

Spatial and temporal isolating mechanisms: the formation of discrete breeding aggregations of sockeye salmon (*Oncorhynchus nerka*)

Andrew P. Hendry, Frank E. Leonetti, and Thomas P. Quinn

Abstract: This study examined the spatial and temporal isolation of breeding aggregations of sockeye salmon (*Oncorhynchus nerka*) along a single island beach in Iliamna Lake, Alaska. The density and spatial extent of these aggregations varied among years, but one of the sites (Fuel Dump Point) was consistently separated from another major spawning area (Fuel Dump Bay) by at least 15 m of unused but generally similar habitat. Females settled first at the Point and this site supported higher spawner densities than the adjacent Bay. Male breeding opportunity, estimated from operational sex ratios, was higher in the Bay soon after spawning commenced. However, few males moved from the Point into the Bay and all movement that occurred was late in the season, when breeding opportunities for males were very limited. The reproductive success of males that moved from the Bay to the Point was estimated to be 0.003% of the total reproductive success of all males at the Point. The reproductive success of males that moved from the Point to the Bay was estimated to be 3% of the total reproductive success of all males at the Bay. Thus, spatial and temporal variation in settling largely isolated the two spawning aggregations within a breeding season. We suggest that variation in habitat quality may interact with the heritability of spawning date, contributing to the formation of distinct breeding groups.

Résumé : On trouvera ici les résultats d'une étude de l'isolement spatial et temporel de groupes reproducteurs de Saumons rouges (*Oncorhynchus nerka*) le long d'une plage insulaire au lac Iliamna, Alaska. La densité et l'étalement spatial de ces groupes variaient d'une année à l'autre, mais à l'un des sites (pointe de Fuel Dump), les poissons du groupe étaient toujours séparés des poissons des autres frayères importantes (baie de Fuel Dump) par une bande d'une largeur de 15 m non occupée, mais offrant des conditions relativement semblables. Les femelles occupaient d'abord la pointe, et à cet endroit, la densité des poissons en fraye était plus élevée que dans les eaux adjacentes de la baie. Chez les mâles, les chances de reproduction, estimées d'après les rapports mâles : femelles réels, étaient plus élevées dans la baie peu après le début de la fraye. Cependant, peu de mâles se sont déplacés de la pointe vers la baie et les déplacements observés ont tous eu lieu vers la fin de la saison, au moment où les chances de reproduction devenaient rares pour les mâles. Le succès reproducteur des mâles qui se sont déplacés de la baie vers la pointe a été évalué à 0,003% du succès global des mâles à la pointe. Le succès reproducteur des mâles qui se sont déplacés de la pointe vers la baie a été estimé à 3% du succès reproducteur global des mâles à la baie. Il faut conclure que la variation spatiale et temporelle du choix d'habitat avait pour effet d'isoler les deux groupes reproducteurs au cours de la saison de reproduction. Nous croyons que la variation dans la qualité de l'habitat peut agir de concert avec l'héritabilité de la date de fraye, contribuant ainsi à la formation de groupes reproducteurs distincts. [Traduit par la Rédaction]

Introduction

Many organisms form breeding aggregations isolated in space and (or) time from conspecifics. Pacific salmon (*Oncorhynchus* spp.) cluster into discrete groups at spawning sites in streams or lakes. Several mechanisms are assumed to contribute to the formation of these aggregations. First, mature

salmon home to natal incubation areas, resulting in the reproductive isolation of spawning populations (Foerster 1968; Horrall 1981; Quinn et al. 1991; Quinn and Dittman 1990). Second, selection of spawning sites within the natal area by females reflects spatial variation in the distribution of conditions suitable for reproduction (Tautz and Groot 1975; Neilson and Banford 1983; Crisp and Carling 1989; Beard and Carline 1991; Vronskii and Leman 1991). The strong fidelity of females for their initial nesting site (e.g., Hanson and Smith 1967; Foote 1990) further limits mixing during the breeding season. Thus, spawning site choice by females results in aggregations of spawners in preferred habitats isolated from each other by areas of relatively poor

Received June 13, 1994. Accepted October 25, 1994.

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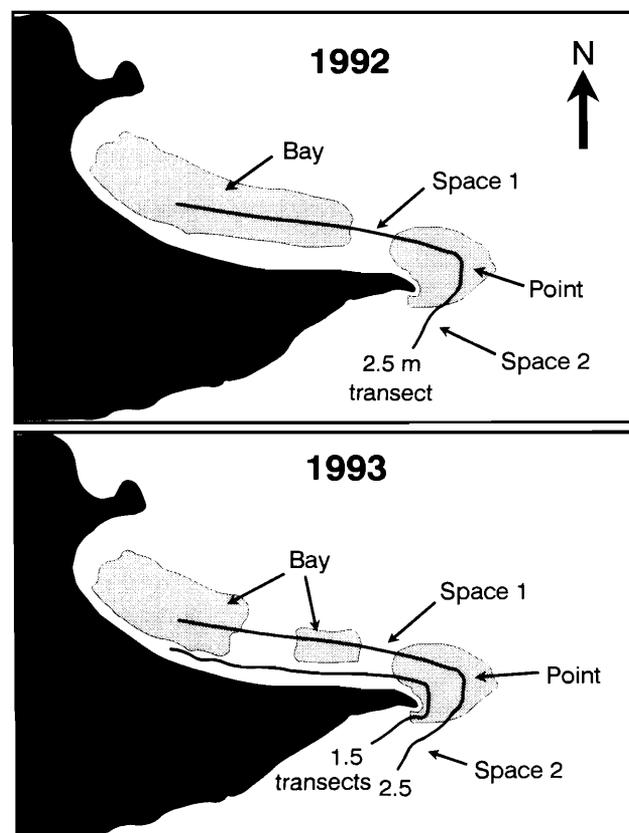
habitat. A third mechanism, temporal separation, can also contribute to isolation as the spawning of adults and the incubation and emergence timing of embryos become synchronized to local conditions (Bams 1969; Brannon 1987).

Reproductive isolation allows selection and random genetic drift to act, resulting in genetic population structure (Quinn et al. 1987; Utter et al. 1989; Altukhov and Salmenkova 1991; Varnavskaya et al. 1994) and local adaptation to specific spawning and rearing environments (Ricker 1972; Taylor 1991). Of the isolating mechanisms, natal homing has received the most attention. However, the tendency of salmon to form distinct populations at varying spatial and temporal scales emphasizes the need to examine other mechanisms that initiate and maintain reproductive isolation. Moreover, processes of isolation are important considerations in conservation genetics as they influence effective population size (Meffe 1987) and the identification of distinct population units (Utter 1981; Waples 1991).

At large scales, spatial separation of spawning sites, and differences in spawning time between sites, clearly contribute to reproductive isolation. For instance, straying is more common between nearby spawning areas than between distant locations (e.g., Labelle 1992; Pascual and Quinn 1994; Tallman and Healey 1994). This parallels studies of genetic population structure that can often distinguish between salmon from different geographical areas or river systems but not between salmon from nearby streams (Grant et al. 1980; Wilmot and Burger 1985; Withler 1985; Wood et al. 1994). Studies of temporal isolation commonly focus on the formation of seasonal races. Leider et al. (1984) reported differences in spawning time and location limited gene flow in steelhead (*O. mykiss*). Gharrett and Smoker (1993) found little gene flow between early and late runs of pink salmon (*O. gorbuscha*) in a single stream. Tallman and Healey (1994) showed that straying was low among chum salmon (*O. keta*) populations that spawned at different times and at different locations. In sockeye salmon (*O. nerka*), Varnavskaya et al. (1994) noted that genetic differentiation in lakes was greatest among subpopulations that had different run timing. At smaller scales the interaction of natal homing, habitat selection, and temporal variation in the establishment and maintenance of reproductive isolation is unknown.

