The Abundance, Distribution, and Habitat Preferences of Adult Sockeye Salmon in Streams Tributary to Takla Lake and the Middle River of Central British Columbia

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Abstract
The abundance and longitudinal distribution of adult sockeye salmon (Oncorhynchus nerka) returning to spawn in Gluskie, Forfar, and O'Neill creeks have been determined annually since 1992 to identify spawner habitat use and preferences. Spawner distribution relative to key physical habitat features is being determined by using aerial and ground-based habitat inventory techniques combined with both total-area enumerations and strip-counts for spawners. Habitat descriptions are obtained at three scales: (1) macrohabitat (stream reach), (2) mesohabitat (features such as pool, riffle, and glide types including channel structure), and (3) microhabitat (substrate texture, water depth, velocity, and spatial indices). The overall goal in this project is to determine how forestry-associated changes in the thermal, hydrologic, and geomorphologic regimes in the selected study watersheds affect variations in (a) the structure, stability, and distribution of fish habitats, (b) sockeye salmon spawner distribution and habitat use, and ultimately, (c) egg-to-fry survival.

Introduction
The Stuart–Takla Fisheries–Forestry Interaction Project is a multi-agency and multidisciplinary investigation of the effects of modern forest-harvesting practices on stream ecosystems, salmonid populations, and fish habitats in the interior of British Columbia. The relationships between forestry activities and the productivity of aquatic ecosystems in the central interior of B.C. are not well known because relatively little research has been undertaken in this region. Research programs in coastal watersheds such as Carnation Creek (Vancouver Island) and on the Queen Charlotte Islands have provided much of the information upon which the provisions of the new (1995) B.C. Forest Practices Code are based (see Hogan and Tschaplinski 1996; Hartman and Scrivener 1990). Because of regional differences in climate, topography, hydrology, and soils, the results of over 25 years of research conducted in coastal B.C. systems is frequently not applicable in the interior. Thus, Forest Practices Code provisions are frequently adapted for interior ecosystems from extrapolations of the knowledge gained on the coast. Operational testing and evaluation of these provisions will aid in distinguishing coastal watersheds from those located in the central interior of B.C.

The Stuart–Takla study was initiated in 1990; it incorporates several watersheds and is the first of its kind in the B.C. interior. The Takla Lake drainage area is located in the northernmost part of the Fraser River...
basin (Macdonald et al. 1992). The area contains valuable forestry, fisheries, and recreational resources. It is especially important for the production of sockeye salmon\(^1\) (*Oncorhynchus nerka*). The Fraser basin is one of the most important salmon producing systems in North America. On average, about 25% of the annual production of sockeye from the Fraser River originates in the Stuart–Takla drainage. Research on fisheries–forestry interactions is vital to ensure that these prime salmonid spawning and rearing habitats are protected in the future and to aid in making ecologically sound decisions about integrated resource management.

Accordingly, the overall objectives of this long-term research project are to: (1) provide an understanding of the physical and biological processes operating within several watersheds in the central interior region of B.C.; (2) determine how forest-harvesting practices conducted according to the Forest Practices Code change these processes; and (3) apply the results to refine the current harvesting and resource protection provisions for interior forests within the new Forest Practices Code.

The project is based on four streams tributary to Takla Lake and the Middle River which serves as the lake’s outlet. Researchers began collecting pre-harvest baseline data in 1990 from three unlogged watersheds, Gluskie, Forfar, and O’Ne-ell (Kynoch) creeks, and from Bivouac Creek which has been partially logged. Each stream contains populations of bull trout (*Salvelinus confluentus*), rainbow trout (*Oncorhynchus mykiss*), “ kokanee” (*Oncorhynchus nerka*), and especially sockeye salmon. Together, these streams sometimes receive over 50% of the total number of adult sockeye returning to spawn in the Takla Lake drainage in summer (Macdonald et al. 1992).

Logging conducted under the provisions of the Forest Practices Code do occur in parts of the study area. The study will feature experimental controls in both area and time. For example, the Forfar Creek watershed will remain unlogged for the duration of the project in order to evaluate the effects of different harvest options conducted in the other sites. A minimum of 4 years of pre-harvest data will be collected from each of the remaining watersheds. The project design and component studies are detailed in other presentations within these proceedings and published elsewhere (Macdonald et al. 1992; Macdonald 1994).

