). In contrast, males invest little in their offspring. They neither protect the female from other females, nor remain with a female to protect the nest. Males spread their reproductive risk by attempting to mate with many females over the course of the spawning season. The costs of losing individual contests are far greater for females than for males. Thus females are expected, and observed, to be much more reluctant to relinquish their positions than males when faced with similar pressures.

The difference in expression of aggressive behaviours between males and females may have evolved in response to the

reproductive needs of each sex. In males, where size is a major factor in determining the outcome of intrasexual competition, body displays form a large part of the behavioural repertoire. In females, where prior residence appears to decide the outcome of most intrasexual interactions, displays form only a small part of aggressive behaviours. The propensity to display may be exaggerated in males because they can afford to lose individual competitions, and may reduce the risk of injury by responding to and transmitting displays. Because the costs of losing individual competitions are great in females, particularly those which have already commenced spawning, territorial females are less likely than males to respond to displays or threats.

The salmonid mating system is more complex than that previously suggested. Both sexes express territoriality, although in different forms and for different lengths of time. The differences between sexes in territoriality, expressions of aggressive behaviour and factors which determine the outcome of intrasexual competitions appear to have evolved in response to different portfolios of energy investment. The determinants of the amounts of energy investment are probably related to the clumped distribution of necessary resources, and the available reproductive options.

CHAPTER 2

FEMALE MATE CHOICE IN SALMON

Introduction

Mate choice describes all instances in which differential mating success in one sex is due to preferences exhibited by the opposite sex (Searcy 1982; Halliday 1983). Females are generally considered to be more selective of mates than males because they are limited in the number of eggs they can produce and the number of young they can raise. Males are often limited only by the number of females they can inseminate (Darwin 1871; Bateman 1948; Orians 1969; Trivers 1972). Therefore, numerous situations exist where it pays males to be indiscriminate by comparison with females.

Female mate choice can depend on a variety of factors, for some of which the reproductive gains through discriminating choice are readily apparent and for others of which they are not. The choice of mates on the basis of the resources they hold (territories), the nuptial gifts they present, and the parental ability they indicate (e. g. courtship feeding), can lead to increased reproductive success for selective females (see Searcy 1982 for review). In mating systems where males invest only their gametes in their progeny, as in salmon, immediate benefits of female mate choice are not obvious (see Bradbury and Gibson 1983). It has been argued that such choice

may be based on physical and/or behavioural characteristics which reflect the genetic fitness of potential mates (e. g. Borgia 1979; Thornhill and Alcock 1983).

Competition among males for access to females can limit the choices available to females (e. g. Davies and Halliday 1979; Cox 1981; Diamond 1981). However, even where restricted by male competition, females may exert some control over which individuals they mate with (Davies and Halliday 1977; Fairchild 1981; Cox 1981; Halliday 1983).

In the semelparous Pacific salmon, females are territorial of nest sites and males compete for access to females and the areas surrounding them (Chapter 1). The outcome of male intrasexual competition depends largely on the relative sizes of competing males (Hanson and Smith 1967; Chapter 1), and not, apparently, on the behaviour of females. While females are often restricted in the direct choice of males, there is evidence to suggest that they prefer to spawn with large males. Hanson and Smith (1967) and Hankin and McKelvey (1985) have observed that Pacific salmon females attack small males more frequently than they attack large males. McCart (1970) and Schroder (1981) have documented that females accompanied by males larger than themselves spawn more rapidly than females accompanied by males smaller than themselves.

In this chapter, I experimentally examine the spawning rate

of kokanee females accompanied by males of different sizes, to test the hypothesis that females vary their rate of spawning dependent on the size of courting males.

Methods

Ten territorial, ripe, 'medium' sized females (20.5 to 21.0 cm fork length) of known weight were placed in each of two 4 by 4 m adjacent experimental arenas. To one arena 10 'small' males (17.0 to 19.0 cm fork length) were added; to the other 10 'large' males (22.0 to 25.1 cm). The fish were left together for 18 hours, after which all were removed and the females weighed. This procedure was repeated six times, alternating the size group of males presented between adjacent arenas to control for possible differences in spawning rate associated with the different arenas (of which there was no difference). The data on female weight loss (egg deposition) were used to test the hypothesis that females accompanied by males larger than themselves spawned a greater number of eggs (*i. e.* lost more weight) over the 18 hour period than females accompanied by males smaller than themselves.

The experiment was conducted in the Meadow Creek spawning channel at the north end of Kootenay Lake, during September 1984. The females were carefully selected from over 1,000 examined. To commence each trial, 30 females were selected from a collection of anesthetized (MS-22) females, weighed and

individually tagged (2 cm Floy dart tags). These females were allowed to recover from the anesthetic for at least one hour, while being kept in 1.5 m square screen holding chambers in the stream. At 17:00 hours, the females were randomly divided into two groups of 15, released into the two experimental arenas and allowed to establish territories overnight. To minimize differences among females in readiness to spawn, ten territorial females were identified at 900 hours on the following morning, and the 5 excess females removed (females readily spawn only if they have established nest sites). The remaining ten females were then left undisturbed until 17:00 hours. At this time, ten tagged males of one of two size groups ('large' and 'small') were introduced into the arena and allowed to remain with the females for 18 hours. Prior to the completion of each trial, the position of each male relative to the females was recorded ('dominant', 'competitor', 'sneak', 'alone'). After this, all females were seined from the arena, anesthetized and weighed. The weight of each female at the end of each trial was subtracted from its initial weight to determine total female weight loss.

The data on female weight loss were examined by two methods: first by assuming the behaviour of each female was independent of the behaviour of all other females they were held with (Mann Whitney U test) and; second, by assuming non-independence of female spawning behaviour both within and between arenas (Wilcoxon signed rank matched pair test). In

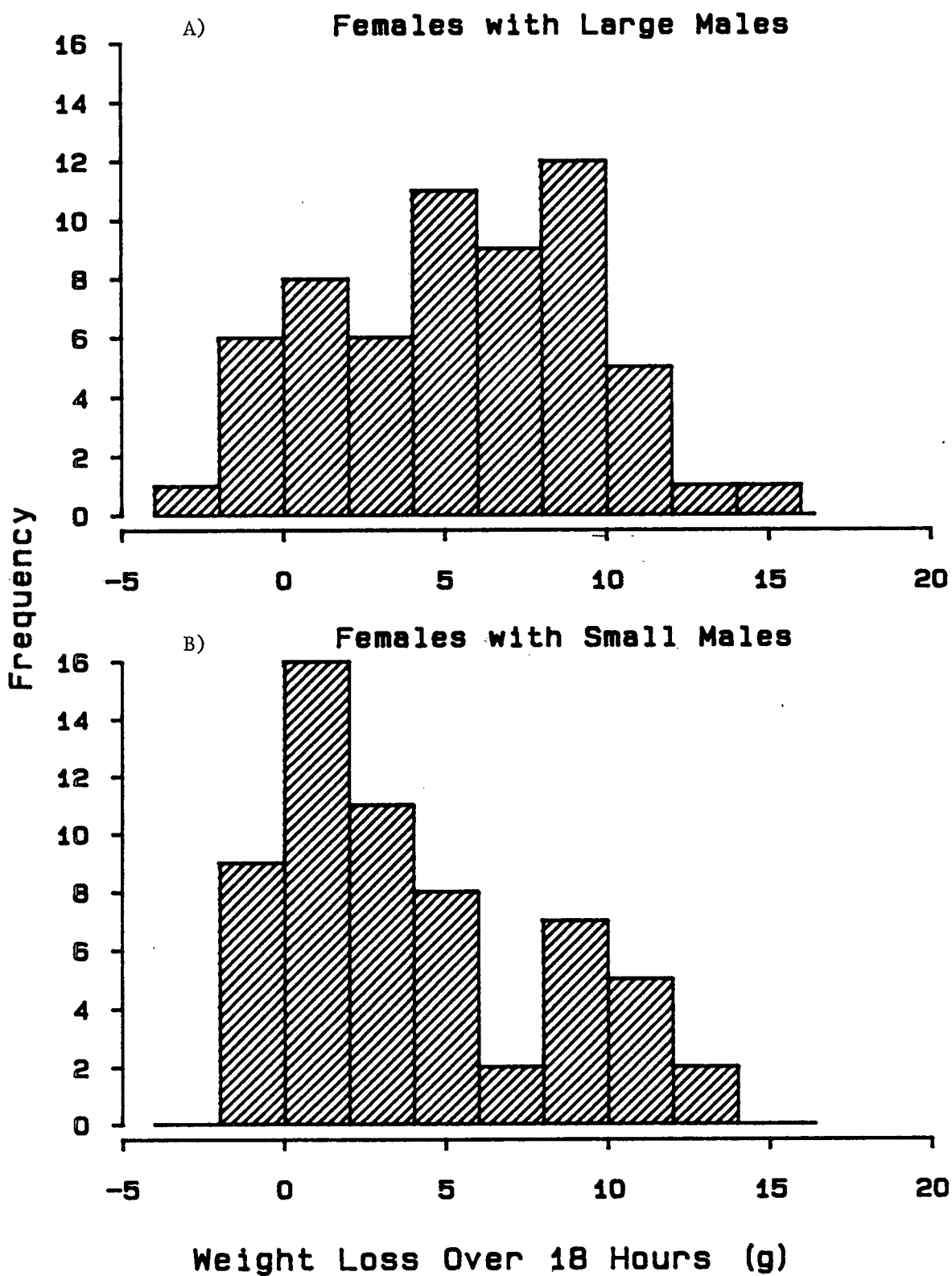
this latter test, the weight loss of all females within an arena was summed and the total weight lost by females accompanied by small males per trial was subtracted from the total weight lost by females accompanied by large males in the adjacent arena. This methodology controlled for possible differences between trials due to climatic conditions, by deriving single scores for groups of females run at the same time.

To determine if female weight loss was related to egg loss, subjective scores of female body cavity distension were recorded for each female. The seven scores ranged from 0 to 30, at intervals of 5 (0 = very distended (full of eggs); 30 = not distended (no eggs left in body cavity)). These subjective scores were compared to the weight loss measurements to determine if there was a relationship between the weight lost by individual females and their body cavity distension.

Results

Female kokanee accompanied by large males over an 18 hour period lost more weight than females accompanied by small males ($p < 0.05$; Fig. 15). On average, females accompanied by large males lost 5.3 g (0.5SE) and females accompanied by small males lost 3.8g (0.5SE), a difference corresponding to approximately 10% of the weight of the egg mass of a medium sized female. In all 6 trials, females accompanied by males which were larger than themselves lost more weight in total than females

Figure 15. The weight loss by females accompanied by (A) 'large' males and (B) 'small' males.



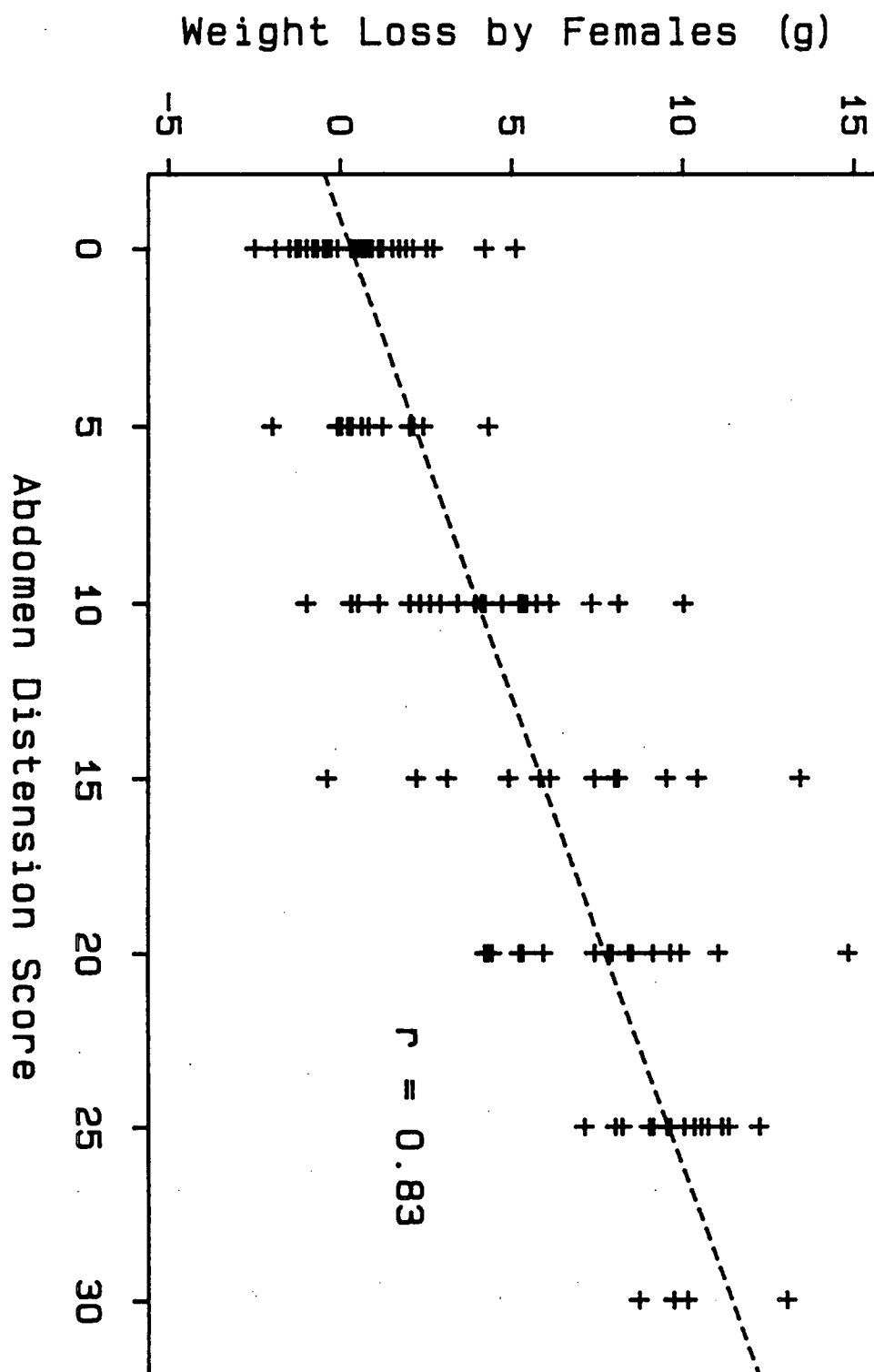
accompanied by males smaller than themselves, independent of the arena occupied (mean difference in weight loss of ten females = $14.95 + 3.84SE$ g; $p < 0.05$).

Some females gained weight between the two weighings within a trial, suggesting measurement error, probably arising from sampling in the field under variable weather conditions and from taking wet weights of females. It is probable that this sampling error was equal between groups.

Female weight loss was related to egg loss. Subjective scores of female body cavity distension were strongly related to the weight lost by each female ($p < 0.001$; Fig. 16). Analysis of body distension data showed that females accompanied by small males had more distended abdomens at the end of the period (closer to the zero score which indicates no egg loss) than females accompanied by large males (Mann Whitney U test; $p < 0.05$).

The difference in weight loss between the groups of females was not accounted for by a significant difference in the number of females attended by males in each treatment. Forty-nine of 60 and 44 of 60 females were attended by large and small males, respectively, at the end of the 18 hour trial (Chi squared contingency test; $p > 0.25$).

Figure 16. The relationship between subjective scores of female body cavity distension (0 = fully distended; 30 = empty) and weight loss.



Discussion

Evidence of female preference for large males

Previous experimental studies on female mate choice in salmon have demonstrated that females vary their rate of spawning depending on the size of the accompanying male. McCart (1970) demonstrated that sockeye females paired with (large) sockeye males spawned much faster than sockeye females accompanied by (small) kokanee males (see also Chapter 5). Schroder (1981) demonstrated that chum salmon females accompanied by males larger than themselves spawned more rapidly than females paired with males smaller than themselves.

Female preference for relatively large males has also been indicated in studies of female intersexual aggression. Salmon females have been shown to attack males smaller than themselves more often than they attack males larger than themselves (Hanson and Smith 1967; Hankin and McKelvey 1985). However, the attacked males in these studies probably occupied subordinate positions in male hierarchies, and female aggression may have been directed towards subordinate males, and not necessarily towards small males, per se. In either case, aggression may not reflect female choice. This behaviour may be an attempt to limit spawning interference by males, or it may simply result from a case of mistaken identity; subordinate males often adopt "female" colour patterns (Schroder 1981; pers. obs.) and

females are aggressive towards other females (Chapter 1). There is no evidence to suggest that females aggressively drive off small males when no other males are present.

In this study, kokanee females accompanied by males larger than themselves lost weight at a greater rate than females accompanied by males smaller than themselves. This is additional evidence that females vary their rate of spawning depending on the size of the accompanying male, because female weight loss was directly attributable to egg loss (Fig. 16), and egg loss was probably related to spawning behaviour. Female intrasexual competition can cause egg loss (pers. obs.), but this does not appear to account for the differences observed here. The density of females in the arenas was not great, minimizing aggressive interactions among females.

Female salmon appear to vary their rate of spawning depending on the size (relative to themselves) of the accompanying male, and not on behavioural characteristics associated with size. Schroder (1981) demonstrated that there were no significant differences in spawning behaviour between relatively large and small chum salmon males which could account for the difference he observed in female spawning rate. Similarly, I found that there was no significant difference in the total number of females attended by large and small males that could account for the observed differences in weight loss.

Schroder (1981) suggested that females affect mate choice by eliciting continued competition among males when they are accompanied by males smaller than themselves, doing so by slowing their spawning rate and thus increasing the chance that small incumbent males will be displaced by larger males. The probability that a small male will be displaced increases with time for three reasons: first, there is great and continued competition for access to females (e. g. Hanson and Smith 1967; Schroder 1981); second, large females attract large males (Chapter 3) and; finally, size is a major factor in male intrasexual competition in salmon, largely outweighing advantages accrued through prior access (Chapter 1).

Possible adaptive significance of female mate choice

Female preference for large males in salmon is probably not related to any immediate benefits associated with size in males. Males provide neither protection nor resources to the females they accompany or to their progeny. Fertilization efficiency, in the absence of competitors, appears unaffected by male size in salmon (McCart 1970; Hutching and Myers 1985).

Females may achieve long term benefits through preference for large males if size is a heritable character, because large size confers an advantage in male and female intrasexual spawning competition (Chapter 1) and at other times in the life history (e. g. Foerster 1968; Healey 1982; West and Larkin

1987). The existence of significant additive genetic variation for growth in salmonids (Ricker 1981; Kinghorn 1983) suggests that mate selection based on size may result in increased fitness of the progeny.

While the reasons females prefer large males are unclear, it is probable that this preference is not free of costs. Females appear to increase the risks of reproductive failure through their discrimination against small males. Pacific salmon females have only limited and finite energy reserves to devote to reproduction. Their energy reserves are divided among the needs of maintaining bodily functions, finding a nest site, constructing and spawning in several adjacent nests, and defending the nest site from other females before and after spawning. It seems probable that by delaying spawning, a female increases the costs of nest defense before spawning completion, and thus decreases the energy available for later nest defense, at the same time increasing the risk of failing to complete spawning, either because of displacement by other females or death.

In conclusion, female kokanee appear to vary their rate of spawning depending on the size of the courting male, spawning more readily with large males. On average, large males will spend less time with individual females than small males and hence will have more time and energy to mate with additional females. Coupled with the advantage of size in intrasexual

competition, female mate choice may have a significant effect on male mating success, increasing the disparity between small and large males within populations.

CHAPTER 3

MALE MATE CHOICE DEPENDENT ON MALE SIZE IN SALMON

Introduction

Mate choice and intrasexual competition are major components of sexual selection. The outcome of intrasexual competition is usually decided by the relative strengths of the competitors, which can often be unambiguously measured by their relative size (e. g. Kodric-Brown 1977; Howard and Kluge 1985; Barlow et al. 1986; McLain and Boromisa 1987). In contrast, mate choice is usually considered to be independent of the physical characteristics of the sex making the choice; criteria of choice such as mate size, dominance and parental care ability are usually not considered dependent on the characteristics of those selecting mates in empirical studies of mate choice (see Searcy 1982; Halliday 1983). Mate choice based on inbreeding avoidance is a rare example of choice dependent on relative characters between the sexes (e. g. Bateson 1983; Smith and Ayasse 1987).

The number of mates available to individuals often differs among members of a population because of the effects of intrasexual competition (e. g. Le Boeuf 1974; Howard 1978; Davies and Halliday 1979; Downhower et al. 1983; McLain and Boromisa 1987). While there is much evidence to suggest that such competition can lead to the evolution of alternative

strategies for seeking mates (e. g. Howard 1978; Davies and Halliday 1979; Rubenstein 1980; Dunbar 1982; Dominey 1984; Gross 1985), there is little evidence to suggest it can lead to the evolution of varying strategies of mate preference (what mates are preferred). Where there are immediate selective advantages associated with discriminating choice, all individuals, independent of their relative strength, are usually assumed to prefer the same potential mates. However, intrasexual competition can cause the expected variance in reproductive success to differ among members of the sex in question if they mated at random with females available to them. For example, if the strongest individuals have the widest range of potential mates (by virtue of their competitive superiority and/or preference by the opposite sex; e. g. Hanson and Smith 1967; Le Boeuf 1974; Burley 1977; Cox 1981) then the variance in the expected reproductive success of these individuals if they mated at random is likely to be greater than that of the weakest individuals. Simply, the strongest individuals could potentially mate with the highest and lowest quality mates whereas the weakest individuals are usually limited to the lowest quality mates. Consequently, the strongest individuals within a sex may be expected to be more selective of mates, having more to gain through such selectivity. Thus, selection might be expected to favour mate choice strategies that are based not only on the absolute characters of potential mates but also on the relative strength of the choosing individual.

Previous work on male choice in fishes, including salmon, suggests that males, independent of size, prefer the largest of available females, probably because of the strong relationship between female size and fecundity (Hanson and Smith 1967; McCart 1970; Jonsson and Hindar 1982; Downhower and Brown 1981; Rowland 1982; Loiselle 1982; Sargent et al. 1986; Berglund et al. 1986). However, there is considerable evidence to suggest the range of available mates increases with male size in fishes because of the effects of size in male intrasexual competition (Hanson and Smith 1967; Kodric-Brown 1977; Fricke 1980; Thresher and Moyer 1983; Downhower et al. 1983) and female preference for large and/or competitively superior males (Schroder 1981; Downhower et al. 1983; Berglund et al. 1986). Therefore, we might expect to see variable mate choice strategies dependent on male size in fishes.

In a series of five experiments, I tested whether kokanee males (which spawn separately from sockeye) select females based on their absolute size or on their size relative to that of the male. If male choice has evolved in response to the variance in mate quality of available females rather than to the variance in mate quality of all females, male selectivity should increase with increasing male size in salmon.

Methods

Male choice was examined in two separate kokanee populations in south eastern British Columbia: Meadow Creek, tributary to Kootenay Lake and Pass Creek, tributary to Arrow Lake. These populations provided a large size range of spawning kokanee. Males and females were broadly categorized into three size groups: small (19-27 cm, all measurements are of fork length); medium (28-40 cm); and large (41-52 cm). In four experiments (A,B,C and D) males of one or two size groups were presented with a choice of two territorial but different sized females. The sizes of males and females used varied among experiments. A fifth experiment (E) examined the effect of male competition on preference by the smallest males. Small males were given a choice between either a small female or a large female accompanied by a large male. Experiments A and B were conducted at Meadow Creek and the rest were conducted at Pass Creek.