The objective of this study was to investigate fine-scale spatial and temporal isolation of spawning populations within a breeding season. Specifically, we hypothesized that a combination of differences in spawning date, coupled with limited movement between sites, would contribute to partial isolation of adjacent breeding groups. To investigate these processes, we chose two spawning aggregations of sockeye salmon separated by only 15 m, a scale at which site-specific natal homing was unlikely. Variation in the number and condition of spawners at the various sites was used to document temporal patterns in spawning and to develop indices of estimated "relative breeding opportunity" (RBO) for males. The observed movement of males was then compared with movement patterns that would have minimized spatial variation in RBO. The estimated reproductive success of males which moved between sites was compared with that of males which did not move. Physical habitat variables that might account for the observed distribution of spawners were quantified to evaluate the role of spawning site selection.

Fig. 1. Transect placement at Fuel Dump Island in 1992 and 1993. The shaded areas correspond to the approximate distribution of spawning groups.



Methods

Study site

In Iliamna Lake, Alaska, sockeye salmon spawn along certain island beaches (Demory et al. 1964; Olsen 1964; Kerns and Donaldson 1968; Blair and Quinn 1991; Blair et al. 1993) as well as in other types of habitat. Qualitative observations from 1988 through 1991 suggested that sockeye salmon spawning on one of these beaches (Flat Island No. 1 in Demory et al. 1964; Fuel Dump Island in Blair et al. 1993) formed several spatially discrete groups. Two of these groups were chosen for this study. The first was in a small area adjacent to a point of land (Fuel Dump Point) and the second was in a larger area in the bay immediately to the northwest (Fuel Dump Bay). Transects placed through these areas (Fig. 1) formed the basis for all subsequent data collection. Each transect consisted of a lead line placed along the bottom at a standard depth. In 1992, a single 120 m long transect was established at 2.5 m depth. This transect extended from an unused section of beach, through a spawning area at the Point and an unused section between the Point and Bay, and into the Bay spawning area. In 1993, transects were established in this area at the 1.5- and 2.5-m isobaths.

Distribution and dynamics of spawning

Transects were surveyed daily (August 15–31, 1992, and August 6–29, 1993) and the number and condition of females in each 2.5 m (along the transect) × 2 m (1 m on

either side) section of the transect were estimated visually. Females were classified as green (distended abdomen, not associated with the bottom), ripe (distended abdomen, associated with a particular location on the bottom), or spawned-out (concave abdomen, associated with a particular location on the bottom). The number of males associated with each female was also recorded. Based on examination of males captured at this site by beach seine in previous years, all males were assumed to be reproductively active (i.e., ripe) for the duration of their residence in the spawning area. Daily transect counts (in 2.5-m increments) of nesting (ripe + spawned-out) females were used to identify spatial groupings. Data collected within each of these groupings were pooled for comparisons among sites (Bay, Point, space 1, space 2; Fig. 1). Numbers of ripe males, ripe females, and spawned-out females along transects were determined by adding counts for all 2.5-m increments on each day within each site. Densities were calculated by dividing these totals by the area covered by the transect at each site. The operational sex ratio (number of ripe males/number of ripe females; Emlen 1976) and the proportion of nesting females that were spawned-out (number of spawned-out females/number of nesting females) were determined for each site on each day.

Transects placed for daily surveys covered a fraction of the total area used by spawners (Fig. 1). On August 22, 1993, a more extensive sampling grid was used to determine the total area of spawning beach used by sockeye salmon, and subsequently to estimate the total number of spawners at each site (Fuel Dump Bay and Fuel Dump Point). For this purpose, the existing 1.5 m depth transect was extended through the Bay and into an unused area to the northwest. Every 10 m along this transect, the extent of spawning was measured along a line perpendicular to the shore. This survey was used to estimate the total spawning area at each site. The total number of spawners at each site on each day was calculated by multiplying the density of spawners along transects by the total spawning area.

Tagging and male longevity

During snorkel surveys, plastic dart tags (Floy Tag, Inc.) specific to the site (Point or Bay) and date of tagging were inserted into the dorsal hump of male sockeye salmon by means of a hollow needle attached to a pole spear (Adkison et al. 1995). All tagging took place within 5 m of a transect and the selection of males was random within this area. Over the 2-year period, only 2 of 248 tagged males appeared to be injured by this technique. During transect surveys, the presence and site-specific identity of all tagged males within 5 m of each transect was recorded. In 1993, 27 other ripe males that showed no deterioration or scarring were tagged with individually color-coded dart tags, using the same technique. Of these additional males, 17 were tagged at the Point on August 8, one day after the first females settled, and 10 were tagged in the Bay on August 12, three days after the first females settled there. The location of each individually tagged male (to the nearest 2.5-m increment along the nearest transect) was recorded each day. The difference between the last day on which a male was observed and the day it was tagged provided an estimate of the average residence time of males at the two sites. To account for a possi-

ble delay between initial settling and tagging (see above), 1 and 3 days were added to the observed residence time of males at the Point and the Bay, respectively. This generated an estimate of the longevity of males at the two sites. The average longevity of individually tagged males was compared between the Point and the Bay using a two-sample *t* test ($\alpha = 0.05$).

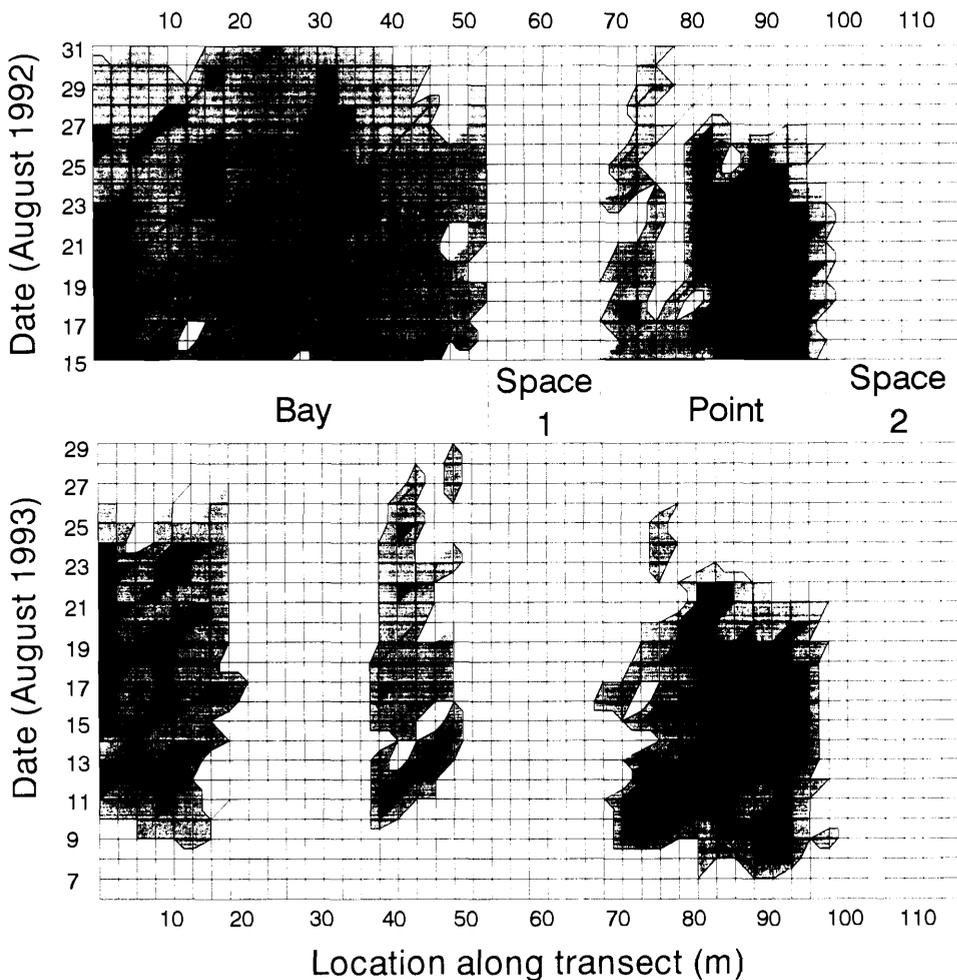
Movement and reproductive success of males