This component of the overall program focuses on adult sockeye spawning habitat ecology. Sockeye use the study streams primarily for spawning and egg incubation (Tschaplinski 1994). Spawners arrive at the mouths of the streams in mid-to-late July after migrating about 1300 km from the mouth of the Fraser River in roughly 18 days. Spawning is essentially concluded by about 18 August. Eggs and alevins develop and remain in the streambed until the following spring. The majority of sockeye fry emerge from the streambed during April and May and almost immediately emigrate downstream to rear for about 1 year in the lake system. Because most fry spend relatively little time in their natal streams, the direct effects of forest harvesting upon sockeye fry production from the study streams will likely be upon (a) adult spawners and the quantity, quality, and stability of stream spawning habitat, and consequently (b) the survival and development of eggs and embryos in response to streambed conditions.

Accordingly, the objectives of this project component are to: (1) determine the abundance and spatial distribution of adult sockeye salmon in Gluskie, Forfar, and O’Ne-ell creeks; (2) determine spawner densities and habitat preferences throughout each stream by (a) habitat type, and (b) microhabitat characteristics including water depths, stream velocities, spatial indices (stream widths and volumes), and substrate texture; (3) interpret spawner site-selection (densities) relative to variations in egg-to-fry survival and fry production determined by other project investigators; and (4) monitor for post-harvest changes in habitat type, stream channel structure and stability, and spatial distribution of adult sockeye.

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\(^1\)For brevity, sockeye salmon are frequently referred to as sockeye in this paper.
Land Management Practices Affecting Aquatic Ecosystems

Methods

Details of all stream survey methods noted here are given by Tschaplinski (1994), and Tschaplinski and Hyatt (1990, 1991). The following summary describes work in progress. Preharvest data on adult distribution and habitat preferences have been collected since 1992.

Sockeye Abundance

It is necessary to accurately enumerate the numbers of adult sockeye entering each stream because the effects of forest harvesting on sockeye production will ultimately be evaluated from long-term trends in egg-to-fry survival. These survivals reflect the study streams capacity to produce fry from a given number of spawners, and are determined by comparing the number of fry migrating from the streams each spring with estimates from the total number of eggs deposited in the previous summer. Egg deposition is calculated from the seasonal abundance of spawners, the sex composition of the spawning run, and estimates of female fecundity.

Because accurate estimates of spawner abundance are critical components of this project, several methods have been simultaneously employed to enumerate adult sockeye on the spawning grounds. The accuracy and precision of each method varies to different degrees according to variations in environmental conditions and other factors (Tschaplinski and Hyatt 1990, 1991). For example, flash floods may damage counting fences and allow migrating fish to escape upstream without being enumerated. By employing different techniques, acceptable estimates of abundance are obtained each year by at least one method.

Staff from Fisheries and Oceans Canada (DFO) obtained daily counts of sockeye by sex at temporary fences located near the mouths of each study stream (Smith 1994; Macdonald et al. 1992). These fence counts were supplemented every second day by visual counts of both live spawners and carcasses obtained by surveyors walking the entire length of each stream occupied by sockeye (Smith 1994).

Alternate estimates of sockeye abundance were produced in this study to further supplement those obtained by DFO. These estimates include those determined by using (1) Petersen mark-recapture techniques, and (2) the area-under-the-curve method with an estimate of stream-residence time for spawners (see Tschaplinski and Hyatt 1990, 1991). Both techniques required the application of tags to large samples of fish when they entered the study streams.

Fish were tagged in two daily sessions for each stream, once at the beginning and again near the chronological mid-point of the seasonal spawning migration. In each stream, up to 500 sockeye or more were tagged per day with brightly colored plastic discs of 25-mm diameter (Tschaplinski and Hyatt 1990, 1991). A unique color of tag was used for each stream on each tagging date.

During each tagging session, sockeye were captured with seine nets downstream of the counting fence. One set of two discs was fixed to the anterior base of the dorsal fin of each fish (Tschaplinski and Hyatt 1990, 1991). Tagged fish were then released upstream of the fence so that they could continue their migration to their spawning sites. A gate in the fence was opened as needed to permit the passage of any fish attempting to return downstream.

Both tagged and untagged sockeye were enumerated throughout the spawning grounds of each stream at intervals spaced at 6–7 days during the spawning season. The first fish survey was conducted 3 days after the tags were first applied in order to allow tagged fish sufficient time to disperse throughout the spawning grounds. These surveys were conducted not only to determine spawner abundance, but also to determine (1) migration patterns and distribution of spawners arriving at different times of the migration period, (2) preferred sockeye habitat prior to forest harvesting, and (3) competition for space between early-arriving and later-arriving spawners.

Sockeye Distribution and Habitat Preferences

Two methods have been employed to determine adult sockeye migration patterns, distribution, and habitat preferences. Both techniques also generated additional estimates of population abundance. One method is the strip-count procedure (Tschaplinski and Hyatt 1990, 1991). This method involves establishing counting stations at regular intervals along the entire length of each stream occupied by adult sockeye. Stations are spaced at 30-m intervals in the present study. The 30-m interval has been found to effectively cover the full range of repeating habitat units (e.g., riffs, pools, glides) in streams 8–10 km long where channel widths in most areas vary, usually between about 8 and 30 m (Tschaplinski and Hyatt 1990, 1991).