Estimates of mean fecundities of females used were derived from a regression of egg number on female fork length for Kootenay Lake kokanee ($\text{Log (egg number)} = 3.09 \text{ Log (fork length)} - 1.75$, $n=68$, $R = 90.5$, $p<0.001$; Ministry of Environment, Province of British Columbia, unpublished data). The relationship of egg number and female fork length has not been measured in Pass Creek kokanee, but was assumed to be similar to the relationship between fecundity and size in the nearby (<100

km) Kootenay Lake kokanee populations.

All experiments were conducted in the spawning streams in two 4 x 4 m experimental arenas constructed of chicken wire in areas of good spawning gravel and water flow. The arenas were enclosed within a larger pen to limit interactions of test fish with free-swimming fish in the creeks. The arenas were large relative to female spawning requirements (Tautz 1977), minimizing possible differences in territory quality between females. Painted white rocks were placed in each arena to delineate a 1 m grid.

Females used in the experiments were chosen to minimize differences in their spawning readiness, a factor in male choice (Schroder 1981; Hutchings and Myers 1985). Only females which displayed territorial defense of nest sites in the arenas were used in the experiments. They were selected by placing 2-4 females of each of two size groups in the arenas on the night before a test. Most established territories overnight and commenced nest construction. In the morning, one territorial female of each size group was selected and the others were released. During the experiments, the number of digging bouts (nest construction movements) performed by each of the two females in the arena was recorded to monitor possible differences in female activity. A female digging bout consists of a rapid series of body flexures each culminating in the scraping of the tail over a small length of substrate as the

female moves slightly upstream. After each digging bout, the female moves or drifts downstream to her original position and usually surveys her nest ('probing'; McCart 1969; Tautz and Groot 1975) before commencing another digging bout (see McCart 1969 for a detailed description of the digging behaviour of O. nerka).

Males to be tested were seined from the stream immediately before the tests. Capture and transport of males appeared to have minimal effect on male behaviour, as most showed an immediate and continued interest in the females after their introduction into the arenas.

For male choice trials, a single male was introduced into an arena with two territorial females and allowed to become oriented for 10 minutes. Behaviour relative to each female was then recorded during two five minute observation periods separated by a seven minute interval. At the completion of each trial, males were removed from the arenas, their fork lengths measured and then they were released. Male choice did not differ between the five minute observation periods and the results were combined for analyses.

To quantify male preference, time spent near the females ('nearness time') and the number of male 'courtship displays' directed toward each female were recorded. Nearness time was defined as the time a male spent within 25 cm of a female, plus

the time it was oriented to the female when at distances from 25 cm to 1 m. A male was considered 'oriented' to a female when its head was pointed toward the female or when the male reacted to female movements when lateral or slightly upstream of the female. If the male went farther than 1m from the female, timing was recommenced when the male approached to within 25 cm. The timing criterion was derived from numerous observations that male salmon usually remain within 1 m while courting females (Hanson and Smith 1967; Gross 1985; Chapter 1). The male was required to approach within 25 cm to reduce subjectivity in timing 'interest'. The 'nearness time' rule was modified slightly for the competition experiment (E). Because the presence of a large male often restricted close access to the large female, the requirement that the male must approach within 25 cm for timing to be commenced was dropped and all time oriented to the female when within 1m was recorded. The courtship displays recorded were 'approaches' (including quivers), 'crossovers' and 'digs' (McCart 1969; Tautz and Groot 1975). Digging bouts by males have not previously been considered as courtship displays in O. nerka but rather as 'displacement activities' (McCart 1969). However, I do not agree with this interpretation. Since male digging (of the type recorded; see Chapter 1) is a behaviour expressed only when with females, I believe it is appropriate to class it as a courtship display, in the same manner that the other displays performed solely in the presence of females are classed as courtship displays. Male digging is an infrequent behaviour (<3% of total

behaviours) and its inclusion as a courtship behaviour did not affect the outcome of any statistical tests. The frequencies of all courtship displays were positively correlated and the data were combined for analyses.

Preference of a male for a female was expressed in two ways: first, as the difference between the total nearness time with the largest female and the total nearness time with the smallest female (Time Difference); and second, as the difference in the number of courtship displays performed with the largest and smallest females (Display Difference). Difference scores were calculated for each male because the time spent near one female and the number of displays directed to her were not independent of the time and displays recorded with the other female. Within male size groups, preference was tested using the Wilcoxon signed ranks test on the Time Difference data and the paired student's t-test on the Display Difference data. Between male size groups, preferences were compared using the Mann Whitney U-test for Time Difference data and a two sample t-test for Display difference data (all tests were two-tailed).

Results

The mean sizes and number of (1) female pairs presented and (2) males tested for each of the five experiments are given in Table 1. A summary of the Time Difference and Display Difference results for each experiment are presented in Figs. 17 and 18. The Time Difference and Display Difference data indicated the same preference by given sized males within each experiment. These preferences are summarized in Table 1.

A. Mate selection of small males when given a choice between small females of slightly different size

When given a choice between females slightly larger and slightly smaller than themselves, small kokanee males displayed more to and spent more time near the larger females ($p < 0.001$ for Time Difference; $p < 0.005$ for Display Difference). The degree of preference, measured in nearness time, for the largest female was positively correlated with the difference in size between the male and the smallest female ($r = 0.289$, $n = 116$, $p < 0.01$; Fig. 19). In contrast, there was no significant correlation between the preference of males and the difference between their own size and that of the largest females ($r = -0.092$; $p > 0.5$).

To examine further the relationship between male preference and the size of the male relative to the smallest female, males were split into two size groups. The size groups were

Table 4. The mean fork lengths (cm; +SE) and size groups of territorial females used and kokanee males tested, plus a summary of the choices made in five experiments.

Experiment	Mean FL of females					Mean FL of males				Choice
	smallest	largest		n1				n2		
A	19.5 +0.1	S(S)	22.3 +0.1	S(L)	36	21.2 +0.1	S	116	S(L)	
B	21.4 +0.2	S	29.2 +1.0	M	5	21.4 +0.2	S	21	none	
	21.7 +0.1	S	30.7 +0.7	M	6	31.7 +0.3	M	15	M	
C	26.6 +0.7	S	47.3 +0.6	L	5	27.0 +0.3	S	20	none	
	24.1 +1.5	S	46.3 +0.7	L	2	34.8 +0.1	M	10	L	
D	35.5 +0.3	M	47.6 +1.2	L	2	34.5 +0.5	M	10	none	
	35.1 +0.1	M	47.4 +0.8	L	3	46.6 +0.5	L	10	L	
E	24.4 +0.6	S	46.2 +0.3	L	4	26.4 +0.5	S	14	S	

S, M, and L correspond to Small, Medium and Large size groups. S(S) and S(L) correspond to the small and large subsets of the small size group in Experiment A only. n1 = the number of female pairs used; n2 = the number of males tested.

Figure 17. Male choice dependent on male size as indicated by the median (+ 95% CI) of the difference in time spent near a choice of females.

The symbols represent the choice of females (in white, on the outside of the vertical axes) presented to males (in black, at the median in the difference in time spent near the largest and smallest females of a choice over ten minutes of observation in an experimental arena). The size of the symbols are proportional to the mean sizes of the fish used. A scale of actual sizes appears in the upper left corner of the figure. Males were tested individually in all experiments, except E, where a large male was paired with the large female during the testing of small male choice. The presence of the large male is indicated on the outside of the right vertical axis. Male symbols to the right of the broken line indicate preference for the largest of a choice of females, those to the left indicate preference for the smallest of a choice of females. Note that in experiment A the smallest females, on the left, are only slightly smaller than the largest presented females, on the right (means of 19.5 versus 22.3 cm).

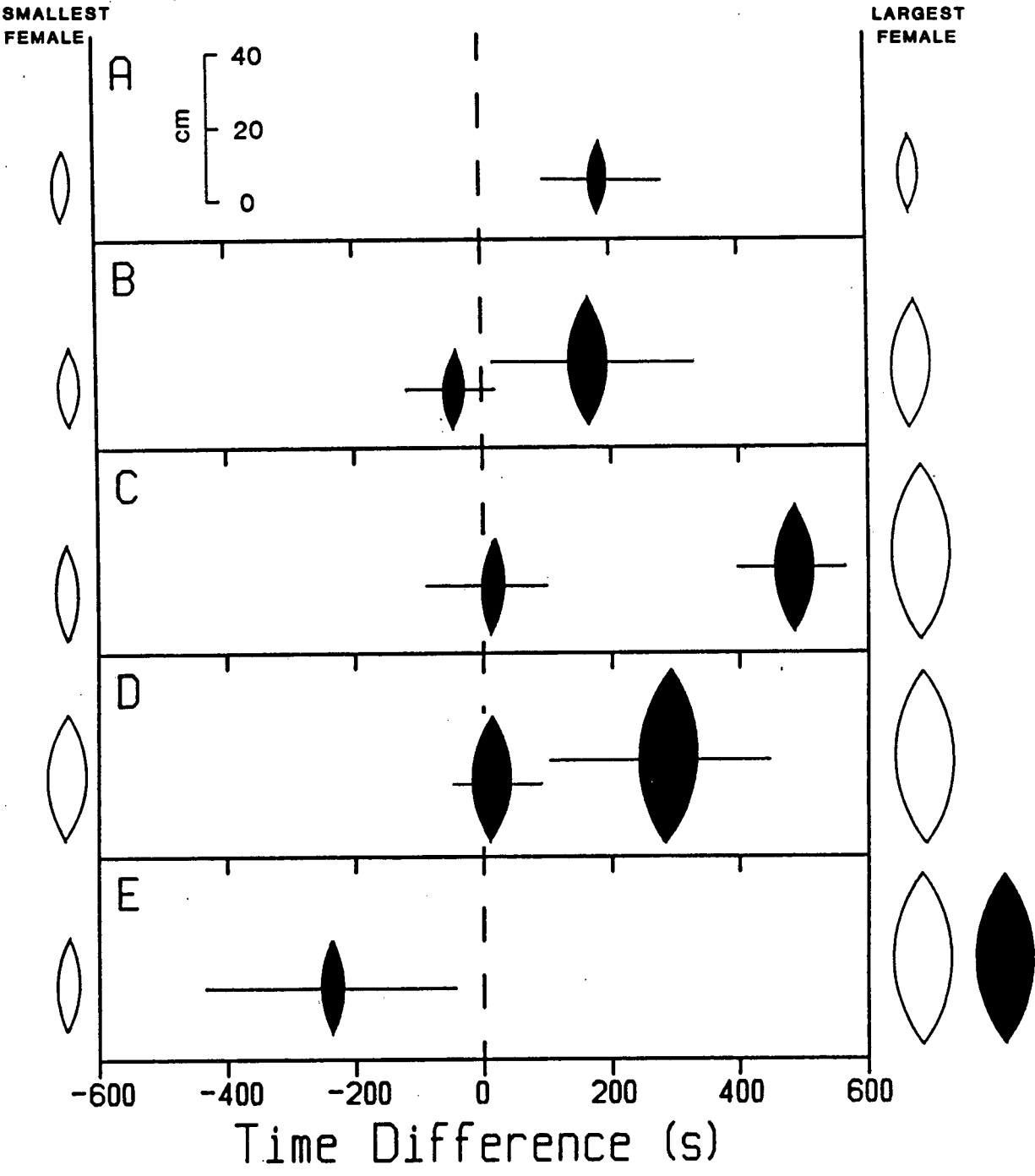


Figure 18. Male choice dependent on male size as indicated by the mean difference (+ 95% CI) in total courtship displays performed to a choice of two females in five separate experiments. See Fig. 17 for a description of symbols and layout of figure.

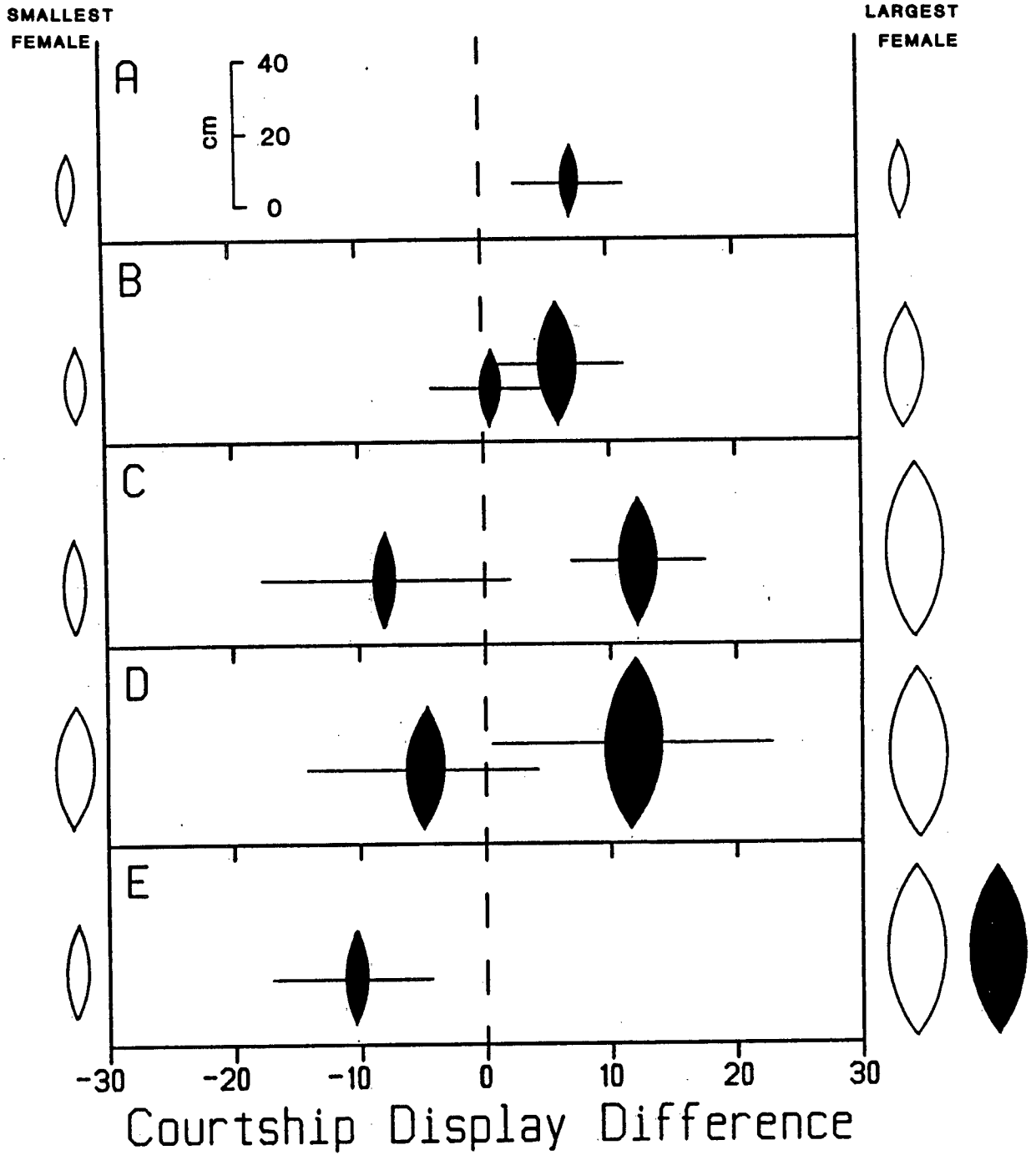
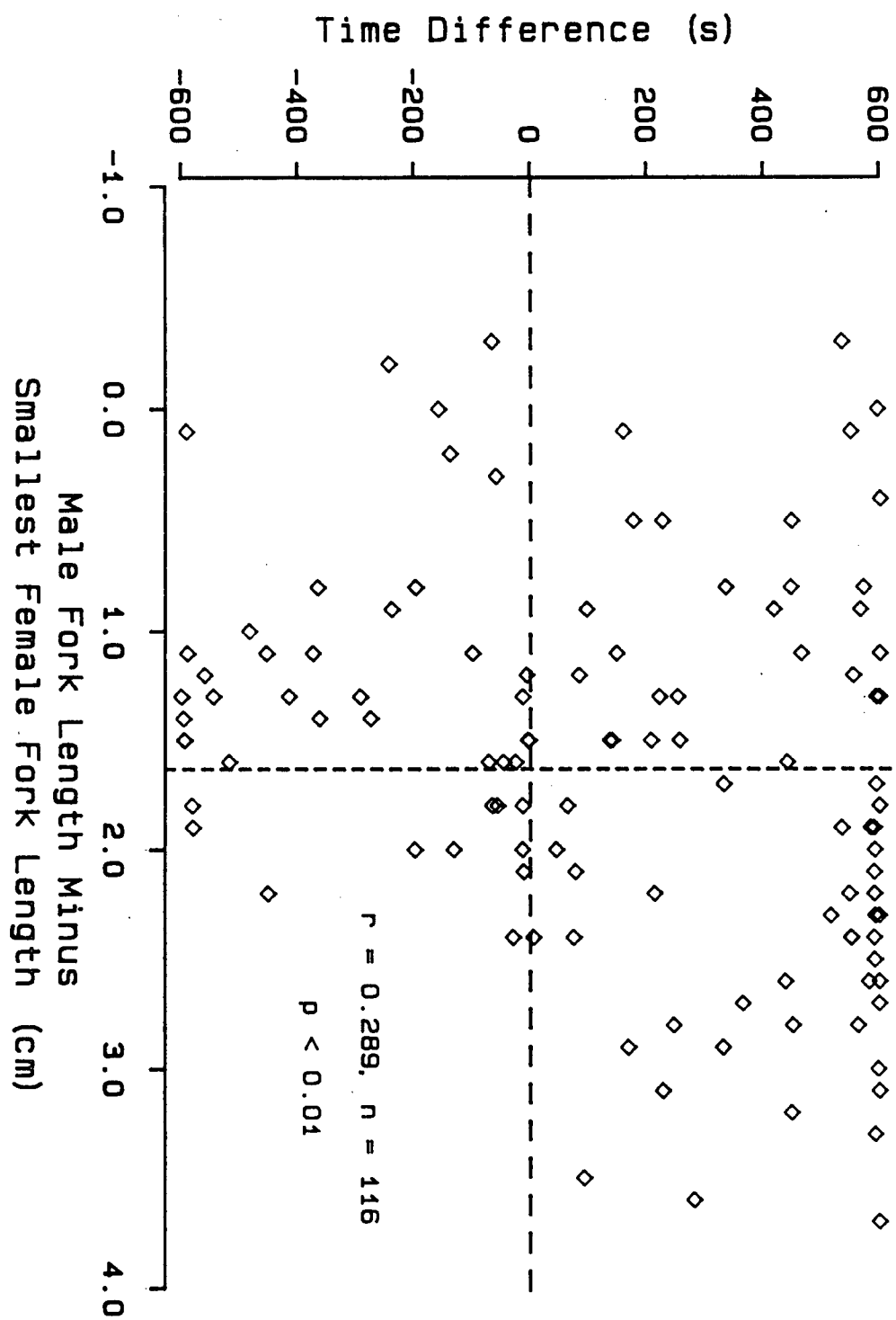


Figure 19. Male choice dependent on the size difference between the test male and the smallest presented female in experiment A.

Points to the right of the vertical broken line are those of males greater than the mean (1.63cm) size difference between test males and the smallest females. Points above the broken horizontal line indicate individual male preference of the largest of a presented pair of females. Note that relatively few males which were greater than 1.63cm larger than the smallest female spent the majority of their time near the smallest female (lower right quadrat).



determined by subtracting the size of the smallest female from the size of each male, and then by dividing the males into two groups (slightly smaller, slightly larger) at the mean (1.63 cm) of this size difference. The slightly larger males showed a strong preference for the largest female ($p < 0.0001$, $n = 54$, for Time (Fig. 19) and Display Differences). In contrast, the slightly smaller males showed no preference among the females presented ($p > 0.4$, $n = 62$ for Time and Display Differences).

B. Mate selection of small and medium sized males given a choice between small and medium females

Small kokanee males showed no preference between small and medium sized females in nearness time or courtship displays ($p > 0.3$ for Time Difference; $p > 0.05$ for Display Difference). In contrast, medium sized males showed a preference for medium females in both choice criteria ($p < 0.05$). The two sizes of males differed significantly in Time Difference ($p < 0.05$) but not in Display Difference ($p > 0.05$).

C. Mate selection of small and medium sized males given a choice between small and large females

Small kokanee males showed no preference between the small and large females in either nearness time or displays ($p > 0.6$ for Time Difference; $p > 0.1$ for Display Difference). In contrast, medium sized males showed a strong preference for large females

($p < 0.01$ for Time Difference; $p < 0.001$ for Display Difference). The preference of small and medium sized males differed significantly ($p < 0.001$ for Time Difference; $p < 0.01$ for Display Difference).

D. Mate selection of medium and large males when given a choice between medium and large females

Medium males showed no preference when given a choice between females of their own size and those much larger ($p > 0.9$ for Time Difference; $p > 0.2$ for Display Difference). In contrast, large males showed a strong preference for the large females ($p < 0.05$ for Time and Display Difference). The preferences of large and medium males were significantly different for both choice criteria ($p < 0.05$).

E. The effect of competition on small male choice

The smallest males in Pass Creek, which showed no preference between small and large females in the absence of competition, preferred the small females when the large female was attended by a large male ($p < 0.05$ for Time Difference; $p < 0.01$ for Display Difference).

Female response to the presentation of males

In all experiments, with the exception of Experiment A, there was no significant difference in the digging behaviour of females (Table 5). Discounting the exception, this suggests that the observed male choice can be related to the size of the presented females and not to different states of female activity. Since the rate of female digging is probably related to female responsiveness to males in salmon (McCart 1970; Schroder 1981; Chapter 5), these results suggest the different sizes of females were equally receptive to the presented males.

In experiment A the largest females dug significantly faster than the smallest females. The difference in the digging rate between females was opposite to that expected on the basis of female choice alone. In salmon, females dig faster when accompanied by males larger than themselves than when accompanied by males smaller than themselves (McCart 1970; Schroder 1981; Chapter 5). In experiment A, the test males were smaller than the large females and larger than the small females, suggesting that smaller females should have been more receptive than larger females to the presentation of the males (see Chapter 2). Thus, the greater rate of digging by the larger females may be related to greater male interest and not solely to female choice.

Table 5. The mean number and Difference (+SE) in digs performed by the smallest and largest females over ten minutes of observation in an experimental arena in five choice experiments.

Experiment	Mean number of digs by females				Difference		N	Male size		P
	smallest		largest					group		
A	3.86	S(S)	7.99	S(L)	-4.13	+0.71	116	S	<0.001	
B	0.05	S	0.00	M	0.05	+0.05	21	S	>0.3	
	1.47	S	2.33	M	-0.86	+1.60	15	M	>0.6	
C	3.85	S	0.05	L	3.80	+2.30	20	S	>0.1	
	1.50	S	1.10	L	0.40	+0.65	10	M	>0.5	
D	4.30	M	2.50	L	1.80	+1.92	10	M	>0.3	
	1.20	M	1.10	L	0.10	+1.09	10	L	>0.9	
E	4.00	S	2.43	L	1.57	+2.41	14	S	>0.5	

see Table 4 for letter designation.

Discussion

Evidence that male choice depends on male size

Previous studies on male choice in fishes suggest males respond to the absolute size of females, preferring the large, hence more fecund, females (Rowland 1982; Loiselle 1982; Downhower and Brown 1981; Sargent et al. 1986; Berglund et al. 1986). The results of this study show that the size of the female relative to that of the male can also be an important factor in male choice. Male preference for large females in kokanee increased with increasing male size. The smallest males did not discriminate between females of their own size and those substantially larger, even where there was a three fold difference in female fecundity. Medium sized males preferred large over small females but did not discriminate between females of their own size and those larger. Large males preferred large over medium sized females, indicating only large males find large females more attractive than all other females. (I did not attempt to demonstrate that large males prefer large females over small females. However, this preference was apparent and formed the basis of Experiment E). Had absolute size been the major factor in male choice all males would have been expected to prefer the largest females, yet this was clearly not the case.