To compare the observed movement of males between sites with that which would be expected if males distributed themselves so as to equalize ratios of ripe males to ripe females (analogous to the "ideal free distribution"; Fretwell and Lucas 1970), we developed an index of relative breeding opportunity (RBO). RBO estimates were based on the reciprocal of the operational sex ratio on each day at each site. An even number of ripe males and ripe females at a given site would produce an estimated RBO of 1.0 for males at that site. As the number of males relative to ripe females increased, the estimated RBO would decrease proportionately. The sum of all daily RBO estimates at a site provided the total estimated RBO for an average male resident at that site for the duration of the spawning season. Predicted optimal male movement (movement that would have maximized an individual male's total RBO) was estimated by comparing the total RBO obtained by settling at a particular site (Bay or Point) and remaining at that site with the total RBO obtained by settling at a particular site and then moving to the other site on a given day. This was calculated by adding the sum of all daily RBO estimates at the initial site before moving to the sum of all daily RBO estimates at the new site after moving.

The estimated RBO was a function of the number of ripe females and males at a given site and did not consider several factors that may affect reproductive success. First, males that move could have a reduced ability to compete with resident males, lowering their relative breeding success at a new site. Second, males weaken as the length of time they spend on the spawning grounds increases, so their ability to obtain a dominant position may decrease as they senesce. The estimated RBO was not sensitive to these differences, as it was an average for all males at a given site on a given day. The use of the estimated RBO as a surrogate for reproductive success would have overestimated genetic exchange, especially late in the breeding season. We also did not quantify male body size, which influences mating success (Schroder 1981; Foote 1990; Quinn and Foote 1994). However, studies at a nearby island beach found no difference in size between tagged males that disappeared and those that remained at the site, or between males that moved throughout the spawning area and those whose movements were very limited (Quinn and Foote 1994). Alternative mating strategies (i.e., sneaking) may influence reproductive success (Gross 1985), but jacks were very rare on island beaches (<2%; Blair et al. 1993).

Reproductive isolation of the two sites (Fuel Dump Point and Fuel Dump Bay) within a breeding season was investigated by comparing the total reproductive success (estimated) of males that moved between sites with those that did not. The relative reproductive success of these two tactics was estimated by the number of males that moved between sites

Fig. 2. Observations of nesting females in 2.5-m increments along the 2.5-m transect by date in 1992 and 1993. Light shading indicates the presence of a single female and dark shading indicates the presence of more than one female.



and the estimated RBO of an average male at a given site on a given day. We assumed that once females had chosen a nesting site, they did not subsequently breed elsewhere and so did not contribute to mixing between sites. This tendency for nest-site fidelity by females has been well documented in studies of the reproductive behavior of stream-spawning salmonids (Hanson and Smith 1967; Foote 1990) and was supported by observations on beaches in Iliamna Lake (Quinn and Foote 1994; Adkison 1994). The estimated reproductive success of males that moved relative to those that did not was calculated using the formula (see the Appendix for the full derivation of this estimate)

$$[1] \quad RS_{A \rightarrow B} = \frac{\sum_{d=6}^{29} \left[\frac{(n_{A,B,d})(F_{B,d})(M_{A,d})}{(n_{A,A,d})(M_{B,d})} \right]}{\sum_{d=6}^{29} (F_{B,d})}$$

where

$RS_{A \rightarrow B}$ is the estimated reproductive success of males that moved from one site (A) to another site (B) relative to all of the males at site B

A is one of the two sites (Fuel Dump Point or Fuel Dump Bay)

B is the other site

d is the date (August 6 through August 29, 1993)

$n_{A,A,d}$ is the number of males originally tagged at site A (A-tagged) and observed at site A on day d

$n_{A,B,d}$ is the number of A-tagged males observed at site B on day d

$F_{B,d}$ is the estimated total number of females at site B on day d

$M_{A,d}$ is the estimated total number of males at site A on day d

$M_{B,d}$ is the estimated total number of males at site B on day d

Environmental variation

Four environmental features (substrate size, water temperature, dissolved oxygen, and water flow) were quantified along transects in 1993. Surface substrate composition was determined in each of 12 quadrats (5×2 m) spaced at 10-m intervals along the 1.5 m depth transect. Prior to any settling or nest building, 100 rocks were collected at random from the surface substrate in each quadrat and the median axis of each rock was measured to the nearest millimetre (Wolman 1954; Kondolf and Li 1992). Measurements of the median axis of all rocks collected within each site (Bay, space 1, Point,

Fig. 3. Proportions of nesting females that were spawned-out (number spawned-out / number nesting) by site and date in 1992 and 1993.