During each fish survey, observers walked the entire length of the spawning grounds but counted fish only at the strip-count stations. At each station, all fish visible (both live spawners and carcasses) in a 1-m wide cross-section or "strip" of the stream...
Habitat cover categories

**Organic**
- Tree-root masses
- Large wood
- Slash/small wood
- Logjams
- Overhanging vegetation

**Inorganic**
- Bedrock
- Boulder
- Cobble (for juvenile salmonids)
- Gravel (for juvenile salmonids)
- Undercut bank

Figure 1. Categories used to classify the habitat occurring at each strip-count station in the study streams.

were counted. Thus, these counts are a sample of the total population. Each count is also a site-specific measure of the density of spawners in terms of numbers per lineal metre of stream. An estimate of the total population was generated when densities at the 1-m wide strips were expanded over the entire length of the stream inhabited by adult fish.

At the same time that strip counts were performed, other observers counted all live spawners and carcasses visible throughout the stream, and summed their counts for each 30-m interval between the strip-count stations. The distribution of all spawners in the stream was thus determined by 30-m interval by this second procedure. This total-population count was performed to evaluate how accurately the population subsample derived from the strip counts reflected the actual longitudinal distribution of sockeye on the spawning grounds.

The accuracy of both population assessment methods was determined by comparing them to sockeye abundance estimates based upon fence counts. Except when fish fences are damaged or submerged by floodwater, the most accurate estimates of adult salmon abundance entering streams are always generated from counts of migrants made at fences located at stream mouths. In the present study, the numbers of live sockeye on the spawning grounds on any given day was determined from the cumulative seasonal count of sockeye passing through the fish fences adjusted by (1) adding the numbers of sockeye distributed downstream of the fences at the mouths of the streams, and (2) subtracting the cumulative numbers of sockeye carcasses counted upstream of the fences up to the day in question. Fence counts that supplement the data are termed “adjusted fence counts” in this report, and serve as our primary reference for sockeye population abundance on any given date. The numbers of sockeye occurring downstream of the fish fences, and the cumulative carcass counts were provided by stream surveys conducted by DFO crews.

**Macrohabitat-Level Assessment**

Sockeye habitat was determined at three spatial scales. The broadest scale employed was at stream reach level (British Columbia Ministry of Forests and British Columbia Ministry of Environment 1995). At this macrohabitat level, the longitudinal distribution of adult sockeye was mapped from the mouth of the stream to the their upstream limit. A reach is a relatively homogenous section of a stream having a sequence of repeating structural characteristics (or processes) and fish habitat types (British Columbia Ministry of Forests and British Columbia Ministry of Environment 1995). The key physical factors used to determine reaches in the field are channel pattern, channel confinement, gradient, and predominant streambed and bank materials. Stream reaches generally show uniformity in these characteristics and in discharge (British Columbia Ministry of Forests and British Columbia Ministry of Environment 1995).

Reach boundaries were defined to occur at (1) significant changes in stream channel form or confinement, such as from a single channel to braided, multiple channels, or at the change from a wide floodplain to a confined canyon; (2) significant changes in gradient; (3) significant changes in streambed or streambank materials; and (4) potential barriers to fish distribution such as major waterfalls. The physical characteristics that differentiate stream reaches also define the fish habitats they contain, and determine their ability to support fish populations.

**Mesohabitat-Level Assessment**

Spawner preferences at the mesohabitat or intermediate scale were determined by using logistic regressions (McCullagh and Nelder 1983) to compare spawner densities observed at strip-count stations with the frequency of habitat types occurring across all strips. The habitat at each strip was classified into standard categories for pool and fast-water habitats (Fig. 1) by using a scheme adapted from those of Bisson et al. (1982) and Sullivan (1986). The approximate proportions of substrate types were also estimated visually by referring to standard size categories (Fig. 2). Also recorded were features such as cover afforded by pieces of large woody debris (enumerated pieces of LWD; see Hogan and Chatwin
Substrate proportions

<table>
<thead>
<tr>
<th>Substrate Type</th>
<th>Size (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boulder</td>
<td>&gt; 256</td>
</tr>
<tr>
<td>Cobble</td>
<td>&gt; 64-256</td>
</tr>
<tr>
<td>Gravels</td>
<td>6-64</td>
</tr>
<tr>
<td>&quot;Pea&quot; gravel</td>
<td>&gt; 2-5</td>
</tr>
<tr>
<td>Sand</td>
<td>&gt; 1-2</td>
</tr>
<tr>
<td>Fines</td>
<td>&lt; 1</td>
</tr>
<tr>
<td>Fine organics</td>
<td></td>
</tr>
</tbody>
</table>

Figure 2. Categories used to describe cover features and substrate surface composition occurring at each strip-count station. See text for methods of cover quantification. At most strips, substrate types were ranked in order of approximate surface area of streambed covered. At selected strips, actual proportions of each size class were determined from photographs.