The size dependent nature of male mate choice observed does

not appear to result from previous conditioning on the spawning grounds. Medium and large sized females are extremely rare in Meadow Creek (probably less than 1 in 1,000 females), whereas all sizes of males and females are common in Pass Creek (pers. obs.). This means that the small males tested in Meadow Creek were far less likely to have had previous experience with larger individuals than those tested in Pass Creek, yet the pattern of mate preference observed in the two streams was similar. Males of all sizes given a choice between females their own size and those larger demonstrated no consistent preference between available females (Figs. 17, 18 and 19).

The attractiveness of females to males is strongly influenced by female activity patterns (Schroder 1982). Non-territorial females are largely unattractive to males. In my experiments, I controlled for differences in territoriality between females (see methods) and monitored their nest construction behaviour (digging) to determine if there were fine scale differences in female activity which could account for the observed male preferences. Female digging rates were similar in most experiments (Table 2), which suggests that differences in female activity do not account for the male mate preferences observed. I reached the same conclusion in the examination of male choice between sockeye salmon and kokanee (Chapter 5). In that study, all sizes of males found the large, sockeye females attractive, independent of the varying sockeye female response, whereas only the smaller males found the small, kokanee females

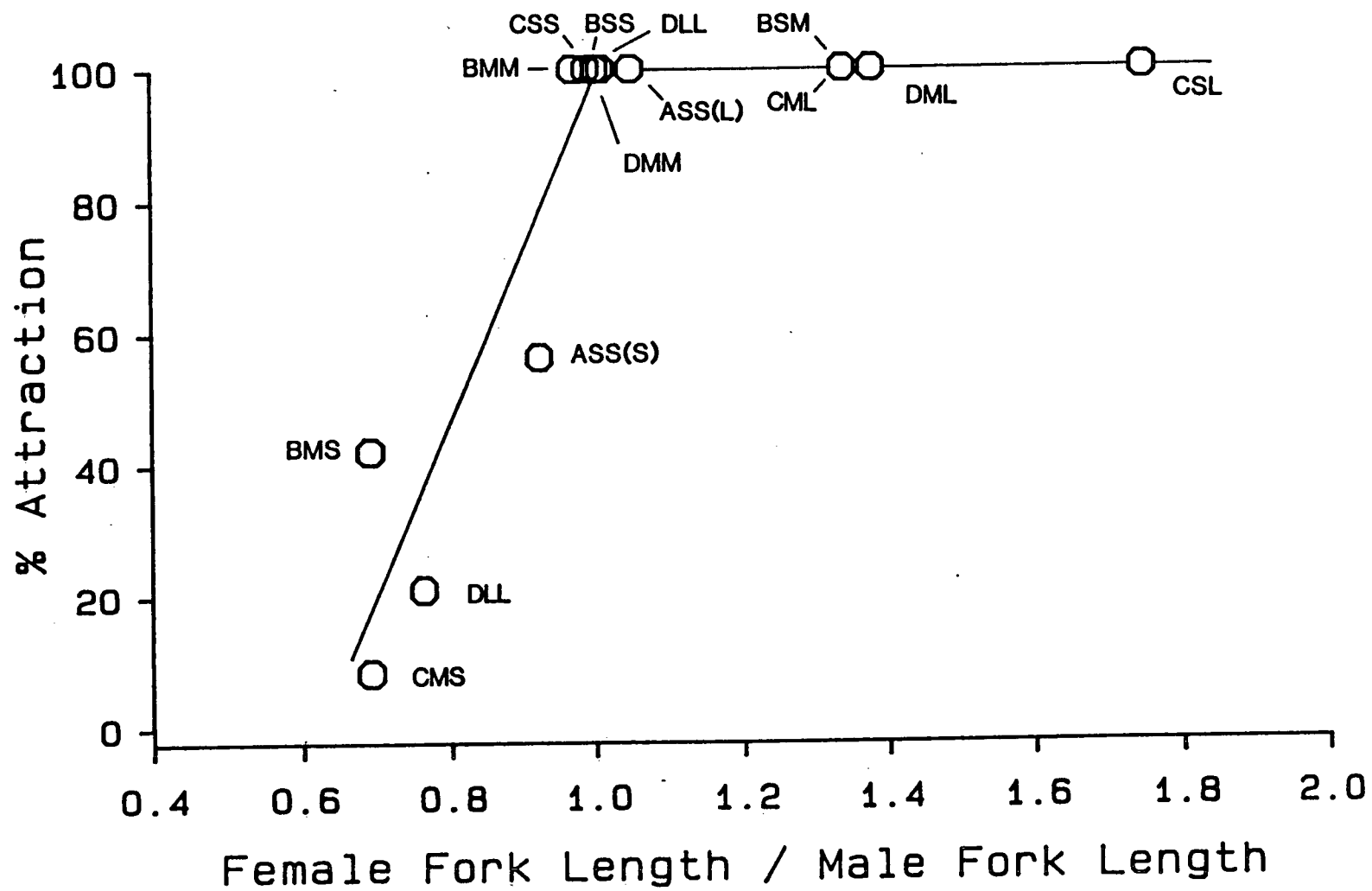
attractive. The discrimination against relatively small females, similar to that observed in the present study, was evident both when a choice of females was available and when it was not.

A measure of female attractiveness based on size of the female relative to the male may be generated by considering the preferred female in each choice experiment as 100% (fully) attractive. The degree of attractiveness of the non-preferred female may then be expressed by dividing the mean time spent near the non-preferred female by the mean time spent near the preferred female. The resulting measure is asymmetric. Females appear to increase in attractiveness to males as they increase in size up to that of the male (Fig. 20). Beyond the length of the male all females are equally attractive. This pattern was evident over the smallest (Experiment A) as well as the largest size ranges (Experiments C and D) of fishes examined. A similar pattern of attractiveness of females was evident in the examination of kokanee and sockeye male choice (Chapter 5). Note that this measure of attraction does not result from any relationship between fertilization efficiency and relative size of partners in salmonids. All males, independent of their size, are equally capable of successfully fertilizing the eggs of large females in the absence of competition (McCart 1970; Hutchings and Myers 1985; Maekawa and Onozato 1986).

This measure of attraction suggests male choice in salmon

Figure 20. Measure of attractiveness of females to males based on their relative sizes.

See text for method of calculation of % attraction. The combinations of letters correspond in order to: 1) the experiment (A, B, C, D); 2) the size group of males tested (S, M, L); and 3) the size group of the females in question (S, M, L, S(S), S(L)). See Table 1 for letter designation. Note that for each experiment and male size group tested there are two size groups of females for which % attraction is calculated. The line through the points was fitted by eye.



involves a variation of decisions suggested by 'threshold' models of mate choice (Janetos 1980; Wittenberger 1983). For each male, females increase in attractiveness with increasing size until they reach a threshold in attractiveness at the male's own size. The interesting feature of male choice in salmon is that the threshold level varies dependent on male size and hence the selection pressure for increased female size generated by male choice will be lower than predicted in models of mate selection based on absolute size or relative size within the sex being selected (e. g. Lande 1981; Kirkpatrick 1982; Seger 1985; Heisler 1985). As long as there are small males in salmon populations small females will have at least some males which find them fully attractive.

Possible adaptive significance of size dependent male mate choice

The rapid increase in the attractiveness of females with increasing female size (which are smaller than a male in size) corresponds to the increase in reproductive potential with size in females. Reproductive potential increases with size in female salmonids because of the strong relationship between body size and fecundity, egg size (Wallace and Aasjord 1984), parental care (van den Berghe and Gross 1984), and competitive ability (Chapter 1). Females smaller than a male are usually available for mating on the spawning grounds because they tend to be courted by smaller, displaceable males (Hanson and Smith

1967; McCart 1970; Campbell 1977; Jonsson and Hindar 1982). That males prefer the larger females when given a choice between females smaller than themselves and those similar to their own size, suggests that selection favours males that take advantage of the greater reproductive potential of larger females.

The plateau in attractiveness of females larger than a male does not correspond to the strong positive relationship between female size and reproductive potential. However, females are not equally available to all males on the spawning grounds (see references above). The larger a female is than a male the lower the probability that a male will successfully court her. The availability of relatively large females decreases with increasing female size for two reasons. First, relatively large females attract relatively large males, which possess a strong advantage in competition for access to females. Second, females accompanied by males which are smaller than themselves take a longer time to spawn than when accompanied by males of their own size or larger (McCart 1970; Schroder 1981; Chapters 2 and 5). This female behaviour increases the time for larger males to find large females and displace smaller males (Schroder 1981; Chapter 2). Once displaced, males may leave to search for other females, or they may become 'sneaks' to the spawning pair. As 'sneaks' they usually fertilize only a small proportion of the female's eggs (Schroder 1981; Chebanov et al. 1983; Maekawa and Onozato 1986). Therefore, the plateau in female attractiveness may have evolved as a result of a trade off between increasing

reproductive potential with size in females and their decreasing availability.

It is well known that the magnitude of variation in the quality of mates is an important factor in the evolution of varying strategies of mate choice both between sexes and between species (Trivers 1972; Parker 1983). Even where there is limited parental investment by one sex (usually males), if the variation in mate quality in the opposite sex is great, mate choice may evolve (Parker 1983). In salmon, males invest little in their offspring but there is great variability in female quality. The evidence presented here suggests that male choice in salmon has evolved in response to variation in available female quality rather than the variance in absolute female quality as is often considered in empirical studies of mate choice (see Searcy 1982; Halliday 1983). Male selectivity increases with increasing male size in salmon, as does the range in size of potential mates. The smallest males are the least selective, having the narrowest range of potential mates, whereas the largest males are the most selective, having the widest range of potential mates.

The pattern of association of males and females on the spawning grounds

The evidence that male mate preference is dependent on male size is consistent with two patterns of association between male

and female salmon on the spawning grounds. First, it is common in salmon for the number of males around females to increase with increasing female size (Hanson and Smith 1967; McCart 1970; Campbell 1977; Jonsson and Hindar 1982; Sargent et al. 1986). Previous studies have suggested this indicates all males prefer the largest females (McCart 1970; Sargent et al. 1986). My results suggest an alternative interpretation. Simply, that as female size increases, the size range (and number) of males which find these females fully attractive also increases. Small females are fully attractive to only the smallest males, whereas large females are fully attractive to all males. Therefore, these results predict large females should attract more males, in accordance with the pattern observed in nature, even though large females are actually preferred over all other females only by large males.

Second, in salmon the sexes often pair assortatively by size (Hanson and Smith 1967; McCart 1970; Campbell 1977; Jonsson and Hindar 1982). My results suggest a degree of assortative mating by size is expected through male choice dependent on male size. Small males are equally likely to mate with females their own size and larger when given a choice, whereas large males are unlikely to mate with females smaller than themselves. Assortative mating by size is further augmented by male intrasexual competition. Once a large male has paired with a large female, access by smaller males is restricted, increasing the probability that small males will mate with females nearer

their own size. The results of experiment E support this interpretation. Small males demonstrated no preference between small and large females in the absence of competitors but preferred small females when large females were accompanied by a large males. Female choice and female intrasexual competition also likely contribute to assortative mating in salmon (Schroder 1981; Jonsson and Hindar 1982; Chapters 1, 2 and 5).

Comparison of male choice in salmon and other fishes

Size dependent male mate preferences have not been documented in studies on fishes, although it is strongly suggested in cichlids (Barlow 1968; McKaye 1986). I believe there are two reasons for this. First, to my knowledge, the question has not previously been experimentally addressed. Second, the mating system of fishes previously experimentally examined are similar to each other and different from that of salmon. In mottled sculpins, Cottus bairdi, three-spined sticklebacks, Gasterosteus aculeatus, and pupfish, Cyprinodon macularius californiensis, the males establish and defend territories which females approach for spawning. Males preferentially court the largest females. Courtship is brief, and females leave the territory immediately after spawning (Downhower and Brown 1981; Rowland 1982; Loiselle 1982; Sargent et al. 1986). Similarly, in pipefishes (Family Syngnathidae), females approach males on their small homeranges (Gronell 1984) and males preferentially select the larger of approaching

females with which they spawn after a relatively brief courtship period (Berglund et al. 1986). In salmon, females are territorial and males usually approach females for spawning. Courtship is extended, often for days, and while males will leave females after a single spawning most appear to remain with the female until she has completed her spawning (approximately 2-4 spawnings in kokanee). Therefore while preference for the largest female may result in immediate reproductive success in sticklebacks, sculpins, pupfish and pipefish, the same is not true in salmon, where extended courtship and direct competition for access to females increase the probability that small males will ultimately be displaced when in pursuit of the largest females.

Choice dependent on individual ability to obtain mates (size) appears advantageous in the semelparous Pacific salmon mating system, where time and energy are extremely limited, rapidly diminishing resources (see van den Berghe and Gross 1986). If male choice were dependent on female absolute size (i. e. comparisons among females, independent of male size), all males would seek out the largest available females ('best of n' strategy). In doing so, all but the largest males would face the risk of learning through costly experience of the limited availability of large females. The costs of such searching would be inversely related to male size; the smallest males would end up searching the most before being displaced to the smallest females. By selecting mates dependent on their ability

to obtain mates (i. e. their own size), individual male salmon reduce their searching costs and thus increase the time and energy available to be spent in courtship and defense of access to females.

CHAPTER 4

A BIOCHEMICAL GENETIC COMPARISON OF SOCKEYE SALMON AND KOKANEE

Introduction

The Pacific salmon Oncorhynchus nerka occurs in two distinct forms, the anadromous sockeye salmon and the non-anadromous kokanee. Sockeye salmon typically spend their first year of life (sometimes longer) in a lake before migrating to the ocean whereas kokanee remain in a lake throughout their lifetime. Sockeye usually attain at least twice the length of kokanee at maturity, largely because of the difference in productivity between the marine and freshwater environments (Foerster 1968). Sockeye salmon and kokanee populations occur either together or separately (Ricker 1940; Nelson 1968a). Where they occur sympatrically, spawning usually occurs in separate localities and at different times (Ricker 1940; Nelson 1968a). In a few localities sockeye and kokanee spawn in the same place at the same time (Ricker 1940; Hanson and Smith 1967; McCart 1970).

It is generally accepted that kokanee have originated from sockeye on numerous independent occasions (Ricker 1940, 1959, 1972; Nelson 1968a; Behnke 1972). This conclusion is supported through an examination of the distribution of the two forms (Ricker 1940; Nelson 1968a) and by observations that non-anadromous populations of O. nerka have appeared after sockeye

salmon were introduced to lakes previously barren of the species (Ricker 1959, 1972; Scott 1984). It seems more probable that kokanee in Japan, Siberia, and western North America (including Vancouver Island) have arisen largely from the marine dispersal of sockeye salmon following the retreat of the Wisconsin continental ice masses, than that they have arisen solely through the freshwater dispersal of kokanee.

There is evidence of genetic divergence between sympatric sockeye and kokanee populations (Nelson 1968b; McCart 1970) and various mechanisms have been proposed to account for this. Selective pressures in freshwater and marine environments probably differ greatly, promoting genetic differentiation between the forms (Ricker 1940). Genetic differentiation is further promoted by the tendency of sympatric sockeye and kokanee to spawn in separate locations at different times, limiting gene flow between the forms (Ricker 1940). Where spawning is coincident, gene flow is probably greatly restricted through assortative mating by form, associated with the great size difference between mature sockeye and kokanee (Hanson and Smith 1967; McCart 1970; Foote and Larkin, in press). Sockeye males mate almost exclusively with sockeye females, whereas kokanee males mate either with kokanee females or attempt to fertilize the eggs of sockeye females by "sneaking".

In this study, the results of an electrophoretic comparison of sympatric and allopatric sockeye and kokanee populations in

British Columbia are used to address questions concerning the recent ancestry and genetic similarity of the two forms. If differentiation has been recent, sockeye and kokanee should be very similar genetically. If one or both forms have given rise to the other form on numerous occasions then sockeye and kokanee should be genetically interrelated rather than members of two distinct genetic lineages. Additionally, if kokanee have arisen in sympatry with sockeye, sympatric sockeye and kokanee may be expected to be genetically more similar to each other than they are to their respective forms in other lakes.

Sockeye and kokanee populations were sampled from throughout British Columbia, including three localities where the forms spawn sympatrically. Sympatric genetic differentiation would seem to be the least likely in localities where sockeye and kokanee spawn sympatrically because of the great opportunity for gene flow between the forms. Genetic differentiation in these localities would suggest that mechanisms in addition to segregation to different spawning grounds are important in the genetic differentiation of salmonid populations.

Methods

Kokanee and sockeye were each collected from 11 and 12 localities, respectively, in British Columbia (Fig. 21, Table 6). Five populations were sampled annually for two or three years. All samples, with the exceptions of those from Cultus and Cowichan lakes and Okanogan River, were collected with gaffs and small seines in streams where fish were spawning. Sockeye smolts were collected by trap in the outlet of Cultus Lake. Kokanee were captured with a mid-water trawl in Cowichan Lake. Electrophoretic data for the Okanogan River sockeye were taken from Utter et al. (1984). Where spawning populations were small (<10,000 fish), mainly moribund or freshly dead specimens were collected. Where sockeye and kokanee spawned sympatrically, they were distinguished by size; most sockeye were greater than 45 cm fork length and kokanee ranged from 16-28 cm. Jack sockeye (precocious males) were rare in the populations sampled and were greater than 30 cm fork length.

Heart, liver, eye and muscle tissues were collected from freshly killed fish, or rarely, from those recently dead as judged from redness of the gills. Samples were placed on ice immediately and frozen as quickly as possible, usually within 12 hours of collection, and stored at -40 C until assayed. Samples were assayed electrophoretically using standard extraction and gel techniques (e. g. May et al. 1979). The system of nomenclature suggested by Allendorf and Utter (1979) was used to

Figure 21. The location and form of O. nerka populations sampled for electrophoresis. Population numbers correspond to those in Table 6.

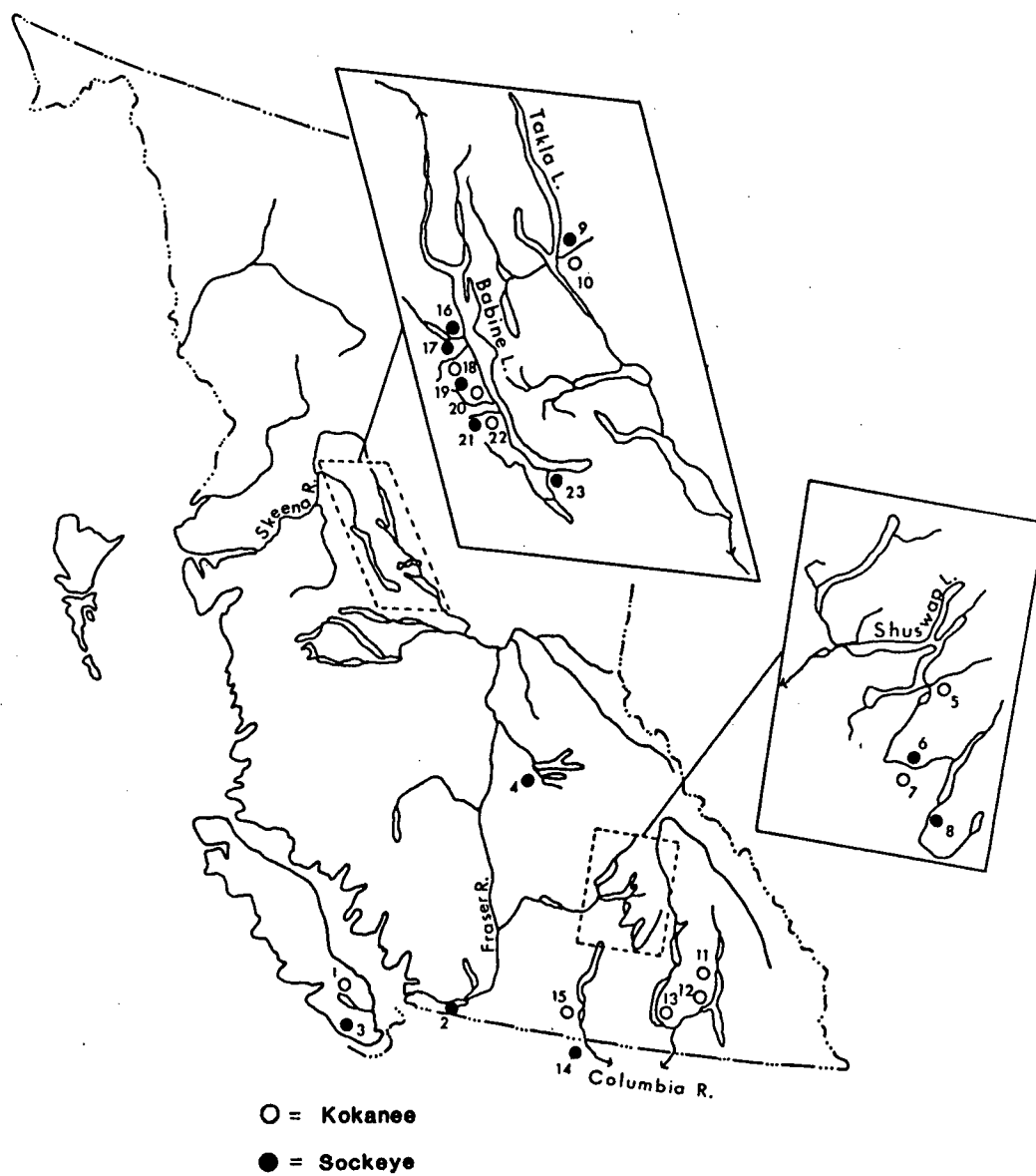


Table 6. Allele frequencies at polymorphic loci for sockeye and kokanee populations sampled in British Columbia

Site	Form	Yr	PGM-1 N (100)	PGM-2 N (100)	LDH-4 (100) (115) (85)	N	GL-2 (100)	N	ALAT (91) (100) (108) (95)	N
Coastal Populations										
1. Cowichan L.	K	85	0.460 150	0.840 150	1.000 0.000 0.000	150	-----	---	-----	---
2. Cultus L.	S	85	0.147 158	0.837 95	1.000 0.000 0.000	99	-----	---	-----	---
3. Chewhat L.	S	85	0.375 100	0.865 100	1.000 0.000 0.000	100	-----	---	-----	---
Upper Fraser River Populations										
4. Horsefly R.	S	85	0.624 93	0.805 100	1.000 0.000 0.000	100	0.995	96	0.330 0.569 0.000 0.101	94
5. Eagle R.	K	86	0.348 99	0.828 99	1.000 0.000 0.000	99	1.000	99	0.505 0.111 0.354 0.030	99
6. L. Shuswap R.	S	83	0.414 99	0.842 101	0.995 0.005 0.000	97	1.000	80	0.172 0.754 0.030 0.045	67
7.	K	83	0.132 76	0.842 76	0.987 0.006 0.006	77	1.000	78	0.355 0.158 0.480 0.007	99
	K	86	0.142 53	0.783 53	0.991 0.009 0.000	58	-----	---	0.336 0.052 0.586 0.026	58
8. M. Shuswap R.	S	86	0.583 144	0.870 142	0.993 0.007 0.000	145	1.000	141	0.132 0.688 0.066 0.115	144
9. Takla L.	K	82	0.357 77	0.903 77	1.000 0.000 0.000	76	-----	---	-----	---
	K	83	0.340 381	0.865 381	1.000 0.000 0.000	300	-----	---	-----	---
	K	85	0.367 124	0.846 123	1.000 0.000 0.000	124	0.992	119	0.721 0.119 0.000 0.160	122
10. Takla L.	S	83	0.467 83	0.837 83	1.000 0.000 0.000	79	-----	---	-----	---
	S	85	0.588 97	0.813 96	1.000 0.000 0.000	97	1.000	100	0.149 0.819 0.000 0.032	94
Columbia River Populations										
11. Meadow Cr.	K	83	0.586 151	0.870 151	0.993 0.003 0.003	151	-----	---	-----	---
12. Redfish Cr.	K	83	0.595 42	0.964 42	0.977 0.023 0.000	38	-----	---	-----	---
13. Arrow L.	K	85	0.575 100	0.910 100	1.000 0.000 0.000	98	0.995	100	0.360 0.615 0.000 0.025	100
14. Okanogan R.	S	--	0.493 71	0.782 71	1.000 0.000 0.000	72	1.000	62	0.285 0.590 0.007 0.000	72
15. Skaha L.	K	83	0.284 88	0.875 88	1.000 0.000 0.000	85	-----	---	-----	---
Skeena River Populations (Babine Lake)										
16. Fulton R.	S	85	0.158 291	0.776 290	0.973 0.017 0.010	293	-----	---	-----	---
17. Tachek Cr.	S	85	0.290 50	0.800 50	0.940 0.010 0.050	50	-----	---	-----	---
18.	K	85	0.238 103	0.607 103	0.861 0.000 0.139	102	1.000	35	0.500 0.390 0.000 0.110	41
19. Pierre Cr.	S	84	0.215 100	0.735 100	0.968 0.016 0.016	94	-----	---	-----	---
	S	85	0.202 94	0.766 94	0.953 0.010 0.036	92	0.989	91	0.529 0.382 0.006 0.082	85
20. Pierre Cr.	K	84	0.270 111	0.698 111	0.850 0.000 0.150	110	-----	---	-----	---
	K	85	0.228 114	0.702 114	0.870 0.004 0.126	115	0.980	74	0.649 0.299 0.000 0.052	77
21. Twain Cr.	K	85	0.239 92	0.678 101	0.865 0.005 0.130	95	-----	---	-----	---
22.	S	85	0.214 103	0.830 103	0.971 0.010 0.019	103	-----	---	-----	---
23. Pinkut Cr.	S	85	0.231 193	0.725 193	0.972 0.005 0.025	198	-----	---	-----	---

designate loci and alleles (Table 7), the same nomenclature has been previously used for sockeye salmon populations (Grant et al. 1980; Utter et al. 1984; Wilmot and Burger 1985). A few samples were assayed at 24 loci but the majority were assayed at a subset of 4 or 8 loci known to be polymorphic in at least some sockeye and kokanee populations. All 27 samples were assayed at Pgm-1, Pgm-2, Ldh-4, and Aat-3 and 16 were also assayed at Ada-2, Pgi and Sdh. In addition, 12 of these samples were reassayed at Gl-2 and Alat (previously designated Gpt-2; this locus had been too difficult to score reliably until a new staining procedure was developed by P. Aebersold (Northwest and Alaska Fisheries Center, 2725 Montlake Boulevard East, Seattle, WA 98112, pers. comm. to C. C. Wood, Pacific Biological Station, Nanaimo, B.C.)).