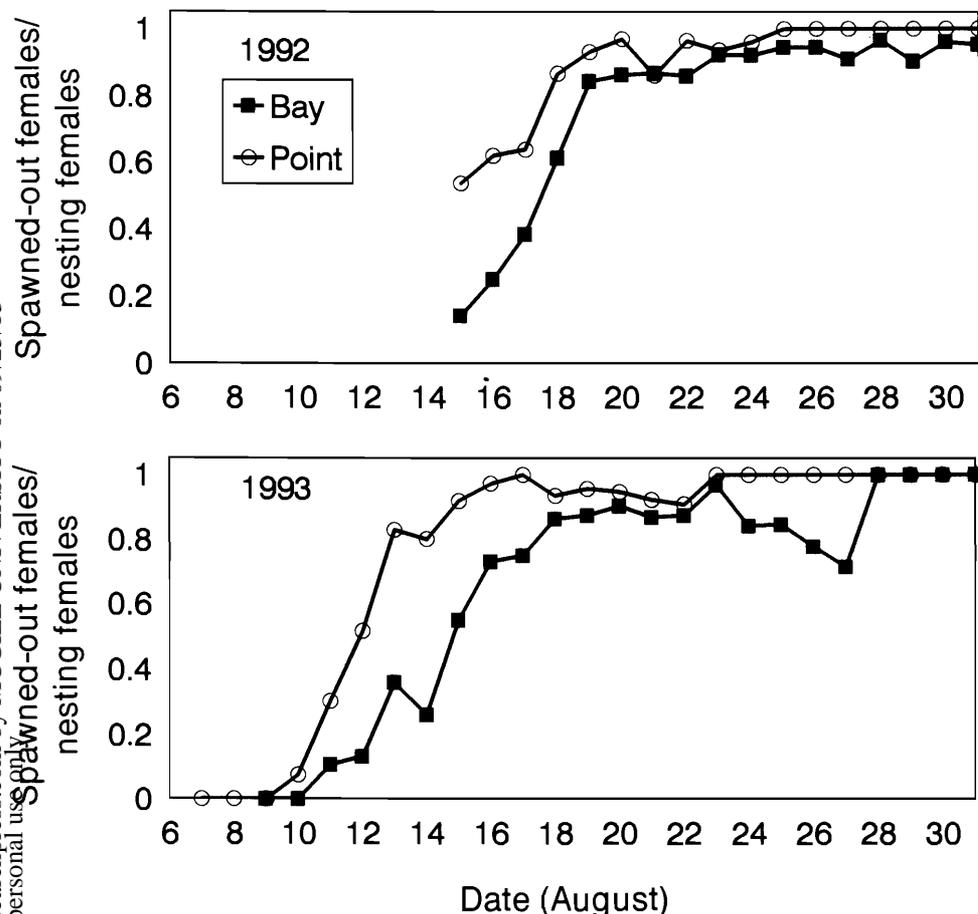


Table 1. Timing of specific phases of spawning (first settling by females, 50% of nesting females spawned-out, maximum density of ripe females, maximum density of all spawners) at Fuel Dump Point and Fuel Dump Bay in 1992 and 1993.

	1992		1993	
	Point	Bay	Point	Bay
Date (August) first females settled	9 ^a	13 ^a	7	9
Date (August) 50% of females spawned-out	15 ^b	18	12	15
Maximum density of ripe females	15 ^b (0.26)	15 ^b (0.30)	9 (0.60)	12 (0.31)
Maximum density of nesting females	15 ^b (0.59)	19 (0.43)	15 (0.74)	23 (0.49)
Maximum density of all spawners	15 ^b (1.62)	15 ^b (0.82)	9 (1.96)	16 (0.78)

NOTE: Numbers in parentheses are the maximum observed densities (number/m²) for each date and location.

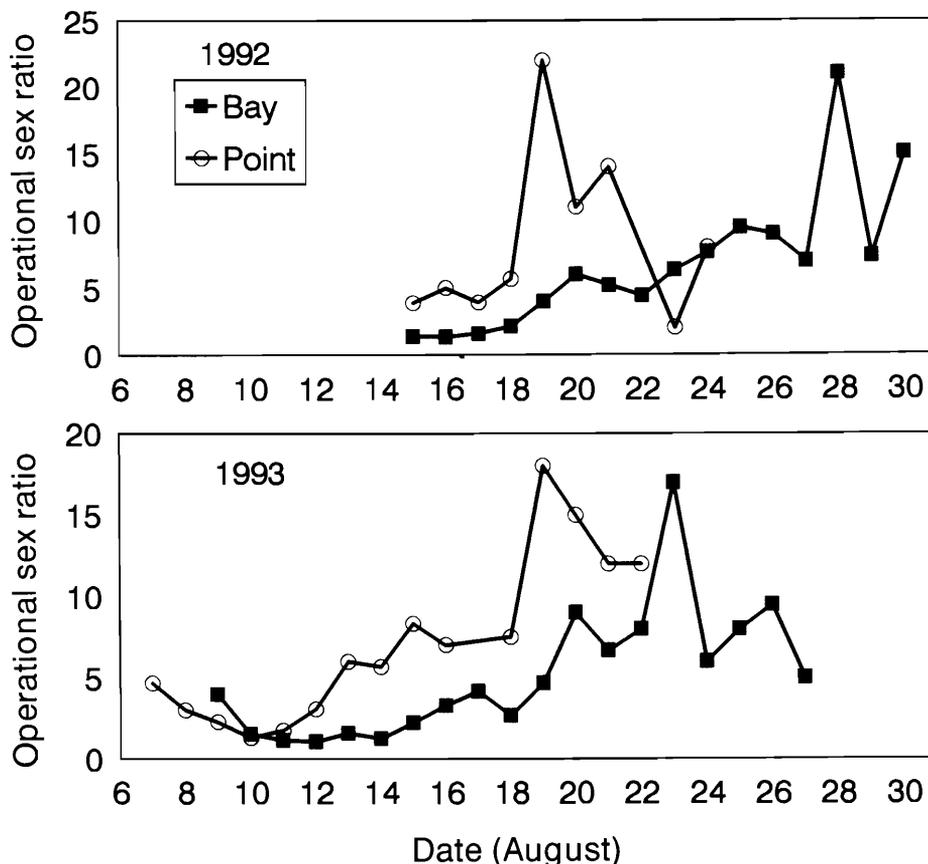
^aThe initiation of spawning in 1992 was determined on the basis of qualitative snorkel surveys prior to the commencement of transect surveys.

^bIn 1992, August 15 was the first day of transect surveys.

space 2) were used to establish frequency distributions of surface substrate composition. Geometric mean particle size was determined for each area and pairwise differences between cumulative distribution functions were compared using two-sample Kolmogorov–Smirnov tests.

Water temperature (°C) and dissolved oxygen (% saturation) were measured with a temperature–oxygen probe (Oxyguard Handy Oxygen Probe, Point Four Systems Inc., accuracy 2% at 0–50 ppm) held directly over the substrate at 24 locations (5-m intervals) along the 1.5 m depth transect

Fig. 4. Operational sex ratio (number of ripe males / number of ripe females) by site and date in 1992 and 1993. The lines end when no ripe females were present (earlier at the Point than in the Bay).



each day from August 5 to August 29. These measurements were also taken along the 2.5 m depth transect on 14 of these days. Daily average temperatures and daily within-site standard deviations in temperature were compared among sites using one-way ANOVA with repeat measures. As dissolved oxygen was close to saturation in all samples (>96%), statistical analyses were not performed.

Water flow was quantified using laboratory-calibrated plaster of Paris cylinders (35 cm² surface area) that dissolved at a rate correlated ($r^2 > 0.94$) with average water velocity and temperature (Petticrew and Kalff 1991; F.E. Leonetti and T.P. Quinn, in preparation). A total of 64 cylinders were deployed at Fuel Dump Island for 48–72 h to allow continuous dissolution or “flux” rates (g·cm⁻²·h⁻¹·°C⁻¹) of cylinders between and within transect sites to be compared. On August 10, 36 cylinders were placed on threaded steel rods 5 cm above the gravel at 6 sites along the 2.5 m depth transect. On August 25–27, 18 cylinders were placed at 10-m intervals on the 1.5 m depth transect and 10 additional cylinders were deployed along the 2.5 m depth transect at irregular intervals. Water flow (flux) was compared among sites using one-way ANOVA for each set of cylinders deployed. All statistical analyses were performed using $\alpha = 0.05$.

Results

Transect surveys in 1992 and 1993 confirmed previous observations: sockeye salmon spawning at Fuel Dump Point and

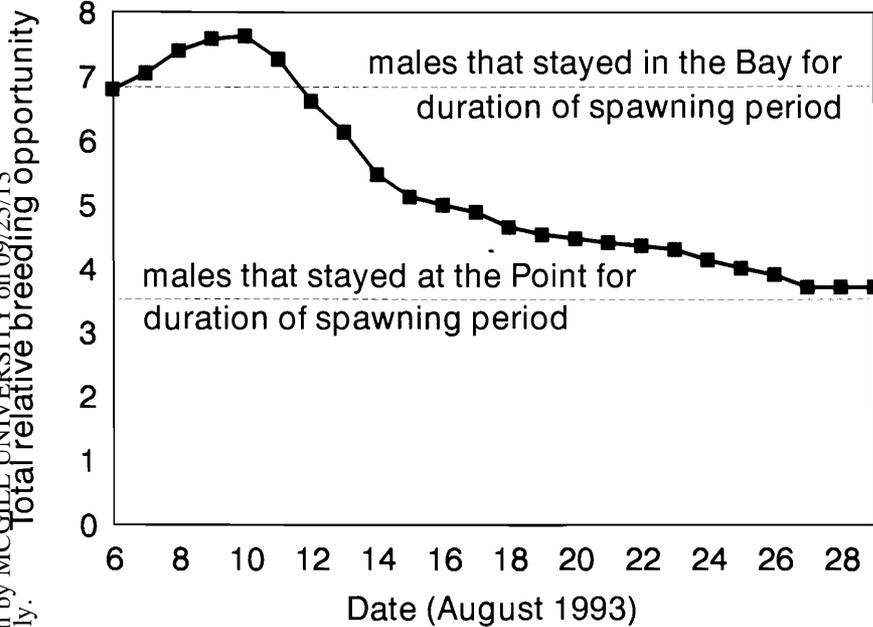
Table 2. Number of males that were tagged at each site in 1992 and 1993 (N) and the total number of observations of individuals in each of these tagging groups at each site.

	n	At observation site					
		1992		1993			
Tagging site		Point	Bay	Point	Bay 1	Bay 2	Bay 3
1992							
Point	44	125	8				
Bay	44	1	121				
1993							
Point	95			393	17	3	24
Bay 1	55			2	219	10	7
Bay 2	10			0	6	33	5

NOTE: In 1992, tags were counted in the Bay within 5 m of the 2.5 m depth transect from 0 to 52.5 m. In 1993, the Bay was divided into 3 areas for the enumeration of tagged males. All tagged males within 5 m of the transect were counted daily in Bay 1 (0–22.5 m along the 2.5 m depth transect) and Bay 2 (37.5–50 m along the 2.5 m depth transect). Bay 3 (an additional spawning area not covered by transects) was surveyed each day from August 13 through August 20 and every other day thereafter.

Fuel Dump Bay were separated by 15 m of unused beach (Fig. 2). These groups (Point and Bay), the space between them (space 1), and the unused area south of the Point (space 2), formed the basis for our comparison of adjacent

Fig. 5. Theoretical total “relative breeding opportunity” (RBO) of an average male that initially settled at the Point and then moved to the Bay on a specific date (the sum of all daily RBO estimates at the Point before moving plus the sum of all daily RBO estimates in the Bay after moving). For males that stayed at the Bay and the Point for the duration of the spawning period, the estimated total RBO was 6.8 and 3.7, respectively.



Spawning aggregations (Fig. 1). In 1993, the spawning population at the Point extended 32.5 m along the 2.5 m depth transect and 22.5 m along the 1.5 m depth transect. This distribution was very similar to that observed in 1992. In 1993, the spawning population in the Bay extended 100 m along the 4.5 m isobath. In 1993, the estimated maximum number of nesting females was 244 (0.74/m²) at the Point (August 15) and 995 (0.49/m²) in the Bay (August 23). Although no salmon were observed along the 1.5 m depth transect in the Bay, spawning began only 30–50 cm deeper (1.5–2 m from the transect). The only observed difference in spawner distribution between the two years was an additional unused section in the Bay (20 m along the 2.5 m depth transect) in 1993 (Figs. 1 and 2). Salmon were not observed in space 1 or space 2 in 1992 and 1993. Qualitative observations in 1994 revealed similar distribution patterns to those in 1993.

Settling of female sockeye salmon at Fuel Dump Island occurred explosively. At the Point, more than 80% of all females had established nesting sites within the first 2 days of settling. In the Bay, 80% of all females had established nesting sites within the first 5 days of settling at that site. As settling began several days earlier at the Point (Table 1), many females settled there before any settled in the Bay. Spawner density peaked sooner and at a much higher level at the Point (Table 1) and the proportion of females that were spawned-out was higher at the Point throughout the period of overlap between the sites (Fig. 3). The operational sex ratio increased for most of the spawning period at both sites, peaking at the Point 4 (1993) and 9 (1992) days before it did so at the Bay (Fig. 4). In 1994, these variables were not quantified but the general pattern was the same.

In both years, approximately 30% of all tagged males were never seen again during transect surveys at Fuel Dump

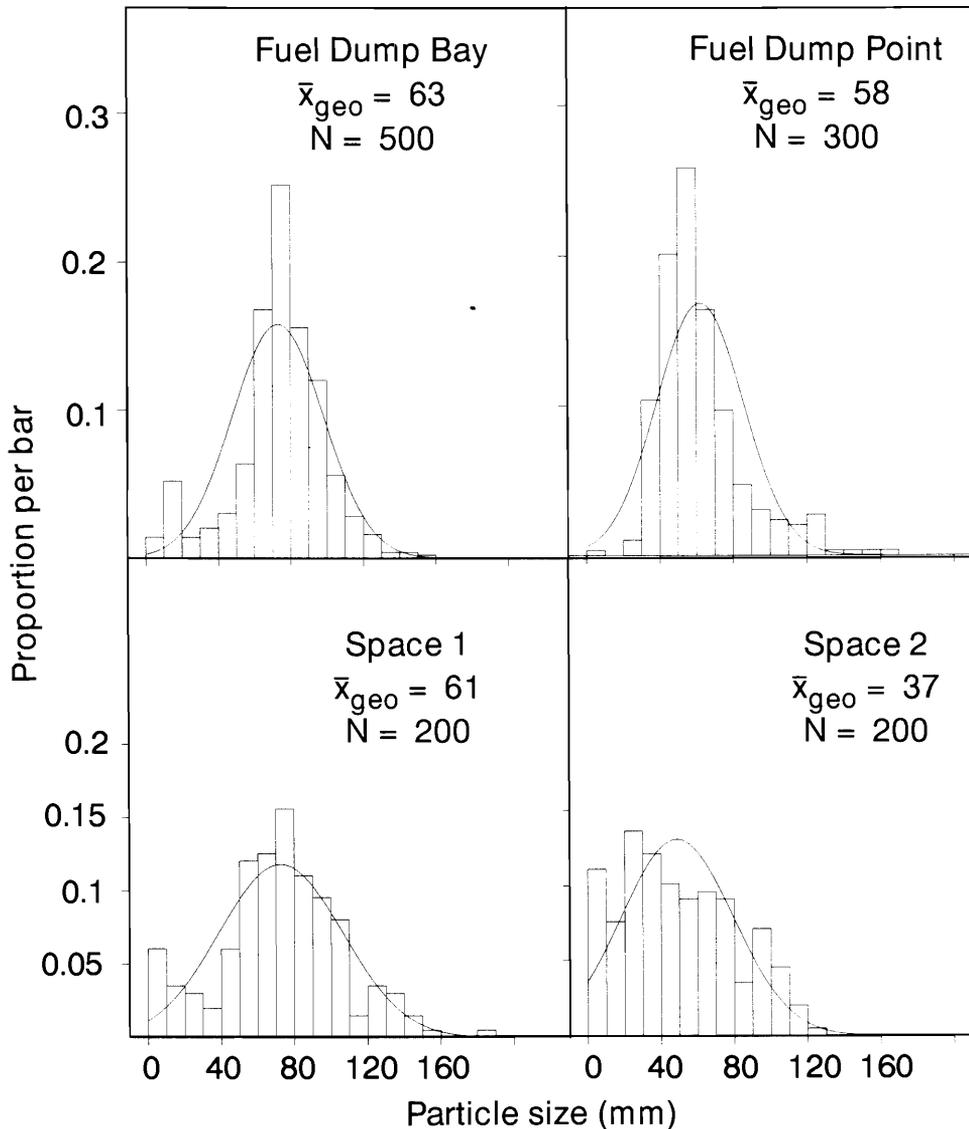
Island or during one-time surveys at 9 other island beaches. Daily observations along transects at Fuel Dump Point and Bay indicated a steady decrease in the number of tagged males from the initial day of tagging to the end of the spawning period. The large majority of observations of tagged males occurred at the initial tagging site, although a few males initially tagged at the Point (Point-tagged males) were later observed in the Bay (Table 2). Movement of tagged males between sites was not detected until 6–9 days after tagging. The estimated average longevity of males at the Point and the Bay, estimated from individually tagged fish, was similar (6.7 and 7.5 days, respectively; $p = 0.875$).