Differences in genotype frequencies between years and among populations were tested by likelihood ratio (i. e., G-test, Sokal and Rohlf 1981) for individual loci and all loci considered simultaneously (using modified critical values for multiple comparisons). Genotype frequencies within populations were compared with those expected under Hardy-Weinberg equilibrium using the Chi-squared goodness-of-fit test. Allele frequencies at either three to five polymorphic loci, depending on the samples, were used to construct similarity phenograms using the unbiased genetic identity statistic (Nei 1978) and the unweighted pair group methods (Sneath and Sokal 1973).

Table 7. Enzymes and tissues used to investigate genetic variation in sockeye salmon and kokanee. Buffers used were (AC) an amine citrate buffer described by Clayton and Tretiak (1972), (RW) a Tris, citric acid, lithium hydroxide, and boric acid buffer described by Ridgway et. al. (1970), and (MF) a Tris, boric acid, EDTA buffer, described by Markert and Faulhaber (1965).

Enzyme	Tissue	Locus	Buffer
Aspartate aminotransferase	Eye	Aat-1,2	AC
Adenosine deaminase	Muscle	Ada-2	AC
Alanine aminotransferase	Muscle	Alat (Gpt-2)	MF
Peptitdase (glycyl leucine substrate)	Eye	Gl-2	MF
Lactate Dehydrogenase	Liver	Ldh-4	RW
Phosphoglucosomerase	Muscle	Pgi	RW
Phosphoglucomutase	Heart	Pgm-1	AC
Phosphoglucomutase	Muscle	Pgm-2	RW
Sorbitol dehydrogenase	Liver	Sdh	RW
Superoxide dismutase	Muscle	Sod	RW

Variation in allele frequencies (arcsine square-root transformed) was investigated using Method 3 of Henderson (1953) for the following ANOVA model:

$$Y_{ijklm} = u + F_i + D_j + F*D_{ij} + L_{jk} + S_{jkl} + e_{ijklm}$$

where: Y_{ijklm} is the transformed value of the individual observation of allelic frequency; u is the overall mean value; F_i is the fixed effect of life-history type ($i = 1-2$, sockeye or kokanee); D_j is the random effect due to drainage ($j = 1-4$, Columbia, Skeena, upper Fraser and Coastal - including Lower Fraser River and Vancouver Island); $F*D_{ij}$ is the effect of the interaction between type and drainage; L_{jk} is the random effect of lake within drainage; S_{jkl} is the random effect of spawning site within lake; and the error term e_{ijklm} , is the effect of annual variability within spawning sites.

The significance of differences in allele frequencies between sockeye and kokanee was examined by an F test of the "form" mean square divided by the "form-drainage" interaction, each with a single degree of freedom due to the unbalanced design. All other effects were considered random, and their individual contributions to the total phenotypic variance were estimated by division of the appropriate variance component by the sum of the drainage, type-drainage interaction, lake, site, and error variance components.

Allele frequency variation was also examined in a

completely nested gene diversity analysis (GDA) (Nei 1973; Chakraborty 1980). In this model, sockeye and kokanee spawning sympatrically were treated as different "forms" of O. nerka, with form nested within spawning sites. Deviations from allele frequencies expected under panmixia due to each level of population subdivision were measured using Chakraborty's (1980) GDA model:

$$H_T = H_W + H_Y + H_S + H_L + H_D + H_F$$

where: H_T is the total diversity among and within sites; H_W is the diversity within single samples; H_Y is the diversity among years within sites; H_F is the diversity between sockeye and kokanee within sites; H_S is the diversity among spawning sites within lakes; H_L is the diversity among lakes within drainages; and H_D is the diversity among drainages.

Results

Annual variation in allele frequencies

Five of the loci assayed were polymorphic in some of the kokanee and sockeye populations examined (Table 6). These were Pgm-1, Pgm-2, Ldh-4, Alat and Gl-2. The observed genotype frequencies did not differ significantly ($p > 0.05$) from those expected under Hardy-Weinberg equilibrium in any of the populations sampled. In addition, there were no significant differences in genotype frequencies over years at any of the

individual loci examined, or for all loci combined, for the three kokanee (Takla Lake; Pierre Creek, Babine Lake; Lower Shuswap River) and two sockeye (Takla Lake; Pierre Creek, Babine Lake) populations sampled repeatedly (Table 6). This suggests that the genetic structure of O. nerka populations is stable over relatively short time periods. Accordingly, the electrophoretic information over years within populations was pooled for most subsequent comparisons among populations.

Comparison of sympatric sockeye and kokanee in three lake systems

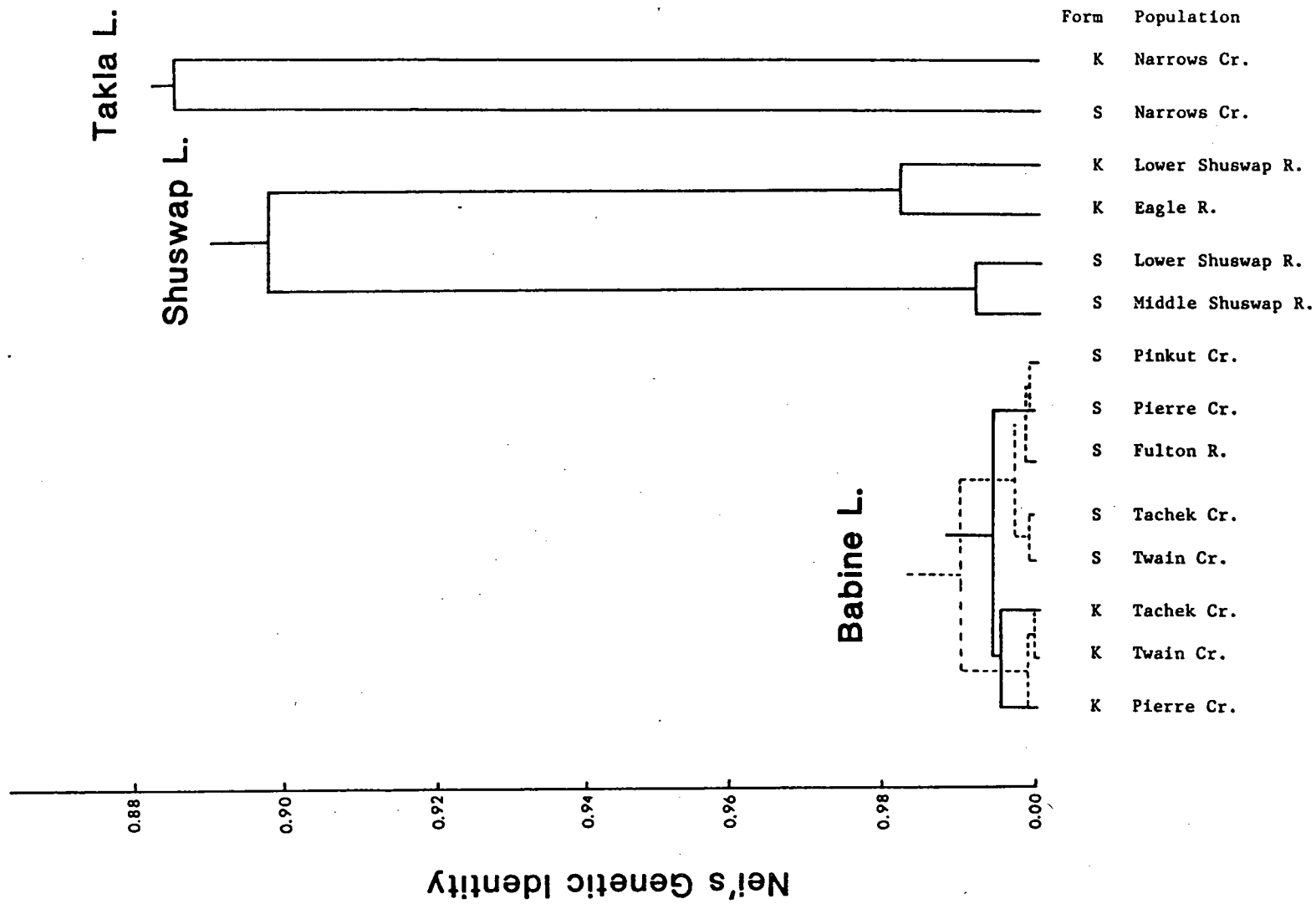
Sockeye from three streams in Babine Lake where sockeye spawn sympatrically with kokanee (Pierre, Twain and Tachek creeks) and from two larger systems where spawning kokanee are absent (Fulton River and Pinkut Creek) showed no evidence of genetic differentiation at any of the three polymorphic loci examined ($p > 0.05$). Similarly, there was no evidence of differentiation among the kokanee populations at any of the three to five polymorphic loci examined ($p > 0.05$). In contrast, there were significant differences between sockeye and kokanee in all systems where they spawn sympatrically ($p < 0.05$). In Twain and Tachek creeks, sockeye and kokanee differed significantly in genotype frequencies at Pgm-2 and Ldh-4, whereas in Pierre Creek differentiation was significant at only Ldh-4 (although the direction of difference at Pgm-2 was similar to that observed in the others). Thus, there were high

similarities within forms and consistent differences between forms across the Babine Lake spawning localities sampled (Fig. 22). Sockeye spawning in the presence of kokanee were no more similar to kokanee than were sockeye spawning in their absence.

Kokanee and sockeye were sampled from three localities in the Shuswap Lake system: the Middle Shuswap River where spawning kokanee are absent; the Lower Shuswap River where the forms spawn sympatrically and; Eagle River where the forms spawn sympatrically but sockeye are rare (and not sampled). Significant differences exist at Pgm-1 between the the Middle and Lower Shuswap River sockeye populations ($p < 0.05$). Similarly, significant differences exist at both Pgm-1 and Alat between the Lower Shuswap River and Eagle River kokanee populations ($p < 0.05$). However, there were greater differences between sockeye and kokanee than between populations within form (Fig. 22). The frequency of Pgm-1 100 were consistently higher, and those of Alat 91 and 108 consistently lower, in sockeye as compared to kokanee populations in the Shuswap Lake drainage ($p < 0.01$).

Sockeye and kokanee from Narrows Creek, Takla Lake, sampled over two and three years respectively, were consistently different at Pgm-1 ($p < 0.05$) and Alat ($p < 0.01$) (Alat was examined only in 1985). Narrows Creek kokanee expressed the Alat 91 allele in the highest frequency observed in this study whereas

Figure 22. Phenograms based on measurements of genetic similarity for each of the systems examined where sockeye and kokanee spawn sympatrically: Babine Lake; Shuswap Lake and; Takla Lake. Phenograms based on data taken from five polymorphic loci (all lakes) are drawn in solid lines, those based on three polymorphic loci only (Babine Lake) are drawn in broken lines.



sockeye had the highest observed frequency of Alat 100. As a result, genetic differentiation between forms in Takla Lake was greater than that for other sympatric sockeye and kokanee populations (Fig. 22).

In summary, there were significant and consistent genetic differences between sympatrically spawning sockeye salmon and kokanee in all systems examined. Within systems, the extent of genetic differentiation within forms was always less than that observed between forms, but the extent of this differentiation varied greatly between lakes. While sympatric sockeye and kokanee differed consistently in allele frequencies, they shared the same alleles at the loci examined. This indicates greater similarity between sympatric forms than that suggested through the use of Nei's genetic identity, which compares only differences in allele frequencies and not the presence or absence of alleles. For example, all sockeye and kokanee populations sampled from the Shuswap Lake system expressed the Alat 108 allele, which was largely absent from all other localities (Table 6). Similarly, all sockeye and kokanee populations sampled from Babine Lake expressed the Ldh-4 85 allele, also largely absent outside this system (Table 6; Withler 1985). Takla Lake sockeye and kokanee expressed the same allele compositions at the loci examined, although they displayed none unique to the system.

Overall comparison of sockeye and kokanee in British Columbia

O. nerka populations from across British Columbia cluster into two broad groups (Fig. 23). One cluster includes all sockeye and kokanee populations sampled from the upper Fraser and Columbia River watersheds (with the exception of Skaha Lake and Lower Shuswap River kokanee). The other cluster includes the sockeye and kokanee populations of Babine Lake (Skeena River system). The three coastal O. nerka populations examined are split between the two clusters, with Cultus Lake sockeye clustering closely with Babine Lake sockeye and Cowichan Lake kokanee, and Cheewat Lake sockeye clustering with upper Fraser and Columbia River O. nerka populations. There is no obvious separation among populations based on form (sockeye or kokanee). The broad grouping of Columbia and upper Fraser River O. nerka populations, coupled with the separation of the Skeena River populations (Babine Lake) and the splitting of coastal populations between the groups is very similar to that reported by Utter et al. (1984) in their extensive geographic examination of sockeye salmon at 50 loci.

The genetic relationship of sockeye and kokanee was investigated using analysis of variance on allele frequencies at three loci. There were no significant differences between forms in allele frequencies at Pgm-1, Pgm-2 or Ldh-4 alleles (Table 8). Differences among drainage systems and the interaction of drainage system and form accounted for most of the observed

Figure 23. Phenograms of the relationship among of sockeye salmon and kokanee populations based on measurements of genetic similarity at three polymorphic loci.

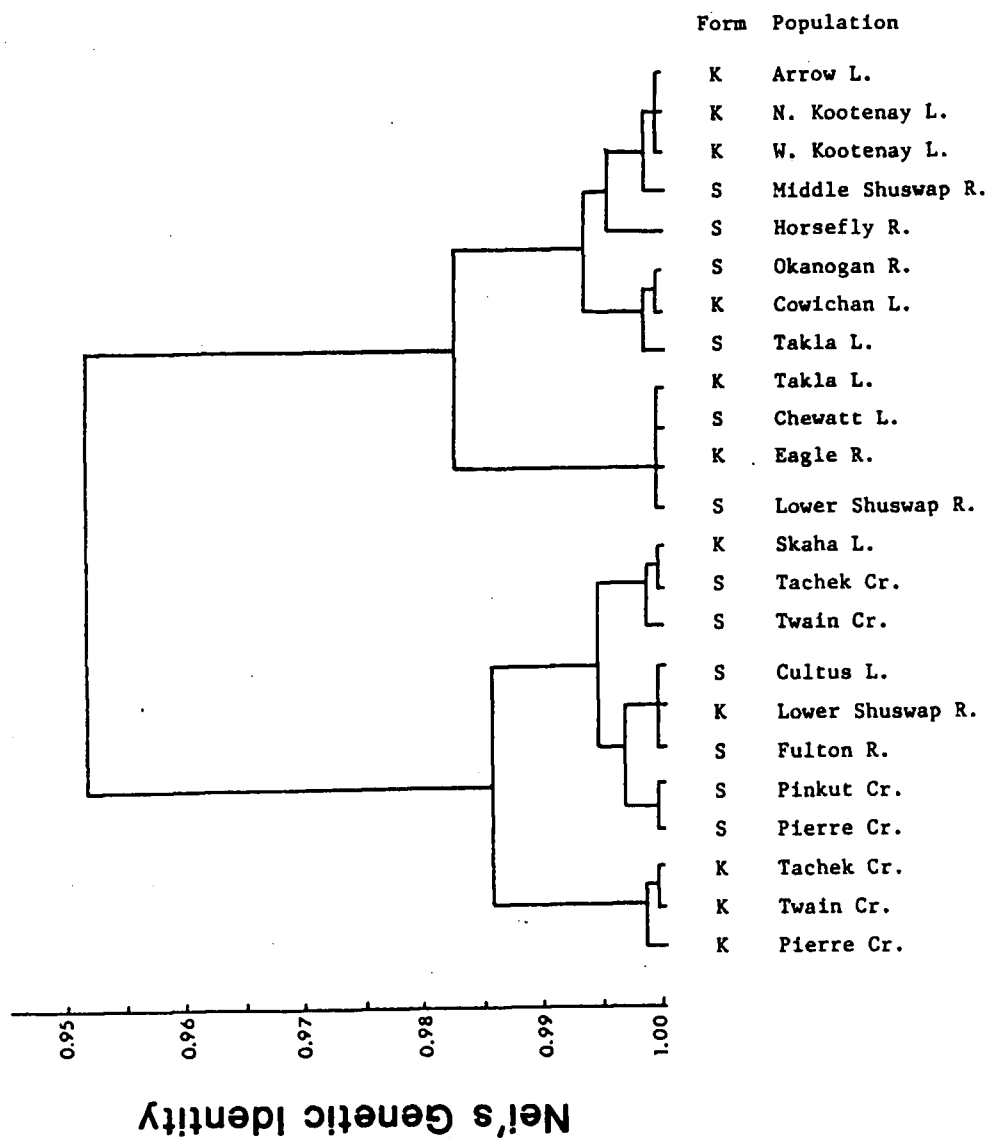


Table 8. Percentage variation in allele frequencies of 23 sockeye salmon and kokanee populations accounted for by sources of variation included in an ANOVA model.

Source	% of Total Variation				
	Pgm-1 100	Pgm-2 100	Ldh-4 100	115	85
error	5.31	18.26	1.87	8.91	2.35
(among years)					
sites	12.67	0.00	1.22	46.55	0.56
lakes	25.14	0.00	0.00	1.55	0.00
drainage	17.05	38.14	29.35	0.00	14.96
form * drainage	39.84	43.60	67.56	42.99	82.13
form	0.78	0.50	1.09	0.68	1.04

variance in allele frequencies. These results indicate that it is not possible to classify O. nerka populations as sockeye or kokanee solely from knowledge of the allele frequencies at the loci assayed, but classification might be possible given knowledge of the drainage system sampled. These conclusions are supported by the more limited data for Alat and G1-2, which also displayed no consistent differences between sockeye and kokanee.

Gene diversity analysis (Nei 1973) yielded similar results. On average, over 90% of the variation in allele frequencies at the three polymorphic loci assayed was due to variation within populations (Fig. 24). Differences among drainage systems were consistently the second greatest source of variation at each locus, followed usually by differences among lakes, between forms and among years (Table 9).

Discussion

The relationship of sockeye and kokanee

Sockeye and kokanee occur naturally in Japan, Kamchatka, Alaska, British Columbia (including Vancouver Island) and the northwestern United States (Nelson 1968a; Ricker 1972; Scott and Crossman 1973). It seems likely that sockeye originally colonized these diverse regions and subsequently gave rise to non-anadromous populations (kokanee) (Ricker 1940; Nelson 1968a).

Figure 24. Hierarchy used in gene diversity analysis of sockeye salmon and kokanee. Percentages in right column are the average proportions over three loci of total genetic variation occurring at different levels. Population numbers correspond to those in Table 6.

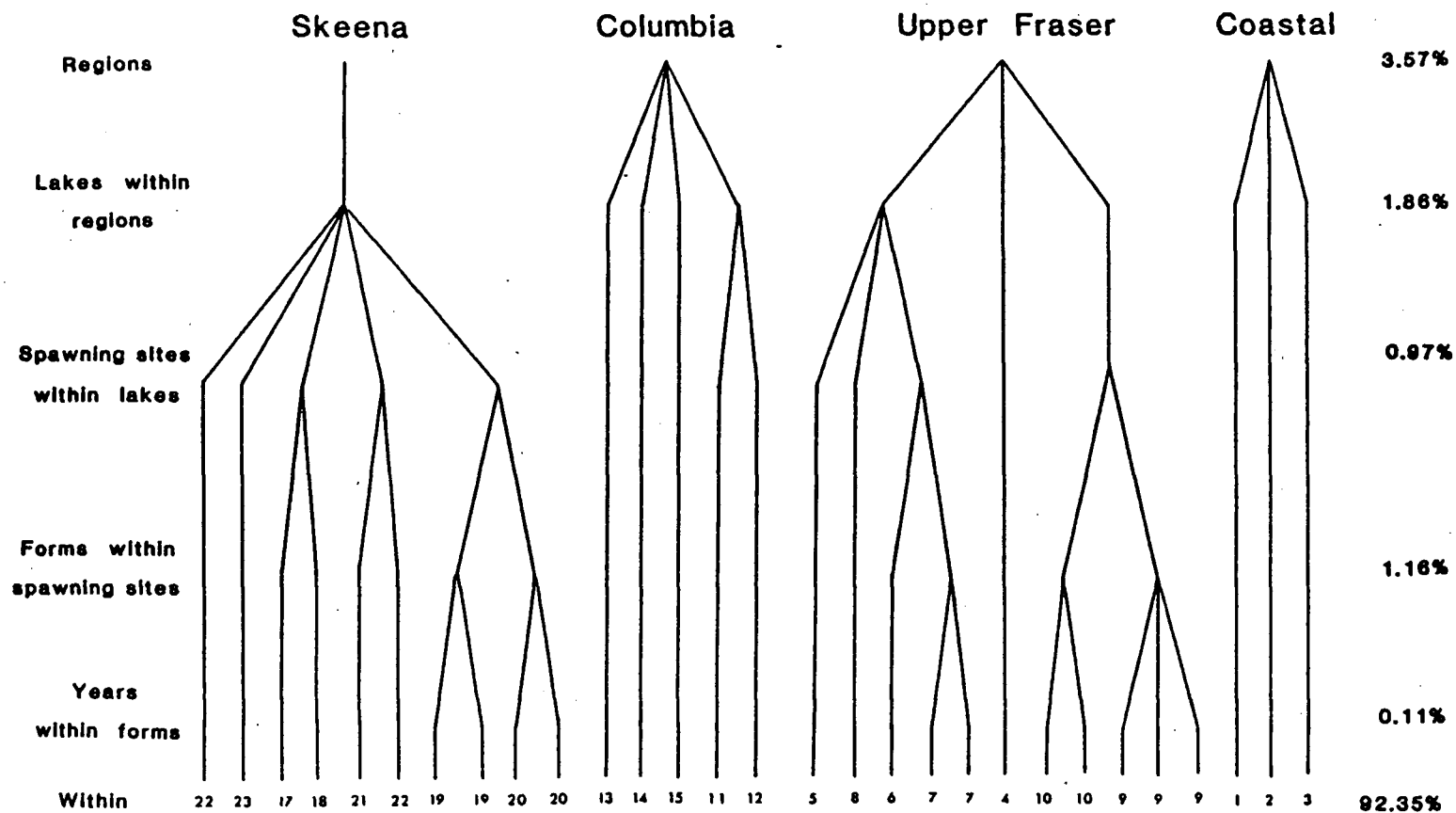


Table 9. . Percenatge distribution of electrophorectically detectable gene diversity at three polymorphic loci among 29 collections of sockeye salmon and kokanee.