Males that stayed in the Bay for the duration of the spawning season had a higher estimated total RBO than males that stayed at the Point, owing to more favorable operational sex ratios (Fig. 4) and a much larger number of nesting females in the Bay. However, a male that initially settled at the Point and then moved to the Bay between August 7 and August 11 would have had a higher estimated total RBO than males that settled at either site and did not move (Fig. 5). That is, the Point was more favorable for the first few days (females did not settle in the Bay until August 9; Fig. 2) and the Bay was more favorable later (operational sex ratios were lower in the Bay than at the Point after August 10; Fig. 4). Estimates of the number of males that moved and their RBOs indicated that the estimated reproductive success of Point males in the Bay was approximately 3% of the total reproductive success of all males in the Bay. The estimated reproductive success of Bay males at the Point was 0.003% of the total reproductive success of all males at the Point.

Fuel Dump Point and Bay spawning beaches lacked woody debris or other structural features likely to affect spawning site quality. The only visible aquatic plants were 18 macro-

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Fig. 6. Size distributions of surface substrate particles sampled, using the Wolman (1954) pebble count. Normal curves with the same mean and standard deviation as the sample are superimposed over observed counts for purposes of comparison. The geometric mean particle size (\bar{x}_{geo}) and total sample size (N , number of rocks measured) are shown for each site.



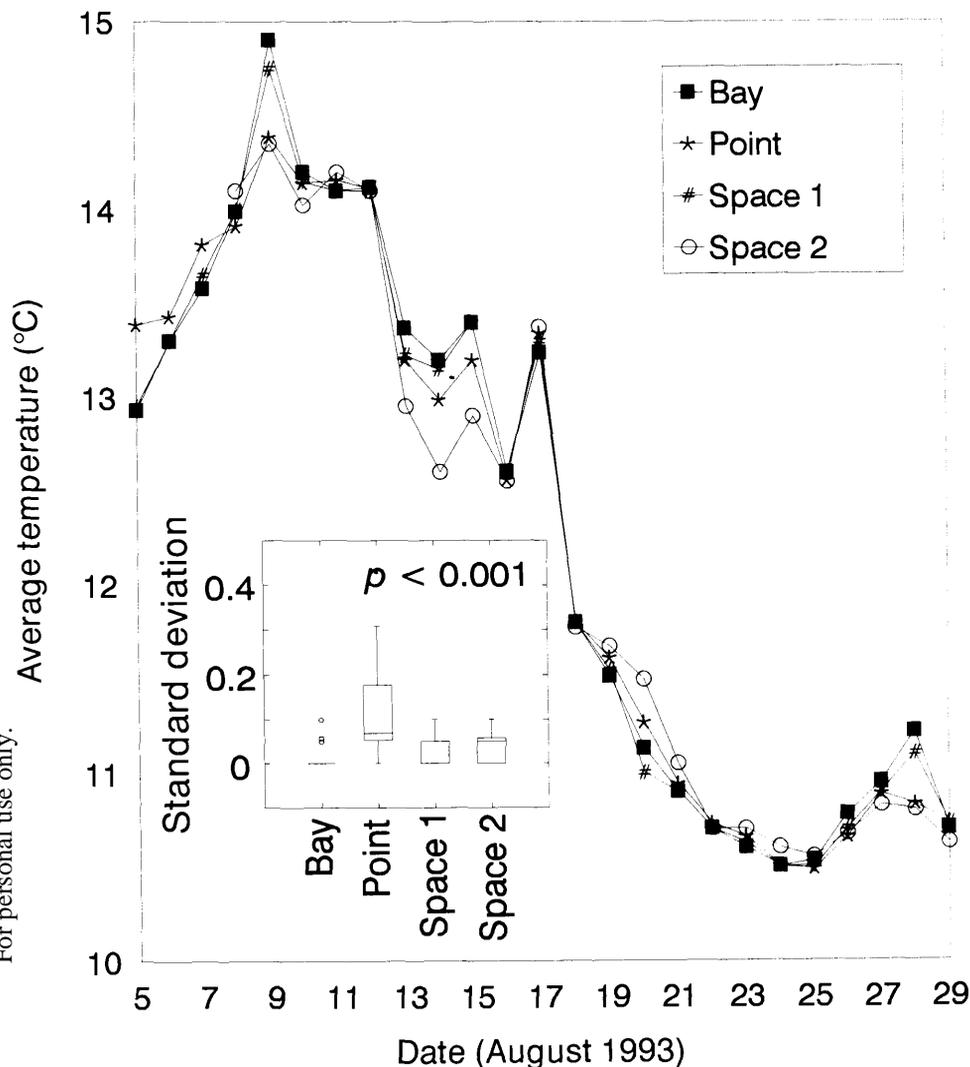
phytes in the area previously defined as space 1. Surface substrate composition varied among the four discrete areas (Bay, Point, space 1, and space 2), based on samples taken along the 1.5 m depth transect ($p < 0.01$ for the Bay against space 1 and $p < 0.001$ for all other pairwise comparisons). Frequency histograms showed that nonspawning areas (spaces 1 and 2) had broader substrate size distributions than spawning areas (Fig. 6). Space 2 had the smallest geometric mean particle size and more fine particles than the other sites. Mean water temperature ranged between 14.9°C (Bay, August 9) and 10.5°C (Point, August 25), with a generally decreasing trend through the spawning period (Fig. 7). Although water temperatures varied by as much as 0.6°C among sites within a day, these differences were not significant when considered for the entire spawning period ($p = 0.154$). Temperature varied considerably within a site and average daily within-site standard deviation in temperature was highest for the

Point and lowest for the Bay (Fig. 7 inset). In water immediately above the gravel surface, dissolved oxygen levels never fell below 96% saturation and were similar within and among sites. Surface water flow at 1.5 and 2.5 m depth, as measured by cylinder flux was greatest in the area between the Point and the Bay (space 1), decreasing toward the spawning aggregations at the Point and in the Bay, with a minimum in the area beyond the Point (space 2; Fig. 8).

Discussion

Sockeye salmon spawning along a single beach at Fuel Dump Island formed at least two spatially discrete breeding aggregations. The density and extent of these aggregations varied between years but one of the areas used by spawners (Fuel Dump Point) was consistently separated from the major spawning area (Fuel Dump Bay) by 15 m of unused beach.

Fig. 7. Average within-site water temperatures by day for each of the four sites. Inset: Average daily within-site standard deviations in water temperature.



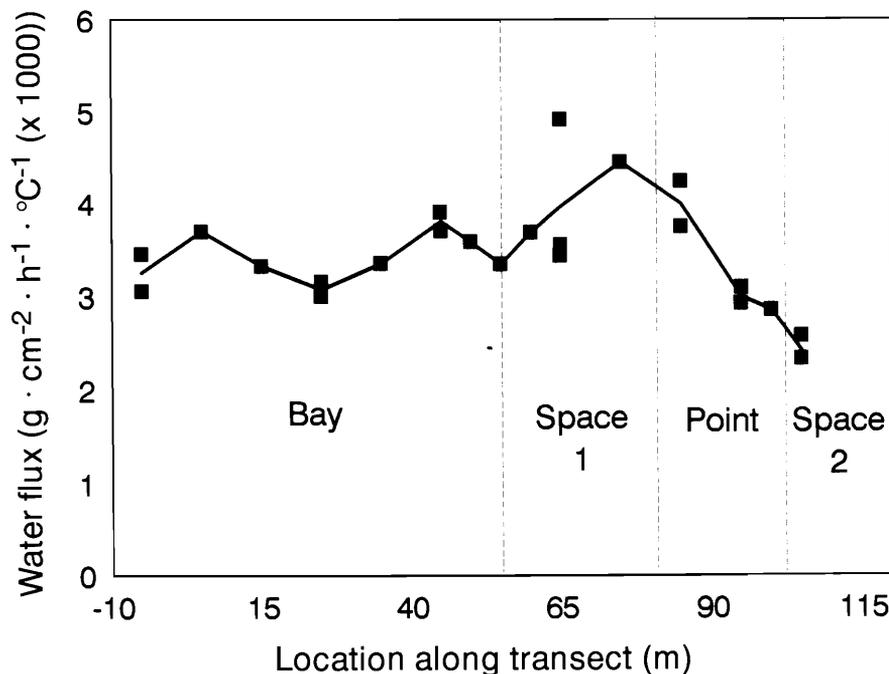
This isolated Point was the first area to be settled by females and supported higher densities of spawners than adjacent aggregations at Fuel Dump Island and other spawning beaches (C.J. Foote and P. Schlenger, unpublished data). Despite the fact that the Bay soon surpassed the Point in potential breeding opportunities, few males that initially settled at the Point ever moved to the Bay. Those males that moved did so late in the breeding season, when almost all females were spawned-out, and so contributed little to spawning in the Bay. Virtually no males moved from the Bay to the Point. In our discussion we evaluate how the lack of movement between sites may contribute to the isolation of these groups within a breeding season, consider a possible environmental basis for spatial and temporal variation in spawning between sites, and integrate our results into a consideration of mechanisms that may initiate and maintain reproductive isolation.

Male movement, relative breeding opportunity, and estimated reproductive success

While female salmon show a strong affinity for their nest site (e.g., Hanson and Smith 1967; Foote 1990), males spawn

with several females at different sites during the spawning period (Mathisen 1962). Males often desert a female immediately after spawning and attempt to replace males attending other ripe females (Keenleyside and Dupuis 1988). Male-biased sex ratios induce competition among males, increase energy expenditure, reduce the average contribution of an individual's sperm to the fertilization process, and increase the time between spawning events (Schroder 1981; Semenchenko 1987). As the density and condition of breeding females vary through space in a spawning environment, males in a freely mixing population should respond to this heterogeneity by minimizing spatial variation in operational sex ratios (analogous to an "ideal free distribution"; Fretwell and Lucas 1970). However, the operational sex ratio was higher and the absolute number of ripe females lower at the Point than in the Bay (i.e., less favorable for males) for most of the spawning period. The optimal movement pattern (predicted from ratios of ripe males to ripe females) of a male faced with this pattern would have been to settle at the Point and then move to the Bay several days later. Surprisingly, only a small fraction of males tagged at the Point were ever

Fig. 8. Average water flux for gypsum cylinders 5 cm above the substrate (F.E. Leonetti and T.P. Quinn, in preparation). Each marker represents the average flux for a group of cylinders placed at the specified location on a given date.



observed in the Bay and movement was not observed until at least 6 days after tagging. Thus, for most of the survey period, the distribution of males across the two areas did not reflect apparent breeding opportunities. Spatial variation in operational sex ratio has also been observed on another island beach where ratios were higher in shallow water, an area presumed to provide a superior reproductive environment (T.P. Quinn, M.A. Adkison, and M.B. Ward, in preparation). Although there was some movement, interbreeding between fish at the Point and in the Bay must be slight within a season because (i) females probably remained at their initial nest site (Hanson and Smith 1967; Foote 1990; Quinn and Foote 1994), (ii) males seldom moved between sites, and (iii) males that moved did so when their breeding chances were poor. The lack of mixing between sites within a breeding season was reflected in our estimate that males which initially settled at the Point contributed to approximately 3% of spawning in the Bay, while those which initially settled in the Bay contributed to less than 0.003% of spawning at the Point.

Once males chose a particular spawning area they tended to remain at that site. This is in accord with the conclusions from other tagging studies on sockeye salmon wherein males rarely stray from their tagging location (Varnavskiy and Varnavskaya 1985), displaced males tend to return to their site of capture (Blair and Quinn 1991), and males that are blocked from their spawning stream do not initially seek another location (Hartman and Raleigh 1964). As in other studies (Blair and Quinn 1991; Quinn and Foote 1994), a substantial fraction of the tagged males disappeared. Very few of these fish subsequently reappeared at the tagging site or in nearby areas. The fate of these males is unknown, but their disappearance was probably not an artifact of the tagging procedure because the density of untagged males in each

transect segment also fluctuated over time. Furthermore, the chosen tagging technique was one that causes a low incidence of injury and does not appear to result in substantial behavioral alterations by fish (Adkison et al. 1995).

Environmental features

The first females to mature in a particular area are presented with the greatest choice of spawning sites and presumably select areas that allow maximum reproductive success. As the spawning season progresses, areas with the best spawning habitat should support the highest spawner densities. At Fuel Dump Island, the Point was settled first. By the time females began to settle in the Bay, the density of females at the Point was already higher than the maximum density ever observed in the Bay or at 8 other beach spawning sites within 6 km of Fuel Dump Island (C.J. Foote and P. Schlenger, unpublished data). We infer that the Point is an excellent incubation environment because it projects into a narrow channel that separates Fuel Dump Island from Porcupine Island. Wind-driven currents funnel through this channel, creating a noticeable current on many days. Seiches would provide a regular source of water circulation at the Point; however, water movement in the Bay would result primarily from onshore winds, which initiate wave-driven circulation. Water temperature varied by more than 0.5°C over a 5- to 10-m distance at the Point on several of the survey days but was largely invariable within the Bay on any given day (Fig. 7 inset). This difference likely reflects a complex pattern of water circulation. Water flux measurements suggested that flows peaked immediately to the north of the Point, tapering off to both sides (Fig. 8). These flow patterns may account for the apparent preferred status of the Point spawning area.