Source of Variation	Relative Gene Diversity			Mean
	Pgm-1	Pgm-2	Ldh-4	
Within populations	89.35	96.10	96.13	92.35
Among years	0.12	0.09	0.02	0.11
Among forms	1.38	0.81	1.16	1.16
Among sites	1.55	0.20	0.44	0.97
Among lakes	3.07	0.40	0.04	1.86
Among drainages	4.52	2.39	2.22	3.57

The present study supports these conclusions regarding the polyphyletic relationship between sockeye salmon and kokanee. There were no consistent electrophoretic differences between sockeye and kokanee in British Columbia by which the forms could be separated. There were greater differences among O. nerka populations among drainages than there were between sockeye and kokanee. Therefore, it seems unlikely that the existing sockeye and kokanee populations in British Columbia are derived from separate genetic lineages.

The anadromous and non-anadromous forms of other salmonids also appear to have given rise to one another on numerous occasions throughout their range. Nordeng (1983) demonstrated that both anadromous and non-anadromous forms of Arctic char, Salvelinus alpinus, can produce anadromous and non-anadromous progeny, the propensity to do so depending on parental form and environmental conditions. Johnson (1980) compared the distribution of anadromous and non-anadromous stocks of arctic char, and concluded that one form gave rise to the other on numerous occasions throughout the species' range. Similarly, Osinov (1984) concluded that anadromous and non-anadromous forms of brown trout, Salmo trutta in U.S.S.R. were "interchangeable". Supporting this, Ryman (1983) demonstrated that anadromous and non-anadromous brown trout Salmo trutta from Sweden were not members of distinct genetic lineages. Allendorf (1975) found that anadromous (steelhead) and non-anadromous

rainbow trout populations, S. gairdneri, were genetically interrelated. Stahl (1987) demonstrated that non-anadromous and anadromous Atlantic salmon, S. salar, within broad geographic regions were genetically more similar to each other than they were to their respective forms between regions.

Genetic differentiation between sympatric sockeye and kokanee

Genetic differentiation among local populations of salmonids has been documented on numerous occasions in a variety of salmonid species (e. g. Vernon 1957; Frost 1965; Ryman et al. 1979; Ferguson and Mason 1981; Parkinson 1984; Osinov 1984; Wilmot and Burgner 1985; Crozier and Ferguson 1986; Hindar et al. 1986; Campton and Utter 1987). Such differentiation is commonly attributed to the virtual isolation among populations which results from accurate homing to separate spawning grounds (philopatry) (e. g. Vernon 1957; Hartman and Raleigh 1964; Frost 1965; Behnke 1972; Ryman et al. 1979; Crozier and Ferguson 1986), coupled with the effects of genetic drift (Allendorf and Phelps 1981; Campton and Utter 1987). However, genetic differences between sympatric sockeye and kokanee are difficult to explain solely on these grounds. Genetic differences exist between the forms even where they spawn predominantly in the same place at the same time, indicating isolation through homing to separate spawning areas cannot account for observed differences between forms. Because spawning populations of O. nerka at my study sites were usually large (>1,000 to

>500,000 individuals), differences between forms are not likely to have arisen from recent genetic drift, although historical bottleneck effects cannot be ruled out. It is improbable that the observed differences are due to sampling error or yearly variation as my sample sizes were large and replicated.

It is not yet clear how genetic differences between sympatrically spawning sockeye and kokanee originate or how they are maintained. McCart (1970) concluded that sockeye and kokanee spawning in the small tributaries to Babine Lake were part of the same polymorphic population. He noted that sockeye and kokanee intermixed on the spawning grounds and that kokanee males (like jack sockeye males) showed a strong propensity to act as "sneaks" to spawning sockeye pairs, suggesting that significant interbreeding occurred between the forms. McCart (1970) demonstrated kokanee males fertilized the eggs of sockeye females in the absence of competition and showed that the progeny of such crosses were fully viable in hatchery conditions. However, the present electrophoretic comparison of sockeye and kokanee clearly demonstrates genetic differentiation between forms in Babine Lake tributaries. Despite apparent interbreeding, there is an effective restriction in gene flow between sockeye and kokanee that indicates they do not constitute a single polymorphic population.

Possible sympatric origin of sockeye and kokanee

The observed genetic similarity between populations of sockeye and kokanee in Babine, Takla and Shuswap lakes strongly indicates that, in each case, one form has arisen from the other in sympatry. The plausibility of sympatric divergence is supported by knowledge of the biology of O. nerka. Native and introduced populations of sockeye salmon are known to have given rise to non-anadromous individuals (Ricker 1938, 1940, 1959, 1972; Smirnov 1959; Krokhin 1967; Krogius 1981) and in some cases self-sustaining populations (Ricker 1959; Scott 1984). Similarly, kokanee are known to be able to give rise to sockeye (Foerster 1947). However, there is no conclusive evidence that the genetic similarities observed between forms within lakes are the result sympatric divergence. Other mechanisms can be proposed to account for the patterns of similarity observed. The forms may have evolved in allopatry and subsequently introgressed and/or have been subjected to convergent selection pressures in sympatry. However, neither of these alternative hypotheses appears to be tenable. If introgression between the forms had occurred, one would expect to find greater genetic similarity between sockeye and kokanee where they spawn sympatrically than where they spawn in separate localities within the same lake because of the opportunity for continuing introgression. The extensive comparison of Babine Lake sockeye and kokanee spawning populations provides no evidence of such continuing introgression. Sockeye that spawn in the absence of

kokanee in Fulton River and Pinkut Creek were genetically indistinguishable from sockeye that spawn sympatrically with kokanee in Pierre, Twain and Tachek creeks. Similarly, in the Shuswap Lake system, sockeye that spawn sympatrically with kokanee in the Lower Shuswap River are genetically no more similar to kokanee than sockeye that spawn in the absence of kokanee in the Middle River system.

It seems even more improbable that convergent selection pressures within lakes could account for the observed genetic similarity of sympatric sockeye and kokanee, since alleles at the loci examined are generally considered to be neutral or nearly neutral to selection (e. g. Ryman 1983). Alternatively, if these alleles are not selectively neutral, and convergent selection pressures were responsible for the observed genetic similarity, one might expect O. nerka populations in neighbouring lakes to be genetically similar as well. Babine Lake, in the Skeena drainage, and Takla Lake, in the Fraser Drainage, are separated by a distance of less than 100 km and are morphometrically similar; they occur in the same climatic zone and have similar geological and colonization histories, and fish species compositions (Lindsey and McPhail 1986). The physical and biotic similarities between lakes should give rise to similar selective regimes and, in the absence of founder effects, sockeye and kokanee in the two lakes might be expected to be genetically and phenotypically similar. In fact, very substantial differences were found both in allele frequencies

and allele compositions among sockeye and kokanee populations in Takla and Babine lakes. Moreover, sympatric sockeye and kokanee in Takla Lake show greater differences in allele frequencies and gillraker counts (Nelson 1968b) than do those in Babine Lake. These results suggest that lacustrine selection pressures alone do not account for the genetic similarity observed between sympatric forms.

This study, together with previous studies of anadromous and non-anadromous O. nerka occurring in sympatry, suggests that genetically isolated populations of sockeye and kokanee have arisen in sympatry, probably on numerous occasions throughout the species' range. The sympatric origin of different forms followed by genetic divergence is theoretically possible (e. g. Maynard Smith 1966; Rosenzweig 1978; Pimm 1979; Rice 1984) but its occurrence in nature is extremely difficult to substantiate and widely disputed (Mayr 1970; Futuyma and Mayer 1980; Templeton 1981). The biology of O. nerka meets two critical requirements of models for sympatric speciation. First, the selective pressures experienced by anadromous and non-anadromous individuals are probably very different, and would be expected to promote the genetic divergence of the forms (Ricker 1940). Second, rather strict assortative mating by form would occur within a single generation of the sympatric origin of the forms because of the great size difference between them at maturity. Even within forms, assortative mating by size is conspicuous in wild populations (Hanson and Smith 1967; Chapter 3). Strong

assortative mating greatly facilitates genetic differentiation caused by selection (Maynard Smith 1966). Once differences of selective value have accrued, "hybrids" would likely have lower fitness than either "pure" sockeye or kokanee. Such selection can lead to the evolution of premating ethological isolating mechanisms (Maynard Smith 1966), which may partially account for the premating isolation observed between sockeye and kokanee in Babine Lake tributaries (Chapter 5). In Pierre Creek, kokanee males prefer to mate with kokanee females rather than with the larger, and more fecund, sockeye females.

In conclusion, recent work describing ecological, morphological and biochemical differentiation of sympatric forms in salmonids suggests that divergence in sympatry is possible and may be widespread (Johnson 1980; Savvaitova 1980; Balon 1980; Balon and Penczak 1980; Hindar et al. 1986). This study provides further evidence to support this hypothesis.

CHAPTER 5

AN EXPERIMENTAL EXAMINATION OF ASSORTATIVE MATING BETWEEN
SCKEYE SALMON AND KOKANEEIntroduction

Numerous theoretical models have examined the conditions under which sympatric speciation is possible (Maynard Smith 1966; Rosenzweig 1978; Pimm 1979; Rice 1984). A general tenet of these studies is that genetic differentiation can result when polymorphisms are maintained by disruptive selection. Such differentiation will probably lead to selection for reproductive isolation. Factors that promote an initial degree of assortative mating between forms greatly facilitate the process. However, while sympatric speciation is a possible outcome of disruptive selection, there is little empirical evidence of its occurrence in nature (Futuyma and Mayer 1980; West-Eberhard 1986).

The anadromy/non-anadromy polymorphism of salmonids exhibits many of the elements necessary for models of sympatric speciation. The polymorphism has a genetic basis (Neave 1944; Nordeng 1983), but one form can readily give rise to the other (Ricker 1972; Nordeng 1983; Scott 1984). Where the anadromous and non-anadromous forms spawn sympatrically, there is a high degree of assortative mating (Neave 1944; Hanson and Smith 1967; McCart 1970). Finally, the selective differences between the

marine and freshwater environments are probably extreme (Ricker 1940). In association with these factors, there is growing evidence of sympatric genetic divergence between anadromous and non-anadromous salmonids (Neave 1944; Nelson 1968b; McCart 1970; Nordeng 1983; Chapter 4)

The assortative mating observed between anadromous and non-anadromous salmonids may result from the phenotypic differences between the forms, most notably size (anadromous salmonids are usually much larger at maturity than non-anadromous individuals). Assortative mating by size has been documented in many animals, including salmon (e. g. Hanson and Smith 1967; Licht 1976; Davies and Halliday 1977; McLain 1982; Malmqvist 1983; Snead and Alcock 1985; Howard and Kluge 1985; McKaye 1986; McLain and Boromisa 1987). Additionally, assortative mating may result from selection for reproductive isolation between the forms, in association with their genetic divergence. Varying degrees of assortative mating, ranging from complete to none at all, have resulted from disruptive selection and genetic divergence in laboratory studies on Drosophila (e. g. Thoday and Gibson 1962; Crossley 1974; Dobzhansky et al. 1976; Speiss and Wilke 1984; Rice 1985; Koepfer 1987). Thus the assortative mating observed between anadromous and non-anadromous salmonids may be the product of factors involved in sexual selection and/or factors involved in selection for premating isolation.

To determine if assortative mating between anadromous and

non-anadromous salmonids results from the size difference between the forms alone or additional premating isolating mechanisms, I ran a series of male choice experiments on the anadromous (sockeye salmon) and non-anadromous (kokanee) forms of Oncorhynchus nerka from two spawning localities, Pierre Creek tributary to Babine Lake and Narrows Creek, tributary to Takla Lake.

Three mechanisms could account for the assortative mating observed between sockeye and kokanee. First, assortative mating may result from male intrasexual competition, such that larger males outcompete smaller males for access to the (possibly) preferred large females, as has been suggested by Hanson and Smith (1967), McCart (1970) and Jonsson and Hindar (1982). In such cases, assortative mating should break down in the absence of competitors for mates. Second, assortative mating may occur because of male choice dependent on male size in salmon. In kokanee, male selectivity increases with male size; small males do not discriminate between small and large females whereas large males strongly prefer large females (Chapter 3). If this same mechanism accounts for assortative mating between sockeye and kokanee, we expect to find male choice dependent on male size but, as within kokanee, we do not expect to find that males of any size (or form) prefer the smallest females (kokanee) over the largest females (sockeye). Finally, assortative mating may result from mate choice dependent on the form (sockeye or kokanee) of potential mates. If so, we expect to find that

kokanee males prefer kokanee over sockeye females when given a choice, both in the presence and absence of competition. Mate choice dependent on form may be evidence of behavioural character displacement in association with selection for premating isolation between sockeye and kokanee.

The study is in three parts. First, I document the degree of assortative mating between sockeye and kokanee in Pierre and Narrows creeks. Second, I examine male choice in both the presence and absence of male competitors. Finally, in Pierre Creek, the factors that determine the attractiveness of females to males are examined. The results indicate that assortative mating in O. nerka is not simply the result of intrasexual competition or male choice dependent on male size; rather I present evidence that assortative mating between sockeye and kokanee is at least partially based on form, and thus possibly the result of selection for reproductive isolation between the forms.

1. Assortative mating between sockeye salmon and kokanee

Methods

To examine the pattern of association of sockeye salmon and kokanee in Pierre Creek, Babine Lake, and Narrows Creek, Takla Lake, I conducted streamside observations detailing the structure of male spawning aggregations around sockeye and

kokanee females. On August 2, 5 and 15, 1984 I counted the total numbers of sockeye and kokanee in Pierre Creek and recorded the number of sockeye and kokanee males associated with a representative sample of 206 territorial sockeye females and 119 territorial kokanee females. Kokanee males in Pierre Creek ranged from 21 to 26 cm fork length; sockeye males ranged from 30 to 67 cm fork length. On August 5, 6, 7 and 9, 1983, I counted the total number of sockeye and kokanee in Narrows Creek and recorded the number of sockeye and kokanee associated with a representative sample of 302 territorial sockeye females and 100 territorial kokanee females. Kokanee males in Narrows Creek ranged from 17 to 20 cm fork length; sockeye males ranged from 55 to 66 cm fork length. Males associated with females mainly adopted one of two behaviours; they were either dominant to other courting males, assuming a position directly lateral to the rear flanks of a female, or they were subordinate, 'sneak' males, assuming positions behind or beside a female and dominant male. In a few cases there was ongoing competition for the dominant position (the position closest to the female).

Results

In Pierre Creek, Babine Lake, no sockeye males were observed courting the 119 territorial kokanee females selected for observation. Kokanee females were almost always courted by a single kokanee male (Table 10). In only two cases were kokanee females observed to have more than one kokanee male in

Table 10. The total number of kokanee and sockeye observed in Pierre Creek, Babine Lake, and Narrows Creek, Takla Lake on three and four dates, respectively. Mean male/female ratios are shown for kokanee males associated with kokanee females (K) and sockeye females (S; most with sockeye males) and for sockeye males in non-dominant (sneak) positions to sockeye pairs (SP; sockeye females with sockeye males). All repeated measures are presented with standard errors and sample sizes in parentheses.

Date	Number		Mean Male/Female Ratio		Sockeye/SP
	Sockeye	Kokanee	Kokanee/K	Kokanee/S	

Pierre Cr.					
Aug. 2	710	5178	-	3.45 (0.40,29)	0.14 (0.08,22)
Aug. 5	1293	10629	1.03 (0.00,76)	2.49 (0.20,86)	0.07 (0.03,67)
Aug. 15	4553	9295	1.00 (0.00,43)	2.46 (0.15,91)	0.19 (0.04,80)
Narrows Cr.					
Aug. 5	131	593	-	0.91 (0.22,21)	0.05 (0.05,19)
Aug. 6	199	1335	-	1.11 (0.14,55)	0.00 (0.00,36)
Aug. 7	281	1300	1.20 (0.13,10)	1.15 (0.14,91)	0.01 (0.02,64)
Aug. 9	316	2557	0.94 (0.04,90)	1.24 (0.09,134)	0.02 (0.02,86)

attendance. In contrast, almost all (191 of 206) territorial sockeye females had an entourage that included several kokanee males. Unless no sockeye males were present, kokanee males associated with sockeye females assumed subordinate roles in the courtship hierarchy. The ratio of kokanee males to sockeye females decreased over the period of observation (ANOVA, $p < 0.01$). This decreasing ratio may coincide with an increase in the proportion of kokanee females in the kokanee run over time, as has been observed in other kokanee populations (Lorz and Northcote 1965). Sockeye males which assumed subordinate roles to sockeye pairs were much less numerous than subordinate kokanee males and the ratio of sockeye males to sockeye pairs did not change significantly over time (ANOVA, $p > 0.10$).

While no sockeye males were observed courting the kokanee females selected for observation in Pierre Creek, a few of the smallest sockeye males (jacks; 30-41 cm) were observed courting kokanee females at other times. To roughly estimate the proportion of jacks that accompanied kokanee females, I recorded the positions of a representative sample of jack males on August 15. Of the 44 jacks observed, only 9.5% (4) were observed courting kokanee females, while the rest assumed sneak positions behind sockeye pairs (38) or were alone (2). McCart (1970) observed that only 6% of jack males courted kokanee females in Four Mile Creek, another tributary to Babine Lake, suggesting that the limited interest of sockeye males in kokanee females is a relatively constant feature of the relationship between

sockeye and kokanee in Babine Lake.

In Narrows Creek, Takla Lake, no sockeye males were observed courting the 100 kokanee females selected for observation. In addition, I never saw any sockeye males courting kokanee females in my numerous walks of the creek in 1983 and 1985, suggesting that sockeye male pairings with kokanee females are rare events in Narrows Creek, if they occur at all. Territorial kokanee females were almost always attended by a single kokanee male. Of the 100 territorial kokanee females observed, 90 were courted by kokanee males and ten were alone. Only seven of the 90 courted females were attended by two kokanee males. Sockeye females were usually attended by a single sockeye male (only four of 301 sockeye females were attended by more than one sockeye male), and a small number of kokanee males. In contrast to Pierre Creek, a significant percentage of sockeye females were not attended by any kokanee males (33.6% versus 7.2% in Pierre Creek). The number of kokanee males attending individual sockeye females was small and did not change significantly over time ($p>0.5$).

The degree of assortative mating by form in Pierre Creek and Narrows Creek over the course of the spawning run was even greater than that observed during the individual walks of the stream, as the spawning runs of kokanee and sockeye did not completely overlap in either creek. In Pierre Creek, the kokanee spawning run was much shorter than the sockeye run. On

Aug. 28th, 5,315 sockeye were counted in the creek (and more were seen entering), while only 200 nearly dead kokanee were observed. No significant runs of kokanee into the creek were observed past Aug. 14th. In Narrows Creek, the sockeye run starts and ends earlier than the kokanee run. Sockeye first arrive in Narrows Creek during the last week in July to the first week in August, with the run usually complete by the third week in August (International Pacific Salmon Commission unpublished reports). Kokanee do not begin arriving until the first week in August and the run persists at least until the first week in September (no observations were made past this time)(pers. obs.).

2. Kokanee and sockeye male choice in the presence and absence of competitors

Methods

There is a high degree of assortative mating between sockeye and kokanee in Pierre Creek and Narrows Creek. Here I test the hypotheses that assortative mating is the result of (1) male intrasexual competition, (2) male choice dependent on male size and/or (3) male choice dependent on the form of the female (see introduction for how to differentiate between hypotheses).

Kokanee and sockeye male choice between sockeye and kokanee females was examined in experimental arenas under the following

competitive situations: A) no competitors present; B) a large sockeye male present, paired with the sockeye female; and C), as in B, but two males of the type tested were added simultaneously. Kokanee (in Pierre and Narrows creeks) and three size groups of sockeye males (in Pierre Creek) were tested in experiment A, whereas kokanee (in Pierre and Narrows creeks) and jack sockeye (in Pierre Creek) males only were tested in experiments B and C. The three size groups of sockeye males in Pierre Creek were: 1) jacks (31-41 cm); 2) medium (42-51 cm) and large (52-67 cm). The three size groups correspond roughly to three year olds, four year olds and four and five year olds, respectively, according to the size and age data presented in Hanson and Smith (1967). The smaller four year olds (medium sockeye males) were designated as an individual size group because, like jack males, they had no corresponding size class of sockeye females. Unlike jack males, medium males were similar in appearance to the large sockeye males, with hooked jaws, a prominent dorsal hump and bright red colour. Jack males were dull red in colour and did not have the obvious dorsal humps and hooked jaws of larger males. Jack males and medium sized males were absent in Narrows Creek.

Males to be tested were added singly (experiments A and B) or in pairs (experiment C) to a four by four meter enclosure in the spawning stream containing a territorial kokanee and a territorial sockeye female (either attended (B, C) or not attended (A) by a large sockeye male). The behaviours recorded

for each male with respect to each female over ten minutes of observation (two five minute periods separated by a seven minute period) were 'nearness time' and courtship displays. Nearness time was defined as all the time a male spent within 25 cm of a female plus only the time it was oriented to the female at distances up to 1m away from her. To reduce subjectivity in what I called 'oriented', a male had to first approach within 25 cm for any timing to be commenced. Timing was stopped when the male left the 1m range or was judged to be no longer oriented to the female when within the 1m range, and recommenced only when the male approached to within 25 cm. The nearness time rule was modified slightly in experiments B and C where another male was present in the arena, because this presence often restricted close access to particular females. In these experiments all time oriented to a female within 1m was recorded and the 25 cm commencement rule was dropped. Courtship displays consisted of approaches (including quivers), crossovers and digs (see McCart 1969 for description of male digging and Tautz and Groot 1975 for a description of quivers and crossovers). All displays were positively correlated with one another and lumped for analyses. Female digging behaviour was also recorded during the two five minute observation periods. A 'dig' consisted of a series of strong body flexures while turned on one side.

Choice was determined by analyses of the difference in time spent near the two females (Time Difference) and by the difference in the number of courtship displays performed to each

of the females (Display Difference) (see Chapter 3 for further details).

Results

A. Male choice in the absence of competitors

In Pierre Creek, Babine Lake, choice differed significantly among the four size classes of males when presented to a sockeye and a kokanee female (Kruskal-Wallis non-parametric ANOVA, $p < 0.001$ for Time Difference and Display Difference; Figs. 25a and 26b). Kokanee males spent more time near the kokanee female ($p < 0.05$) whereas all three size classes of sockeye males spent more time near the sockeye female ($p < 0.05$; in this and all subsequent within male size group comparisons Time Difference data were analyzed by Wilcoxon matched pairs signed rank test and Display Difference data were analyzed by paired t-test). Similar differences were found in courtship displays, except that jack sockeye did not display significantly more to either type of female ($p > 0.3$). Overall, 13 of 20 kokanee males spent more time near the kokanee female, whereas, 12 of 16 jacks, all medium (10) and all large (8) sockeye males spent more time near the sockeye female. Multiple comparisons (non-parametric extension of Tukey's test; see Zar 1984) revealed kokanee differed from all sizes of sockeye males in both Time Difference and Display Difference ($p < 0.05$). No significant differences in the time and display scores were found among the sockeye males.

Figure 25. Kokanee and sockeye male choice between kokanee and sockeye females in the absence (A) and presence of competitors (B, C) in Pierre Creek, as indicated by the median difference in time (+ 95% CI) spent near females of the two forms.

The symbols represent the choice of females (in white, kokanee on the outside of the left vertical axis, sockeye on the outside of the right vertical axis) presented to kokanee (in black) and three size classes of sockeye males (striped, at the median in the difference in time they spent near a female of each of the two forms over ten minutes of observation in an experimental arena). The height of the symbols is proportional to the mean fork length of the females presented and males tested. A scale of actual sizes is presented in the upper left of the figure. No male competitors were present in experiment A; all size groups of males were tested separately and individually. The male competitors present in experiments B and C are depicted, along with the females they attended, on the outside of the axes. In experiment B, a large sockeye male was paired with the large sockeye female during the separate and individual testing of kokanee and jack sockeye choice. In experiment C, which additional males were present depended on the type of male tested. For kokanee, an additional kokanee male was paired with the kokanee female and a large sockeye male was paired with the sockeye female. For jack sockeye, a large sockeye and an additional jack sockeye male attended the sockeye female and the kokanee female was unattended. Symbols to the right of the broken line indicate preference for the sockeye female, those to the left indicate preference for the kokanee female.

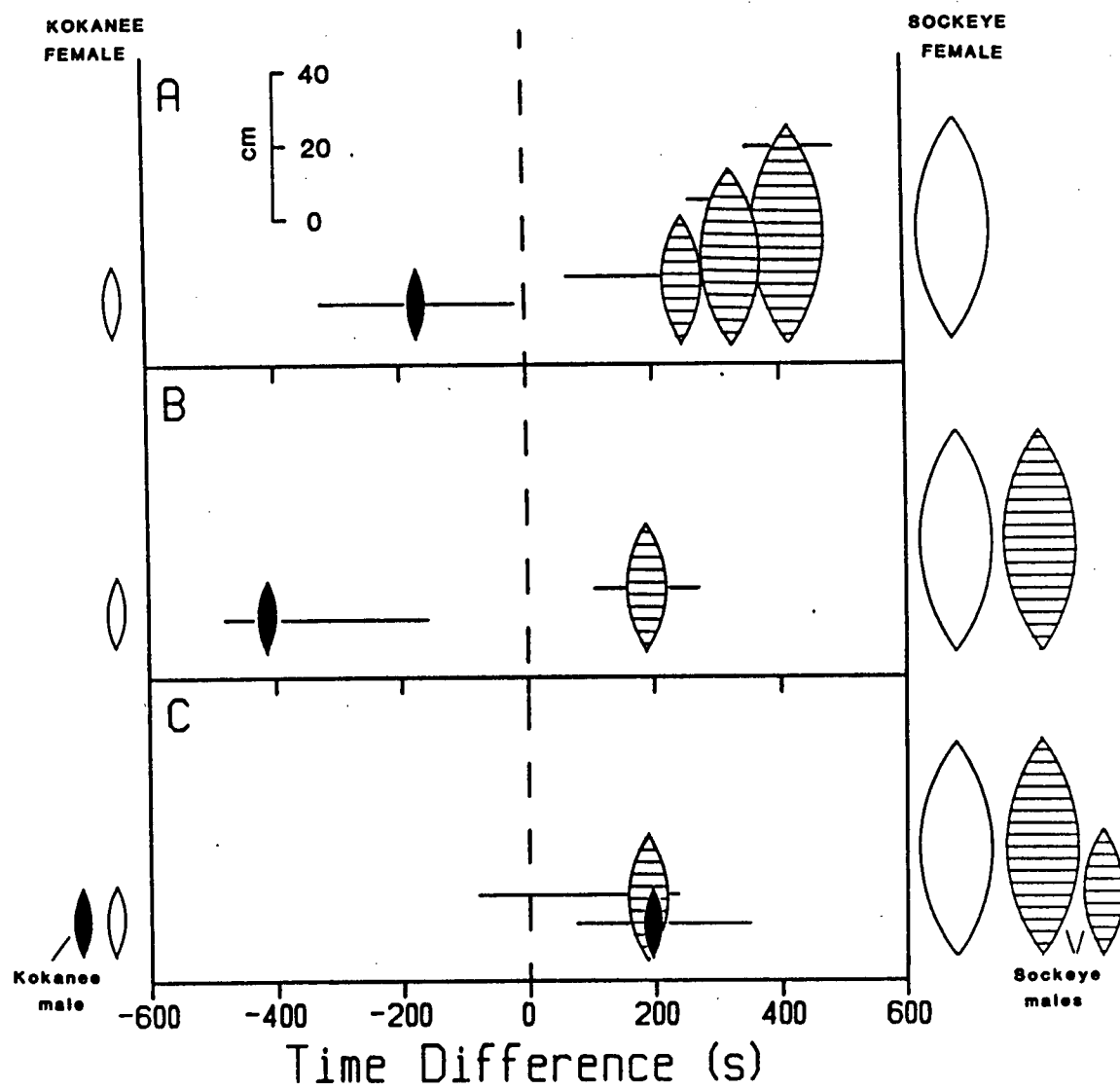
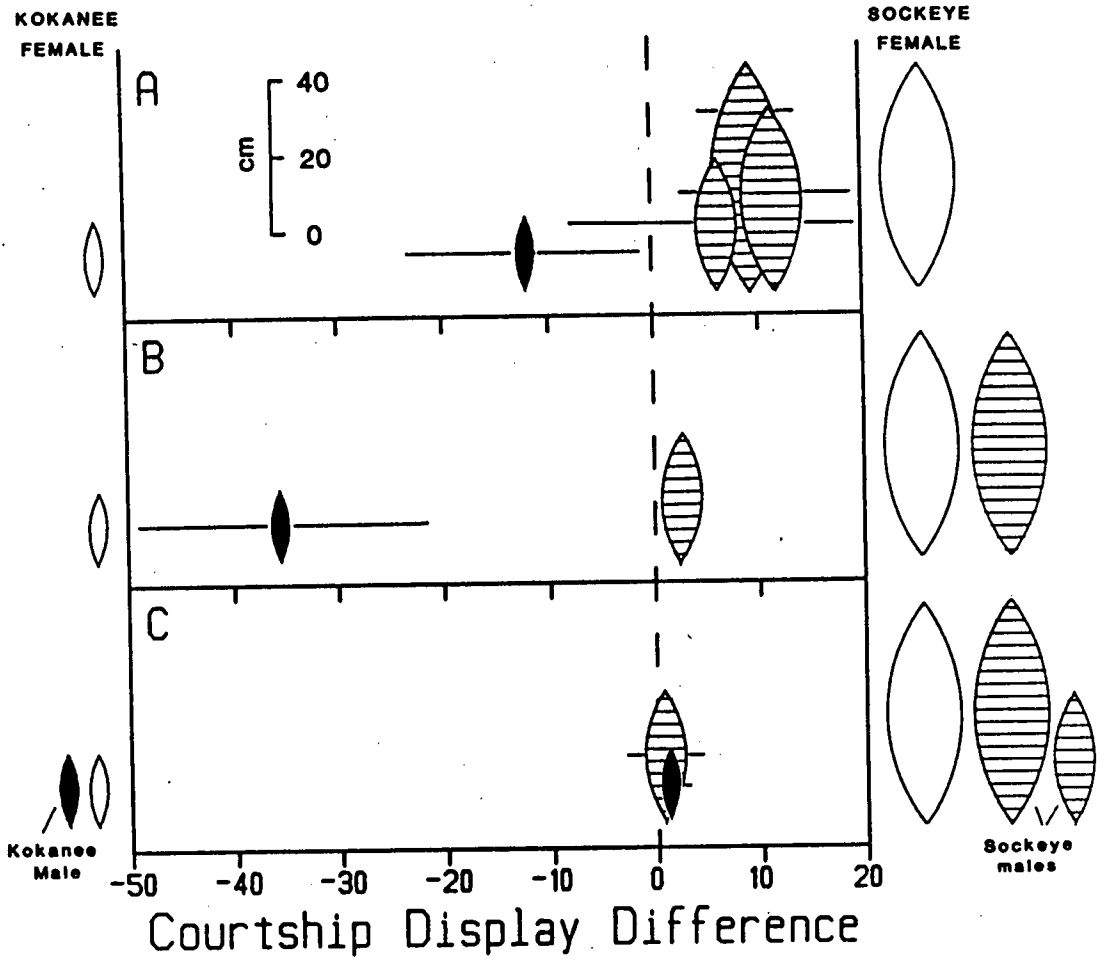


Figure 26. Kokanee and sockeye male choice between kokanee and sockeye salmon females in the absence (A) and presence (B, C) of competitors in Pierre Creek, as indicated by the mean difference (+ 95% CI) in the total number of courtship displays performed to females of the two forms. See Fig. 25 for an explanation of the layout.



However, the difference scores obscured the fact that 55% (9 of 16) of jack males displayed to the kokanee female present whereas none of the medium (0 of 8) and large sockeye males (0 of 10) did. Similarly, while kokanee males displayed more to kokanee females throughout the trials, 70% (14 of 20) of them did display to the sockeye female present.

Kokanee females spawned only with kokanee (1,20; number of spawnings observed, number of males tested) and jack (2,16) males whereas sockeye females spawned with jack (3,16), medium (2,8) and large sockeye males (3,10). The difference in the number of digs performed by the sockeye and kokanee females was positively dependent on the size of the male present ($r=0.64$, $n=22$, $p<0.01$; Fig. 27), suggesting females may also have exerted a choice. However, female digging rate was also probably related to male interest which was confounded with the male size groups.

In Narrows Creek, Takla Lake, kokanee males showed a strong preference for the kokanee female when given a choice between a sockeye and a kokanee female ($p<0.005$ for Time Difference and Display Difference; Figs. 28 and 29). Nineteen of 20 males tested spent more time near and displayed more to the kokanee female.

There was no significant difference in the digging rate of the sockeye and kokanee females used ($p>0.1$; mean number of digs

Figure 27. The regression of Dig Difference (digs by sockeye - digs by kokanee) between paired sockeye and kokanee females on the size of the male present in Pierre Creek.

K = kokanee males; J = jack sockeye males; M = medium sockeye males; L = large sockeye males. The data are taken only from the first time a female pair was presented with a test male to insure independence. One observation for jack males was excluded from the analysis, as the sockeye female spawned and the majority of her digs were nest covering, versus constructing, in nature.

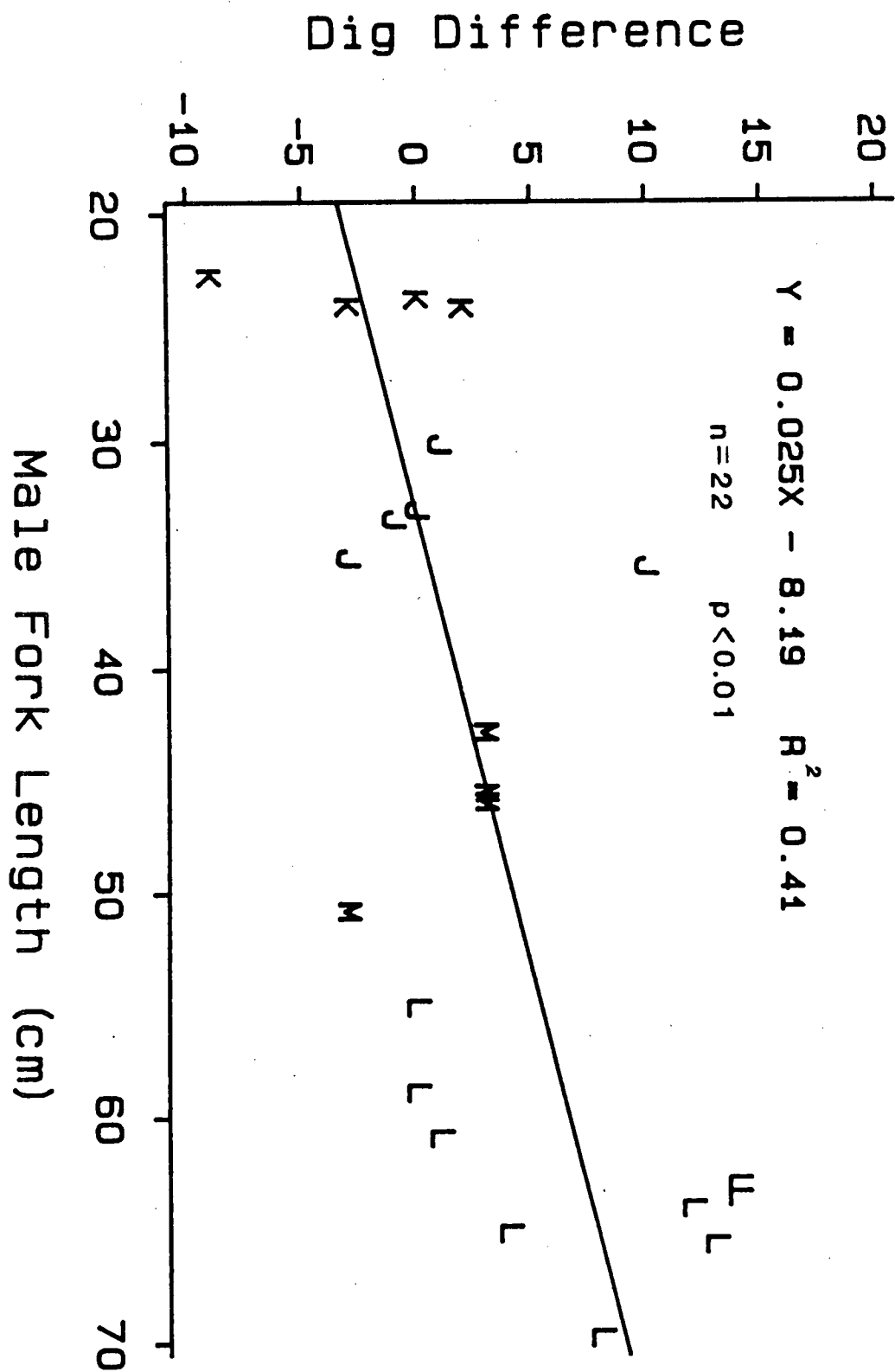


Figure 28. Kokanee male choice between kokanee and sockeye females in the absence (A) and presence (B, C) of competitors in Narrows Creek, as indicated by the median in difference between (+ 95% CI) in the time spent near the females. See Fig. 25 for an explanation of the layout.

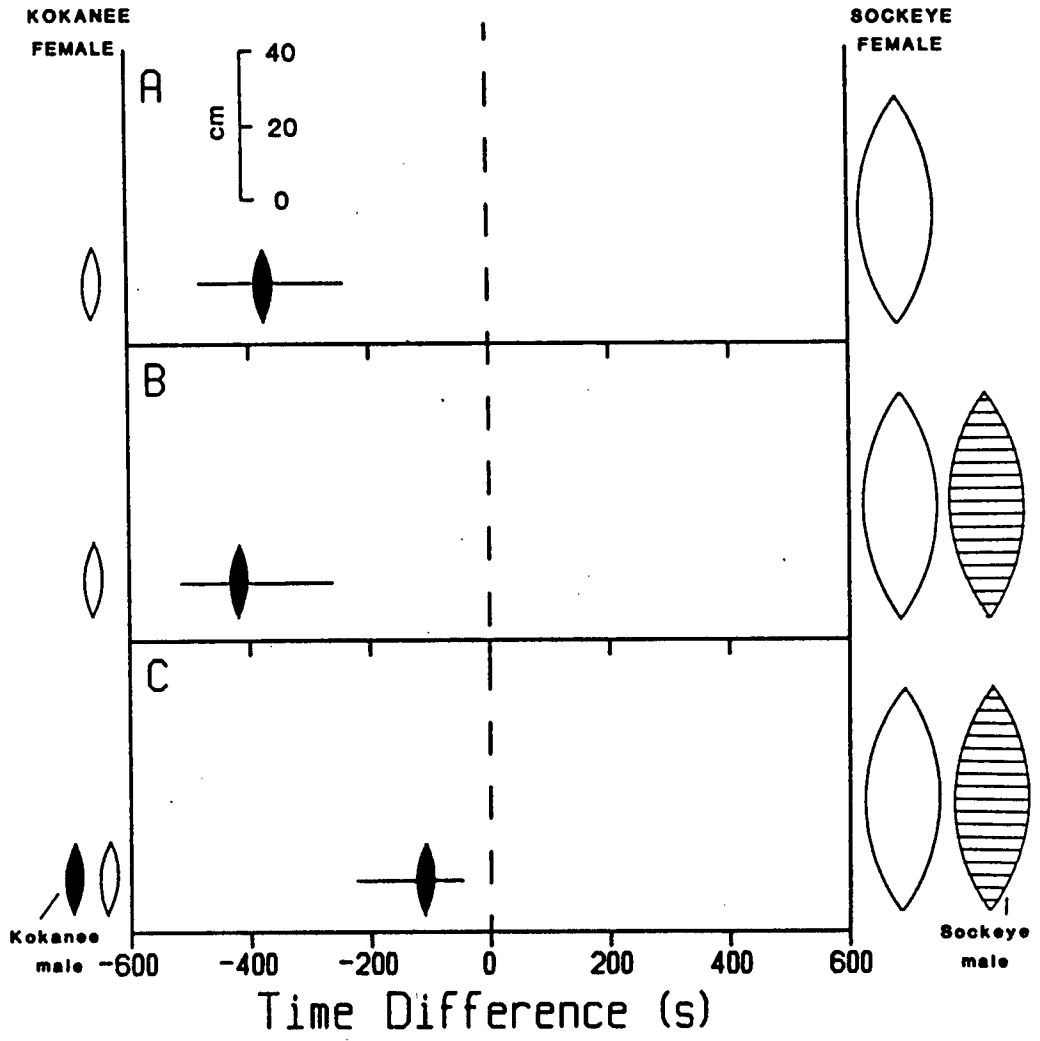
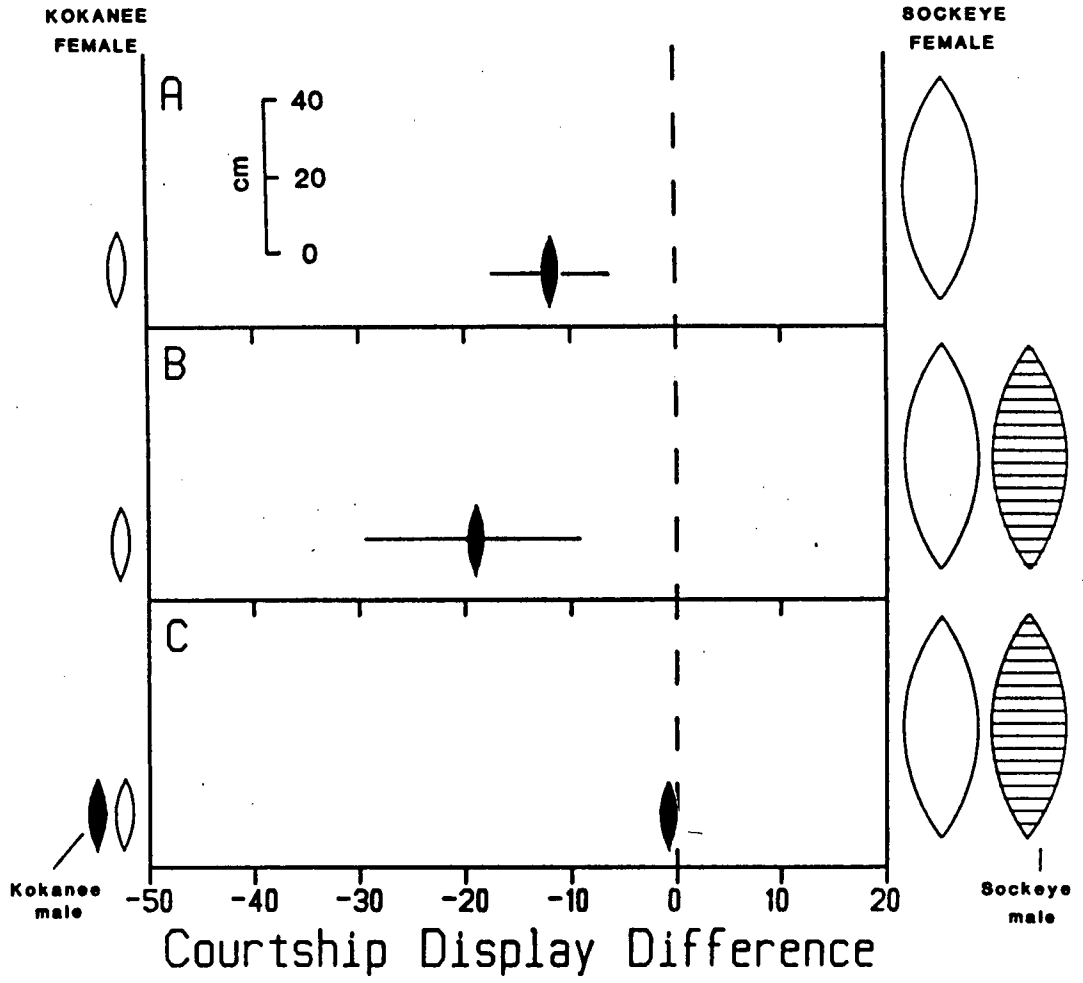


Figure 29. Kokanee male choice between kokanee and sockeye salmon females in the absence (A) and presence (B, C) of competitors in Narrows Creek, as indicated by the mean difference (+ 95% CI) in the total number of courtship displays performed to females of the two forms. See Fig. 25 for an explanation of the layout of the figure.



per sockeye female per ten minutes = $3.4 + 1.4SE$, mean number of digs per kokanee female per ten minutes = $5.0 + 1.8SE$). Two spawnings were observed, once each with a sockeye and kokanee female.

B. Kokanee and jack sockeye male choice in the presence of a large sockeye male

In Pierre Creek, jack sockeye and kokanee males behaved in the opposite manner when presented with a choice of a sockeye pair and a kokanee female (Figs. 25b and 26b; $p < 0.001$; Mann-Whitney U test for Time Difference data, t-test for Display Difference data). Eighteen of 20 kokanee males spent more time near and 19 of 20 displayed more to kokanee females ($p < 0.001$). Sixteen of 20 jack males spent more time near ($p < 0.001$), and 9 of 20 displayed more to the sockeye females (7 jacks displayed to neither female) ($p < 0.05$). These results were qualitatively similar to those obtained when no large sockeye male was present. Quantitatively, only the Display Difference scores of kokanee males differed significantly between experiments, with kokanee displaying more to kokanee females when a large sockeye male was present ($p < 0.05$).

Kokanee males spawned four times with kokanee females throughout the 20 trials but did not participate in the two sockeye pair spawnings. Jack sockeye males did not spawn with kokanee females throughout the 20 trials but participated in one

of the two sockeye pair spawnings.