The distribution of spawning salmon has often been explained in terms of site selection by females, based on

environmental variation (Tautz and Groot 1975; Duker 1977; Neilson and Banford 1983; Crisp and Carling 1989; Vronskii and Leman 1991). At Fuel Dump Island, we quantified spatial and temporal patterns of variation for some environmental features that may influence site selection by females (surface substrate composition, water temperature, dissolved oxygen, and water flow). Comparisons among the two spawning areas and the two nonspawning areas indicated some association between physical factors and the distribution of spawners. Smaller substrates reduce the survival of salmon embryos by reducing water flow, which limits oxygen availability (see review in Chapman 1988). At Fuel Dump Island, one of the nonspawning areas (space 2) had the highest proportion of small gravels and the lowest average water velocity, though in comparison with most spawning streams the particles at all sites were large. The transition between large gravel and small gravel at this site was abrupt (over less than 1 m) and coincided with the border between the dense spawning group at the Point and the area devoid of spawners (space 2). Paradoxically, the unused area between the Point and the Bay (space 1) had a high average surface water velocity. However, the presence of aquatic macrophytes and the somewhat higher proportion of fine particles in this area may reflect reduced subsurface water velocities, lowering reproductive success relative to adjacent areas. Thus, while we have no evidence of variation in egg-to-fry survival among areas, there appears to be some environmental basis for the observed distribution of spawners. Nevertheless, our data would certainly have been insufficient to allow us to make a priori predictions of spawner distribution that would have mirrored those observed.

Synopsis

In Pacific salmon, site-specific natal homing is the primary basis for the reproductive isolation of intraspecific breeding groups (Horrall 1981; Quinn et al. 1987; Utter et al. 1989). However, straying rates are higher among groups that are close together, and homing may be more difficult or less important when habitats are similar (e.g., Blair and Quinn 1991). Our study examined the separation of two breeding aggregations at a level where precise natal homing was unlikely (two groups 15 m apart on a single island beach). In this situation, spatial and temporal variation in spawning contributed to the separation of spawning aggregations within a breeding season. While some mixing of the populations was noted, the level of separation was remarkable because the spawning groups were very close to each other and varied in spawning time by only 3–5 days. Spawning groups farther apart in time and (or) space probably exhibit even less mixing within a breeding season.

Maturation date is highly heritable in salmonids (e.g., 0.38 ± 0.17 , Gall et al. 1988; 0.55 ± 0.07 , Siitonen and Gall 1989; 0.60 , Crandall 1991; 0.57 ± 0.24 , Silverstein 1993). Therefore, a positive correlation should exist between the spawning time of parents and their progeny. In this study, the majority of individuals that matured first and settled at the Point might have been the progeny of fish that had settled early and spawned at the Point in previous years. If specific habitat features consistently made the Point a preferred site, fish that spawned early (Point) could begin to diverge from those that spawned late (Bay) through successive genera-

tions. We do not expect, however, that populations separated by the spatial and temporal scales examined in this study would be isolated enough to become genetically distinct. The spawning season on a given island beach is not protracted (Demory et al. 1964), so only limited genetic isolation may occur in these habitats. In other systems, however, greater variation in spawning time and location might complement natal homing and contribute to stronger reproductive isolation. Precise DNA analysis combined with extensive site-specific tagging of emerging juveniles would provide a logical framework for the examining of population differentiation at varying scales.

Acknowledgments

Greg Blair provided the inspiration for this study by noticing the spatial separation and the difference in spawning time between the Point and the Bay. Milo Adkison, Ole Berg, Chris Foote, and Paul Schlenger were instrumental in the completion of this study through formative discussions, assistance in the field, and helpful reviews of early drafts. Mike Kinnison, Steve Leider, Fred Utter, and two anonymous reviewers provided additional critical reviews of the manuscript. Research support was provided by the Pacific Seafood Processors' Association. Andrew Hendry was supported by a Natural Sciences and Engineering Research Council of Canada Postgraduate Scholarship and the H. Mason Keeler Endowment.

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Appendix

Reproductive isolation of the two breeding groups (Fuel Dump Point and Fuel Dump Bay) was estimated from patterns of male movement and proportions of ripe males to ripe females. Specifically, the degree of mixing between sites was estimated from the relative breeding opportunity (RBO) of males that moved to a site relative to all of the males at that site. That is,

$$RS_{A \rightarrow B} = \frac{\text{total RBO (at site B) of males that moved from site A to site B}}{\text{total RBO of all males at site B over the entire spawning period}}$$

where

$RS_{A \rightarrow B}$ is the estimated reproductive success of males that moved from one site (A) to another site (B) relative to all males at site B.

A is one of the two sites (Fuel Dump Point or Fuel Dump Bay)

B is the other site

The total RBO of males of a given origin at a given site was the daily RBO of those males at that site summed over the entire spawning period. Therefore,

$$RS_{A \rightarrow B} = \frac{\sum_{d=6}^{29} [\text{RBO at site B (on day } d) \text{ of males that moved from site A to site B}]}{\sum_{d=6}^{29} [\text{RBO (on day } d) \text{ of all males at site B on day } d]}$$

where d is the date (August 6 through August 29, 1993).

The RBO of all males (of any origin) at a particular site on a particular day (denominator of the equation) is the total number of males at that site on that day multiplied by the RBO of the average male at that site on that day. The contribution of males that came from another site (numerator of the equation) is the proportion of males that they constitute at the new site multiplied by the RBO at that site on that day. Therefore,

Appendix (concluded)

$$RS_{A \rightarrow B} = \frac{\sum_{d=6}^{29} [(\text{proportion of males at site B that came from site A}) (\text{RBO}_{B,d})]}{\sum_{d=6}^{29} [(M_{B,d})(\text{RBO}_{B,d})]}$$

where

$\text{RBO}_{B,d}$ is the relative breeding opportunity (number of ripe females / number of males) of an average male at site B (on day d)

$M_{B,d}$ is the estimated total number of males at site B (on day d)

Transect surveys indicated the number of males originally tagged at site A (A-tagged) that were observed at site B on each day. However, as only a fraction of the total number of males at site A had been tagged, the actual number of males that moved between sites may have been higher. Therefore, the proportion of males at site A that were tagged was calculated by dividing the total number of A-tagged males observed at site A on each day ($n_{A,A,d}$) by the estimate of the total number of males at that site on that day ($M_{A,d}$). The total number of site A males that moved to site B (the first part of the numerator) was then determined by dividing the number of A-tagged males observed at site B ($n_{A,B,d}$) by the proportion of males at site A that were observed with tags on each day (i.e., $n_{A,B,d}/M_{A,d}$). This yielded

$$RS_{A \rightarrow B} = \frac{\sum_{d=6}^{29} \left[\left(\frac{n_{A,B,d}}{n_{A,A,d}/M_{A,d}} \right) \text{RBO}_{B,d} \right]}{\sum_{d=6}^{29} [(M_{B,d})(\text{RBO}_{B,d})]}$$

RBO was calculated for each day from the number of ripe females and males counted along transects at a given site.

Population estimates for a given site on a given day were also derived from these numbers and the total area of the spawning site. Therefore, RBO at a given site (B) was directly proportional to the total number of females at that site ($F_{B,d}$) divided by the total number of males at that site ($M_{B,d}$). Thus, the daily RBO of males at site B on day d was $F_{B,d}/M_{B,d}$ and

$$RS_{A \rightarrow B} = \frac{\sum_{d=6}^{29} \left[\left(\frac{n_{A,B,d}}{n_{A,A,d}/M_{A,d}} \right) \left(\frac{F_{B,d}}{M_{B,d}} \right) \right]}{\sum_{d=6}^{29} \left[(M_{B,d}) \left(\frac{F_{B,d}}{M_{B,d}} \right) \right]}$$

Algebraic simplification yields the final formula

$$RS_{A \rightarrow B} = \frac{\sum_{d=6}^{29} \left[\frac{(n_{A,B,d})(F_{B,d})(M_{A,d})}{(n_{A,A,d})(M_{B,d})} \right]}{\sum_{d=6}^{29} [F_{B,d}]}$$