In Narrows Creek, kokanee males showed a strong preference for kokanee females when given a choice between a lone kokanee female and a sockeye pair ($p < 0.001$ for both Time Difference and Display Difference; Figs. 28b and 29b). Eighteen of 20 males tested spent more time near and displayed more to the kokanee female. One male approached neither female throughout the trial, while the other spent more time near the sockeye female but displayed to neither female.

Six spawnings were observed, twice between kokanee pairs and four times between sockeye pairs. Kokanee males did not participate in any of the sockeye spawnings.

C. Kokanee and jack male choice in the presence of a large sockeye and a male of their own size

In Pierre Creek, the presence of a similar sized competitor resulted in a switch in behaviour by the 'losing' kokanee male but not by the 'losing' jack male (where 'losing' is defined as spending a lesser amount of time with the kokanee female for kokanee males and with the sockeye female for jacks; Figs. 25c and 26c). Sixteen of twenty kokanee losers spent most time with the sockeye female ($p < 0.05$), and 12 of 20 displayed more often to the sockeye female ($p > 0.3$). Courtship displays to both kokanee and sockeye females were restricted by the presence of

other males. Jack losers did not display more to or spend significantly more time with either kokanee or sockeye females ($p>0.1$). However, in general they oriented toward the sockeye females, but often remained outside the 1 m timing range (note that there were already two sockeye males usually within this range). Only one of ten jacks tested demonstrated a consistent interest in the kokanee female in both Time and Display Difference scores. There was no significant difference between the behaviour of kokanee and jack 'losers' in either Time or Display Difference ($p>0.2$).

No spawnings were observed between the kokanee female and kokanee males but kokanee males did participate as sneaks in all four spawnings between the sockeye pair throughout the 20 trials. Kokanee sneaks disappeared beneath the spawning sockeye pair at the moment of spawning and remained there until spawning was complete. No spawnings were observed during the ten trials of jack sockeye male choice.

In Narrows Creek, the presence of a similar sized competitor did not affect the preference of kokanee males for kokanee females. Kokanee 'losers' spent significantly more time near the kokanee female than near the sockeye female ($p<0.005$) but did not display more to either type of female ($p>0.25$; Figs. 28c and 29c). In total, 14 of the 20 kokanee 'losers' spent more time near the kokanee female than they did near the sockeye female. Three spent no time near either female and

three spent most time near the sockeye female.

Two spawnings were observed, both involving a kokanee female and the dominant kokanee male. In neither case did the kokanee 'loser' participate.

D. Comparison of the behaviour of kokanee males towards sockeye females in Pierre and Narrows creeks

It was apparent that kokanee females were attractive to kokanee males in both Pierre and Narrows creeks. In contrast, the attractiveness of sockeye females to kokanee males appeared to differ between creeks. Kokanee males in Pierre Creek switched their preference to sockeye females when faced with competition for access to kokanee females, whereas kokanee males in Narrows Creek maintained a preference for kokanee females. To further contrast the attractiveness of sockeye females to kokanee males in both systems, I compared the time kokanee males in Pierre and Narrows creeks spent near sockeye females and the number of courtship displays they performed to them in each of the three previous experiments.

In all experiments, Takla Lake kokanee males spent significantly less time near and performed fewer courtship displays to sockeye females than did Babine Lake kokanee males (Mann Whitney U test; $p < 0.01$; Figs. 30 and 31). The greater attractiveness of sockeye females to Babine kokanee males

Figure 30. Comparison of the time kokanee males in Pierre and Narrows Creeks spent near sockeye females in the absence (A) and presence (B, C) of competitors. See Fig. 25 for a description of experimental conditions.

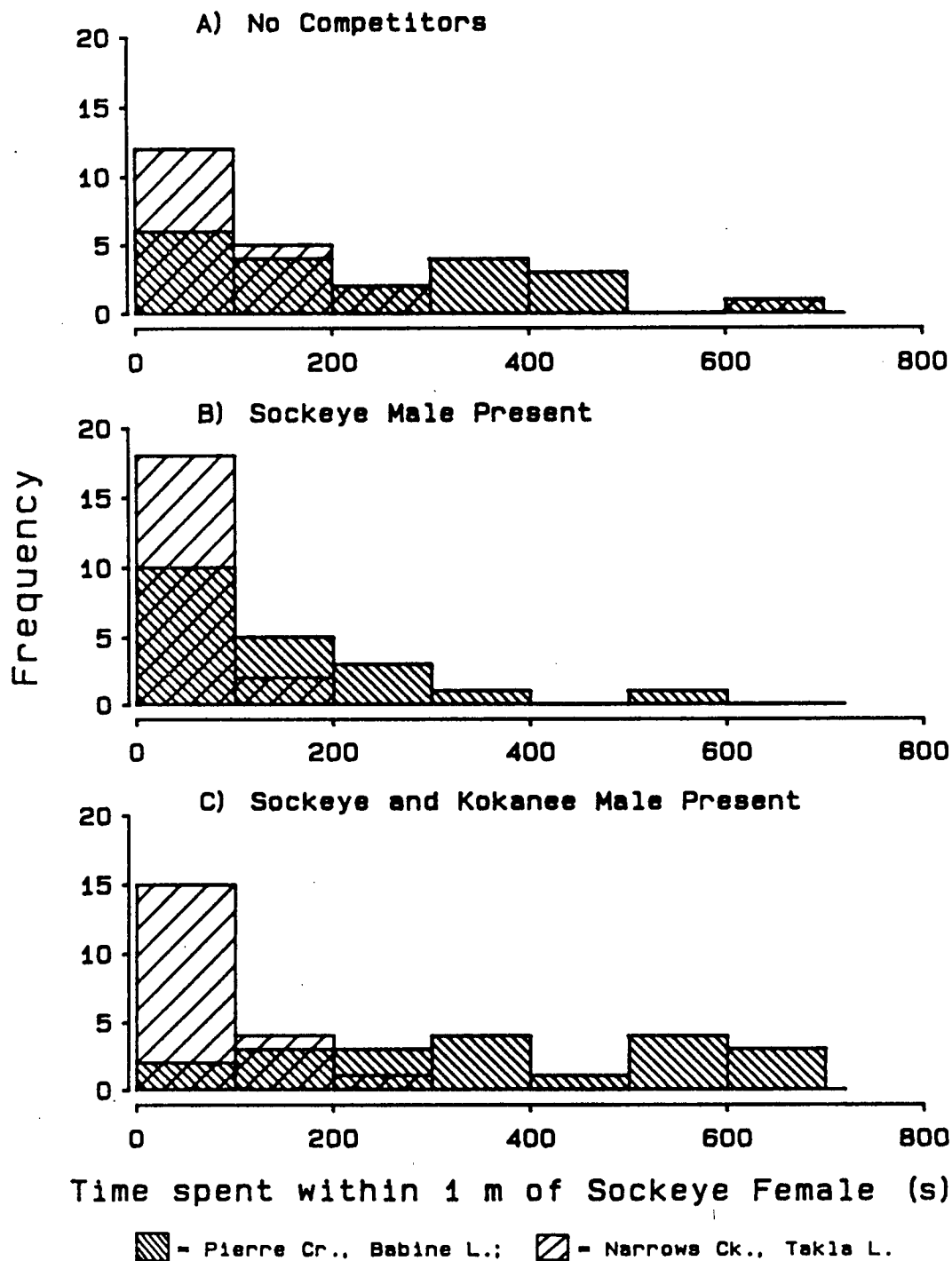
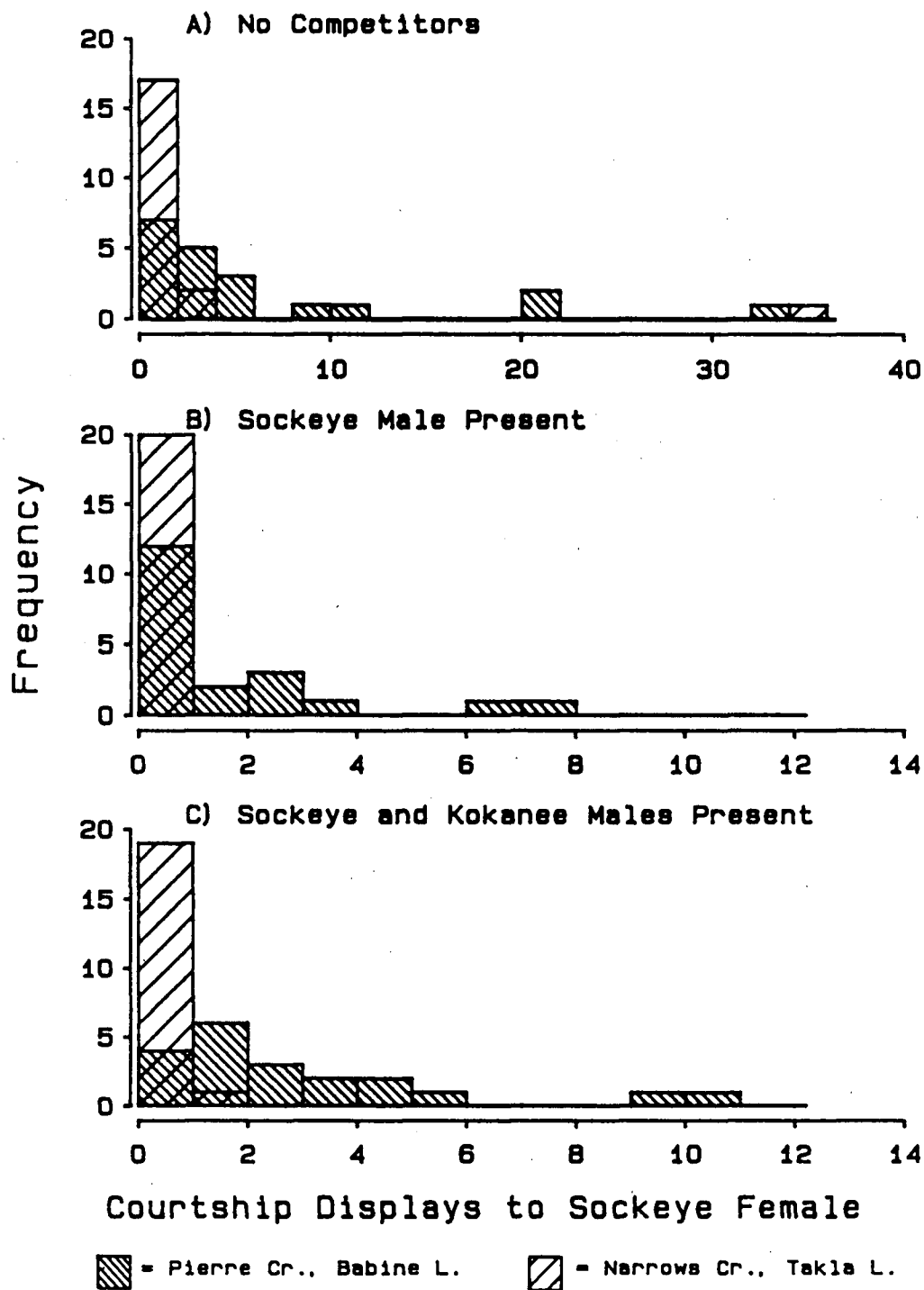


Figure 31. Comparison of the number of courtship displays kokanee males in Pierre and Narrows creeks performed to sockeye females in the absence (A) and presence (B, C) of competitors. See Fig. 25 for a description of experimental conditions.



suggested by these results corresponds to stream observations (Table 10). On average, sockeye females in Pierre Creek, Babine Lake, had many more kokanee males associated with them than did sockeye females in Narrows Creek, Takla Lake ($p < 0.001$), even though the ratio of kokanee to sockeye was higher in Narrows Creek.

E. Comparison of the sneak behaviour of kokanee males from Pierre and Narrows creeks

To compare the propensity of kokanee males in Pierre and Narrows creeks to become sneaks to sockeye pairs, single kokanee males were placed in an arena containing only a sockeye pair and their behaviour was monitored as in previous experiments. Kokanee were tested over two years in Narrows Creek (19 males were tested in 1983, 14 in 1985) and in a single year in Pierre Creek (1985).

There was no significant difference between years in Narrows Creek in the behaviour of kokanee males when presented to a sockeye pair ($p > 0.80$ for nearness time and courtship displays). These data were pooled for comparison with Pierre Creek kokanee.

There were striking differences in the behaviour of Takla and Babine kokanee towards sockeye pairs in both nearness time and total courtship displays (Mann Whitney U-test; $p < 0.0001$;

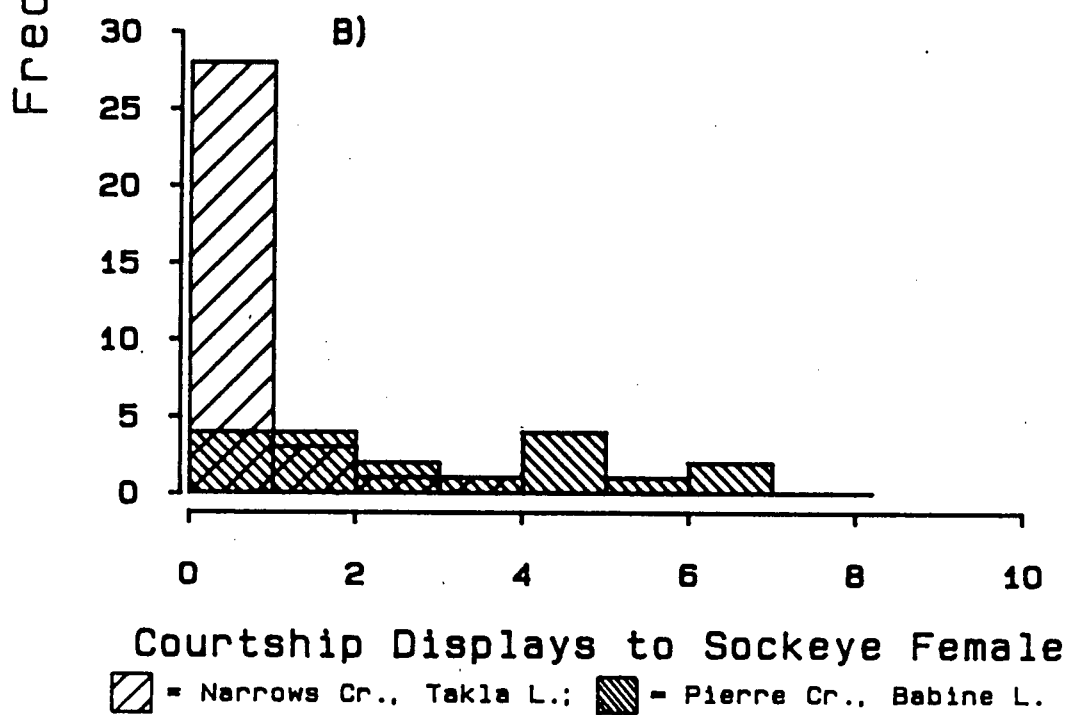
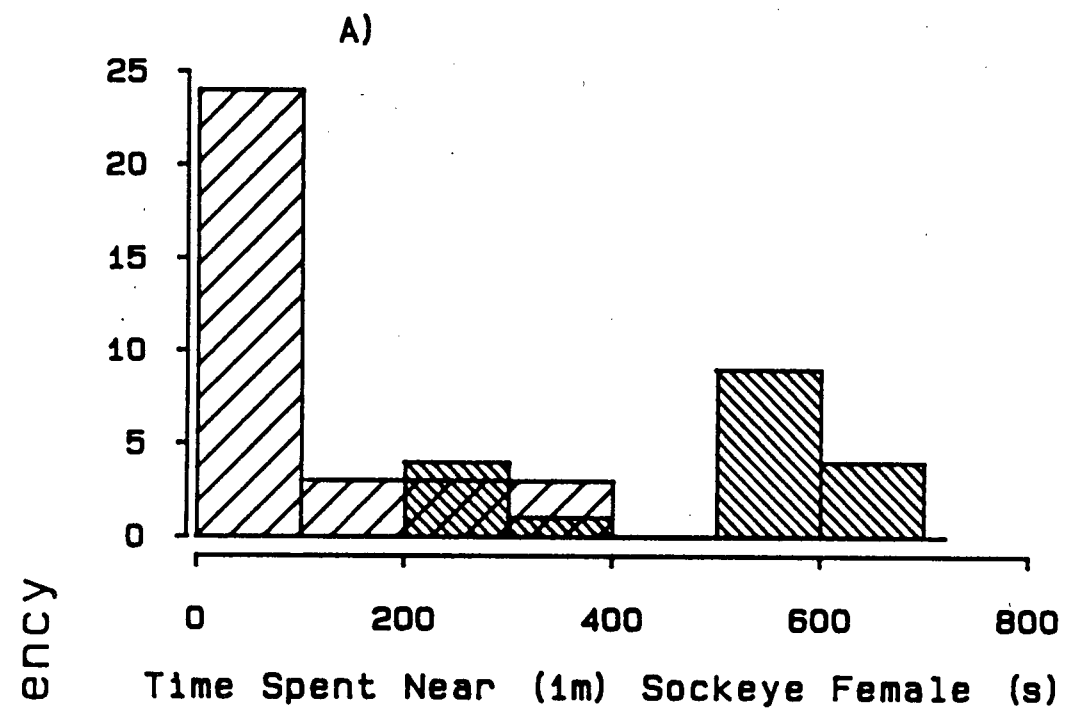
Fig. 32). All 18 Babine kokanee males tested became sneaks to the sockeye pair present. Thirteen of these males spent greater than 83% of their time (>500 seconds) within one meter of the sockeye female. In contrast, only 5 of the 33 males tested in Takla Lake exhibited even weak sneak behaviour towards the sockeye pair. None of the Takla Lake kokanee spent more than 66% of their time (>400 seconds) within 1 m of the sockeye female. Similarly, 78% (14) of Babine kokanee performed at least one courtship behaviour (almost all were rushes (approaches) under the abdomen of the female), whereas only 15% (5) did so in Narrows Creek.

3. Factors involved in determining the attractiveness of kokanee and sockeye females to males

Methods

Female attractiveness to males may depend on one or a combination of the following three factors: a) absolute size of female; b) form (sockeye or kokanee) of female and; c) relative size of the female to the male. If female absolute size is the criterion of male choice, then the attractiveness of females should be independent of male size. If the form of the female is the sole criterion of choice, males should be attracted only to females of their own form. Finally, if relative size of the female to the male is a criteria of choice, the attractiveness of kokanee females should decline with increasing male size and

Figure 32. The amount time (A) kokanee males in Pierre and Narrows creeks spent near sockeye females and the number of courtship displays (B) performed when no other choice was available over ten minutes of observation in an experimental arena.



sockeye females should be attractive to all males (see Chapter 3). To test among these alternatives in Pierre Creek, 12 males of each size class were tested individually with either a single territorial sockeye or kokanee female in the experimental arena. Methods were the same as in the previous choice experiments except that in this case no choice was available as only a single territorial female was present.

To look for possible differences in female response to males of different sizes, each female was alternately presented with males of two size classes. Rates of digging (nest construction) and spawning were recorded. The two size classes used were either kokanee and medium sockeye males or jack and large sockeye males. Each female was used for 6 trials in total, three trials with each of the two size classes of males.

For males, data on nearness time were analyzed with a two-way extension of Kruskal-Wallis non-parametric ANOVA. The behaviour data were analyzed by two-way ANOVA after a Log ($x + 1$) transformation. The set of orthogonal contrasts in both cases were: comparisons between the two types of females for each of the four size classes of males; comparison of kokanee and jack males; comparison of medium and large males and a comparison of kokanee and jack males as a group with medium and large males as a group.

Data on female behaviour were analyzed by first subtracting

the number of digs performed in the presence of the three small males from the number performed in the presence of the three large males (to get a single independent score for each female). The data were then subjected to a two-way ANOVA with female type and male pair type as the independent variables.

Results

There were significant differences: 1) within male groups (between female type) in the time spent near the sockeye and kokanee females; 2) among male groups in the time spent near and displays to either type of female; and 3) in the interaction between male groups and female type in the time spent near and displays performed to females ($p < 0.01$; Fig. 33, Table 11). The major differences in response to the females lay between the group of kokanee and jack sockeye males and the group of medium and large sockeye males ($p < 0.001$). Sockeye females were attractive to males of all size classes (Fig. 33a). All males, except two kokanee males, spent at least 40% of their time near the sockeye female (one of the exceptional kokanee males was oriented to the female throughout the trial but remained mostly just outside the 1m timing area). Eighty-nine percent of all males displayed to the sockeye females. In contrast, kokanee females were attractive to all kokanee and jack sockeye males, but to few medium and large sockeye males (Fig. 33b). All kokanee and jack males spent most of their time near the kokanee females and displayed to them, but most medium and large males

Figure 33. The attractiveness of sockeye (a) and kokanee (b) females to sockeye and kokanee males as indicated by the total time individual males spent near them when no other choice was available over ten minutes of observation in an experimental arena. See Fig. 27 for letter designation.

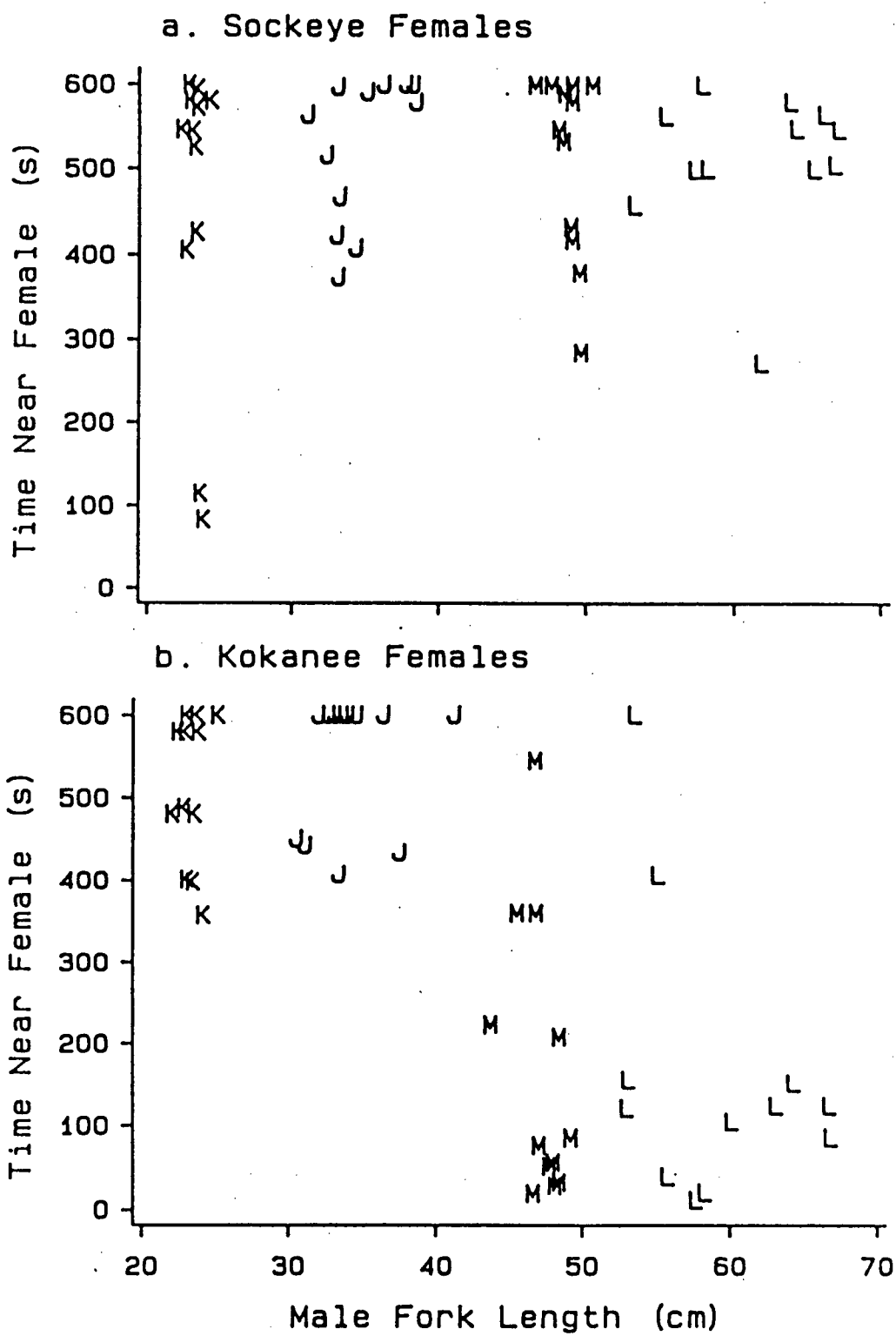


Table 11. The frequency distribution and mean number of courtship displays performed by 12 males of each of four size classes with individual sockeye and kokanee females over ten minutes of observation in an experimental arena.

Male Size Class	Female Size Class											
	kokanee						sockeye					
	0	1-5	6-15	16-25	>25	X	0	1-5	6-15	16-25	>25	X
kokanee		2	2	3	5	29.7	2	4	4	1	1	11.2
jack		1	2	1	8	47.3		7	3	1	1	10.6
medium	9	1	1		1	3.5	1	4	2		5	24.8
large	10	1			1	2.8	2	6	3	1		5.5

spent little time near the kokanee females and only a few of each size class displayed to them. Those large sockeye males which did respond to the kokanee females were the smallest of their class.

Kokanee females spawned only once with kokanee males, four times with jack sockeye males and never with medium and large sockeye males. Sockeye females spawned five times with medium males and once with a large male compared to once with a kokanee male and zero times with jack males.

The digging behaviour of sockeye and kokanee females differed significantly ($p < 0.01$; Table 12). Sockeye females dug more when courted by medium and large males than by kokanee and jack males, but kokanee females dug more often in the presence of kokanee and jack males. The rate of sockeye digging can be related to sockeye female preference for relatively large males as all sizes of males actively courted the sockeye females. It is important to note that the varying sockeye female response did not markedly affect their attractiveness to kokanee and the three size groups of sockeye males. This demonstrates that female choice (as indicated by the rate of nest construction) does not dictate male choice in sockeye and kokanee. Kokanee female digging cannot be related directly to kokanee female preference for kokanee and jack males as most of the medium and large males did not respond to the presence of kokanee females.

Table 12. The difference in the number of digs (+SE) performed by eight sockeye and eight kokanee females when in the alternating presence of three individual males of each of two size classes, over one hour of observation in an experimental arena.

Male size class pair	Female type	
	Kokanee	Sockeye
kokanee and medium sockeye	-3.5 (2.9)	19.3 (5.5)
jack and large sockeye	-15.3 (8.5)	13.8 (8.4)

 The difference in digs was calculated by subtracting the total number of digging bouts performed in the presence of the smallest male from those with the largest male.

Discussion

Proximate mechanisms involved in assortative mating

There is a striking degree of assortative mating by form between sockeye and kokanee in both Pierre and Narrows creeks. Sockeye males mate almost exclusively with sockeye females whereas kokanee males mate with both kokanee and sockeye females. Because of their small size kokanee males are restricted to subordinate, sneak roles in the spawning of sockeye pairs. This pattern of mating is apparently stable over years and localities in Babine Lake (Hanson and Smith 1967; McCart 1970) and over years in Takla Lake (pers. obs.).

Increased fertilization efficiency has been suggested as a factor in the evolution of assortative mating of amphibians and fishes (Davies and Halliday 1977; Malmqvist 1983). This does not account for the assortative mating by form (and size) observed in salmonids, as small non-anadromous and large anadromous males are equally capable of fertilizing large females, in the absence of competition (McCart 1970; Hutchings and Myers 1985).

Male intrasexual competition has been suggested as the major factor behind assortative mating between different size classes and forms (anadromous and non-anadromous) of salmonids (Hanson and Smith 1967; McCart 1970; Jonsson and Hindar 1982).

These studies assumed all males preferred the largest females which is unlikely to be the case (see Chapter 3). My results show that male competition is not the direct cause of assortative mating between sockeye and kokanee, as assortative mating occurred in the absence of competitors in both Pierre and Narrows creeks (Figs. 25, 26, 28 and 29). With an increase in the number of males present in the experimental arenas, assortative mating did not increase between forms as predicted by the competition hypothesis, but decreased in Pierre Creek and remained the same in Narrows Creek. Babine kokanee males, which preferred kokanee females in the absence of competition, switched their preference to sockeye females only when denied access to kokanee females. This switch in preference appears to account for the numerous kokanee males attending individual sockeye females in Pierre Creek, as almost all the territorial kokanee females were attended by kokanee males (Table 10). Takla kokanee males did not switch their preference to sockeye females when denied access to kokanee females, consistent with the relatively few kokanee males observed attending sockeye females in Narrows Creek (Table 10).

Complementary male and female choice appear to be the major factors promoting assortative mating between sockeye and kokanee. Individuals of both sexes find members of the opposite sex of their own form highly attractive. Kokanee females are highly receptive to kokanee males as are sockeye females to sockeye males (Fig. 27; Table 12). In Babine Lake, only kokanee

females and jack sockeye males appear strongly and mutually receptive between forms. Even in this case, jack sockeye strongly prefer sockeye over kokanee females when given a choice (Figs. 25 and 26). I observed no evidence of mutual receptivity between sockeye and kokanee in Narrows Creek, possibly because of the virtual absence of small (jack) sockeye males.

Evidence of a form effect in kokanee male choice

I showed in Chapter 3 that within kokanee, over a size range approaching that between sockeye and kokanee in Babine and Takla lakes, male choice depended on the relative sizes of females to males. Males chose females of their own size or larger; large males chose large females; small males chose small or large females with equal frequency. In the choices between forms in this study, the preference of sockeye males for sockeye females can be accounted for by similar male choice dependent on the size of the female relative to that of the male. The attractiveness of kokanee females to sockeye males declined rapidly with increasing male size in Babine Lake (Figs. 25, 26 and 33). However, the preference of kokanee males for kokanee females cannot so be explained. From the results within kokanee, kokanee males would be predicted not to discriminate between kokanee and sockeye females. Thus the preference of kokanee males for kokanee females in both Pierre and Narrows creeks indicates that kokanee male choice depends on female form. This was particularly clear in Narrows Creek, where

kokanee males displayed little interest in becoming sneaks to sockeye pairs, even in the absence of any other choice.

In Pierre Creek, the suggestion of a form effect in kokanee male choice is supported by the comparison of kokanee and jack sockeye choice. Even though kokanee and jack males are restricted to the same choice of mates on the spawning grounds, that is to be dominants to kokanee females or sneaks to sockeye pairs, their choice differs. Given a choice between a sole kokanee female and a sockeye pair in the experimental arenas, jack sockeye males strongly preferred the sockeye while kokanee males strongly preferred the kokanee female (Figs. 25 and 26). This behavioural difference is not explained by a difference in sneaking ability between kokanee and jack sockeye males. In salmon, the smallest males (in this case kokanee) are thought to possess an advantage in sneak behaviour because of their ability to gain close access to females prior to (Gross 1985) and during spawning (Jones and King 1952; McCart 1970; Gross 1985). In this study, Babine kokanee males were able to sneak directly beneath and between spawning sockeye whereas jack males, because of their larger size, were restricted to positions beside the spawning sockeye pair.

Possibility that the form effect in male choice arose from selection for premating isolation

The evolution of reproductive isolating mechanisms between

sympatric forms in polymorphic populations will probably occur only if there are strong selective differences between the environments the forms occupy (e. g. Maynard Smith 1966; Rosenzweig 1978; Pimm 1979; Rice 1984). As adaptive genetic differences accumulate between forms, the fitness of progeny of between form crosses will decrease, thus promoting the evolution of premating isolating mechanisms. At present, there is no direct evidence of selection against the progeny of sockeye-kokanee matings but it is probable that such selection exists, as the selection pressures of the marine and lacustrine environments probably differ greatly (see Ricker 1940). Differences in selection operating on sockeye and kokanee are indicated by their genetic divergence in vertebra numbers and allozyme frequencies in Babine Lake, and by their divergence in gillraker number and allozyme frequencies in Takla Lake (vertebral count comparisons have not been made on Takla sockeye and kokanee). McCart (1970) found that the vertebra numbers differed significantly between Babine sockeye and kokanee. These differences were maintained in controlled rearing experiments. Vertebral variation within populations of fishes has recently been demonstrated to be adaptive (Swain and Lindsey 1984). Nelson (1968b) showed that Takla Lake kokanee and sockeye differed significantly in gillraker number. Gillraker number is an inherited trait in the family Salmonidae (Svardson 1970), and divergence in gillraker number in sympatric populations is usually associated with ecological divergence (e. g. Lindsey 1963; Bodaly 1979). The frequencies of a few

allozymes also differ significantly between sockeye and kokanee in Pierre Creek, Babine Lake, and in Narrows Creek, Takla Lake and these differences are maintained over years (Chapter 4).

The evolution of genetic differentiation and reproductive isolation in sympatry is greatly facilitated by an initial degree of assortative mating between forms (Maynard Smith 1966). Most models and examples of the evolution of reproductive isolation between forms have suggested breeding habitat differentiation as the predominant factor promoting such initial assortative mating (e. g. Maynard Smith 1966; Bush 1975; Tauber and Tauber 1977; McKaye 1980; Rice 1984, 1985; Rausher 1984). I have demonstrated that physical factors (in this case size) associated with the polymorphism can also result in a significant decrease in gene flow between forms. Gene flow is restricted between size classes within sockeye salmon and kokanee because of assortative mating by size (Hanson and Smith 1967; Chapter 3). Assortative mating by size within forms is partly a consequence of male choice dependent on male size and male intrasexual competition (Chapters 1 and 3). Female mate choice and female intrasexual competition also probably promote assortative mating within forms (Hanson and Smith 1967; Schroder 1981; Jonsson and Hindar 1982; Chapter 2). As such, gene flow is expected to be even further restricted between sockeye and kokanee, as the size difference between forms is far greater than that found within forms. Since this size difference is largely environmentally induced (Foerster 1947; Ricker 1938,

1940, 1959, 1972; Scott 1984), the initial production of both anadromous and non-anadromous individuals within a population will result in a severe restriction in gene flow between forms before any genetic differentiation has occurred. Such an initial severe restriction in gene flow accompanied by strong disruptive selection, may have led to the observed genetic differentiation of sockeye and kokanee in Babine and Takla lakes, and thus to the evolution of the observed premating isolating between the forms. If so, this indicates sexual selection may promote genetic divergence and possibly speciation between sympatric populations of animals in addition to its possible role in the rapid allopatric speciation of animals (see Lande 1981; West-Eberhard 1983, 1986).

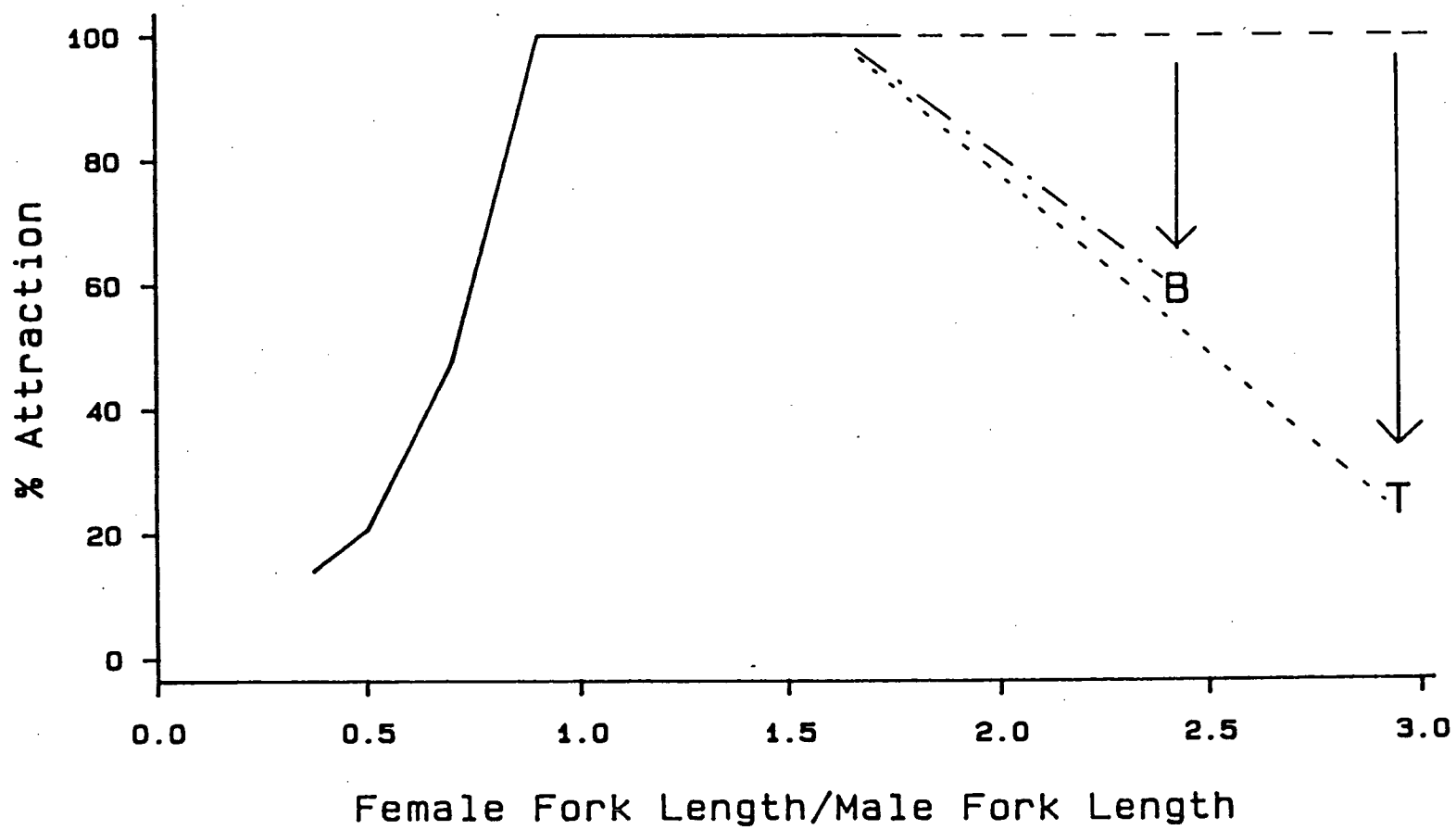
The idea that a polymorphism may result in a substantial decrease in gene flow between forms is not new. The imprinting of parental and sib colour morphs is another character associated with polymorphisms which can lead to assortative mating and possibly sympatric speciation in cichlid fishes (Kosswig 1947; Siepen and Crapon de Caprona 1986).

Finally, it has been argued that the evolution of premating isolation through mate choice is greatly restricted in nature because of complex genetic changes required in the manner in which individuals select mates (Felsenstein 1981; Sved 1981a, 1981b). Unless there is some initial linkage disequilibrium between gene(s) coding for assortative mating by form and those

under selection there can be no isolation between subpopulations. In the case of sockeye salmon and kokanee, little change in kokanee male choice is required to produce significant premating isolation between sockeye and kokanee in localities where the forms spawn sympatrically. In this case, the linkage is not chromosomal but size associated. Where separate, small kokanee males demonstrated no preference between females their own size and those much larger (approaching sockeye female size; Chapter 3). The slight reduction in the attractiveness of sockeye females to kokanee males in Babine Lake resulted in kokanee females being the most attractive and significant assortative mating by form (Fig. 34). The further reduction in the attractiveness of sockeye females to kokanee males in Takla Lake, in association with the greater genetic divergence (see Chapter 4), may simply represent an additional step in the process of the evolution of premating isolation. Thus, the evolution of a form effect in kokanee male choice does not appear to involve a major change in the manner in which males select mates, but rather an adjustment in the manner in which they respond to females of particular sizes, a behavioural characteristic seemingly amenable to selection within forms (see Chapter 3).

In conclusion, I have presented behavioural evidence to suggest assortative mating between sockeye and kokanee in Pierre and Narrows creeks is, in part, the result of male mate choice dependent on form. Male intrasexual competition and male mate

Figure 34. The attractiveness of sockeye females to kokanee males in Pierre Creek, Babine Lake ('B') and Narrows Creek, Takla Lake ('T') as compared to that expected based on the size alone.



choice dependent on male size do not directly account for the preference of kokanee males for kokanee females in both systems. I have argued that such form dependent choice may have evolved as a result of selection against the 'hybrids' of the two forms. Supporting this hypothesis, I demonstrated (Chapter 4) that sympatric sockeye and kokanee populations are genetically divergent, suggesting strong selection exists against 'hybrids'. Such selection, in association with the assortative mating by size and thus form (Chapter 1 to 3), can lead to the evolution of premating isolation. Some degree of premating isolation was observed in both Babine and Takla Lakes. The knowledge of the biology of O. nerka, and the genetic similarity between sympatric forms, suggests that sockeye and kokanee may have diverged in sympatry, thus leading to the possibility of sympatric speciation. Since Babine and Takla lakes have been deglaciated for less than 10,000 years (Lindsey and McPhail 1986), it is possible that the processes of genetic differentiation and evolution of reproductive isolation between sockeye salmon and kokanee are ongoing in both systems.

CONCLUSIONS

The evolution of premating isolating mechanisms between sockeye salmon and kokanee is consistent with models of sympatric speciation (e. g. Maynard Smith 1966; Rice 1984). As has been observed in other salmonids (e. g. Ivankov et al. 1981; Nordeng 1983), either form can give rise to the other (Ricker 1938, 1940, 1959, 1972; Foerster 1947; Scott 1984). The selective pressures experienced by sockeye and kokanee probably differ greatly (see Ricker 1940). For example, sockeye undertake extensive migrations to and throughout the north Pacific Ocean, after which they return to their population specific spawning grounds. The energy demands of these migrations are great (e. g. Mommsen et al. 1980), generating strong selection on swimming performance (e. g. Ricker 1972). In contrast, kokanee undergo no extensive migrations, alleviating the need to allocate large energy stores for migration and probably decreasing the selective pressures associated with prolonged arduous migrations. A difference in swimming performance is indicated by the relative inability of kokanee to navigate barriers compared to sockeye (Seeley and McCammon 1966). Freshwater parasite infestation rates (Salmincola) differ between sockeye and kokanee, with kokanee the more resistant (Ricker 1938). This suggests kokanee have developed specific defenses not necessary to sockeye, as Salmincola are lost upon entering saltwater (Ricker 1940). Genetic differences which accrue because of selective

differences between environments may persist because of the high degree of assortative mating by size, and hence by form (Chapters 1, 2, 3 and 5). That genetic differences do persist between forms was clearly evident in the genetic examination of allozyme frequencies (Chapter 4). Adaptive genetic differentiation promotes the evolution of premating isolating mechanisms. Premating isolation was observed between sockeye and kokanee in two separate systems, with the degree of isolation positively correlated to the degree of genetic differentiation (Chapter 5).

Two factors appear critical for such sympatric divergence to occur: there must be particular ecological conditions if two forms of one species are to occur together and; mechanisms must exist by which one form can give rise to the other.

There are numerous examples of the sympatric occurrence of two very similar forms within the Family Salmonidae (e. g. Lindsey 1963, 1981; Ivankov et al. 1981; Jonsson 1985; Hindar et al. 1986). The sympatric occurrence of two forms appears to be directly tied to the prevailing environmental conditions. Ciscoes (genus Coregonus, subgenus Leucichthys) normally occupy the pelagic zone of lakes, feeding on zooplankton with their numerous long fine gillrakers. Where ciscoes are absent, lake whitefish (Coregonus clupeaformis) normally a benthic feeder, typically have higher gillraker counts (Lindsey 1981), and in some lakes occur in two discrete high and low gillraker forms

(Lindsey 1963; Bodaly 1979). These two forms of whitefish occupy the pelagic and benthic zones, which are normally occupied by ciscoes and whitefish, respectively. Similarly, dwarf and normal sized non-anadromous Arctic char occur sympatrically in many Norwegian lakes, their co-occurrence apparently restricted to lakes deep enough to have a well oxygenated hypolimnion (Hindar and Jonsson 1982). Cherry salmon (O. masu) exist in both anadromous and non-anadromous forms, which may occur together or separately (Ivankov et al. 1981). The co-existence of the two forms is tied to the productivity of the freshwater environment, the greater the productivity the more probable that the two forms will co-exist.

The sympatric occurrence of sockeye salmon and kokanee appears tied to both lake productivity and the presence of competitors. Kokanee are absent from most coastal lakes containing sockeye salmon in British Columbia (Ricker 1940; Nelson 1968a; K. Hyatt, Pacific Biological Station, Nanaimo, pers. comm.). These lakes are typified by low productivity and small sockeye smolt sizes (Hyatt and Stockner 1985), suggesting food resources may not be great enough to support two sympatric forms. Food limitation in coastal lakes is probably further exaggerated by the presence of limnetic threespine sticklebacks, G. aculeatus, which compete directly for zooplankton (Manzer 1976). In contrast, kokanee are present in almost all of the central interior sockeye salmon lakes on the Fraser River system (Nelson 1968a; Goodlad et al. 1974), lakes typified by higher

zooplankton productivity, larger sockeye smolt sizes, and the absence of sticklebacks (Goodlad et al. 1974).

Given the necessary biotic conditions, kokanee appear able to persist in a lake utilized by juvenile sockeye salmon (or vice versa). Ricker (1938, 1940) outlined a mechanism by which kokanee could diverge from sockeye in sympatry. Sockeye salmon give rise to non-anadromous progeny (mainly males, called 'residuals' by Ricker, the non-anadromous progeny of anadromous parents), which Ricker suggested might be precursors of kokanee. It has since been demonstrated that crosses between residuals are viable (Smirnov 1959), and that sockeye introduced into lakes previously barren of O. nerka can give rise to self sustaining non-anadromous populations (Ricker 1959; Scott 1984). These facts, in conjunction with the high genetic similarity between sockeye and kokanee and the similar distribution of the forms support the contention that sockeye have given rise to kokanee on numerous occasions (see Chapter 4).

The strong male bias in residuals suggests they participate as sneaks to sockeye pairs. 'Sneaking' is a alternative reproductive strategy common amongst salmonids, by which (usually) small males participate in the spawning of larger pairs (see Chapter 1). Unlike males, females do not appear able to sneak spawnings; they must establish territories and attract males to reproduce. Since males discriminate against females smaller than themselves, small females are unlikely to attract

mates in the absence of small males (see Chapters 3 and 5). Hence small non-anadromous females are unlikely to persist as a type in the absence of non-anadromous males. However, once small non-anadromous males exist in the population, perpetuated by their ability for sneak fertilization, small non-anadromous females will be able to attract some males, increasing their reproductive chances. Once residual males commence spawning with residual females, the production of non-anadromous progeny from non-anadromous parents (i. e. kokanee) is possible, given a propensity to produce non-anadromous progeny. The propensity to produce non-anadromous progeny is apparent in the perpetuation of non-anadromous populations, originally derived from sockeye introductions (e. g. Scott 1984). Factors involved in sexual selection would then lead to assortative mating by size and form (outlined in Chapter 5), thus increasing the likelihood of genetic divergence between forms, which may lead to the evolution of premating isolating mechanisms and ultimately to speciation.

I conclude that sockeye have given rise to kokanee independently in many places which combine relatively high productivity with the absence of competitors, and that the process can occur sympatrically through the combination of sneak spawning by small males and of assortative mating with respect to size.

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