Habitat inventories were obtained for all strips prior to the spawning season because spawning sockeye can modify some habitat characteristics, especially the particle size composition of the streambed (Scrivener 1994). Prespawning habitat inventories thus permitted the determination of habitat preferences from variations in fish density recorded when spawners were on site. Habitat inventories were repeated after the spawning season to evaluate the effects of adult sockeye on streambed sediment textures. Habitat classifications obtained at each strip during ground-based surveys were supplemented annually with a continuous sequence of stereo aerial photographs (200-mm or 70-mm lenses) taken of the entire stream channel (Hogan 1994).

Microhabitat-Level Assessment

Immediately after strip-count surveys were performed, a subset of strips was selected for each stream by random sampling stratified by fish density. The observed range of spawner densities was thus included within the sample. The sample usually varied between 9 and 13 stations and has represented between about 12 and 20% of all strip-count stations located in the lowermost reach of each stream used by sockeye. At each cross-stream strip, measurements of microhabitat variables were made including stream velocity, streambed surface texture (particle size composition), water depth, and available habitat space (stream wetted width and water volume). Linear correlations were later employed in the laboratory to determine the statistical associations between spawner density and these microhabitat characteristics.

The wetted width of the stream was measured with a metre tape. Water depths, velocities, and 35-mm photographs of the streambed were taken along the cross-stream transect for each strip at either 0.5- or 1.0-m intervals depending upon stream width. One-metre intervals were used when wetted width was ≥10 m. Water depths were measured with metre sticks, and an electronic current meter was used to determine water velocities. Velocity readings were taken at 20 and 80% of the total depth at each 0.5- or 1.0-m interval. For transect locations where the stream was <10 cm deep, a single velocity reading was taken at 50% depth. Mean velocities for each strip were based usually upon 10 to 32 individual readings. Mean depths were based usually upon seven to 20 measurements. Where very shallow water occurred along the banks (i.e., 1-3 cm deep), measurements made within 0.5 m of the bank were not used for subsequent determinations of average depth or velocity. Substrate photographs were taken with a combination of single-lens-reflex land cameras fitted with polarizing filters or similarly-fitted underwater cameras. Photographs were later analyzed in the laboratory (see Tschaplinski 1994 for further details of all methods).

Results and Discussion

Annual trends in adult sockeye abundance and distribution were consistent across all study streams. Therefore, variations in abundance and distribution within and among years are frequently illustrated in this report by using O'Ne-ell Creek as a typical example.

Sockeye Abundance and Comparisons of Assessment Methods

The numbers of adult sockeye returning to each study stream, and the corresponding densities of fish on the spawning grounds have fluctuated widely among years (Table 1). For example, based upon daily fence counts (adjusted), the numbers of live spawners enumerated in early August was over six-fold higher in O'Ne-ell Creek in 1995 compared with 1994 (Table 2). Because fish fences can provide absolute counts of migrating salmon entering streams, the interannual variation in the numbers of sockeye returning to the project study streams has been accurately tracked. However, expansions of
Table 1. Mean densities (numbers per lineal metre) of sockeye spawners in the lowermost reaches of the Stuart-Takla study streams from 1992 to 1995. Densities were averaged across all strips in the lower about 1.3, 2.7, and 3 km of Gluskie, Forfar, and O’Ne-ell creeks, respectively (study section 1). Note that section-1 densities do not vary proportionally with population levels because many spawners move upstream to occupy steeper-gradient reaches in each stream when densities exceed about 4.5 fish/lineal m.

<table>
<thead>
<tr>
<th>Year</th>
<th>Stream</th>
<th>Seasonal (s) or strip-count (*) population abundance for entire stream</th>
<th>Section 1 mean density (no./lin. m) on survey date</th>
<th>Standard deviation (+/−)</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>Gluskie</td>
<td>3 749 (s)</td>
<td>1.5</td>
<td>1.7</td>
<td>Densities based on 1860 live fish on survey date.</td>
</tr>
<tr>
<td></td>
<td>Forfar</td>
<td>12 904 (s)</td>
<td>1.7</td>
<td>2.0</td>
<td>Densities based on 4240 live fish on survey date.</td>
</tr>
<tr>
<td></td>
<td>O’Ne-ell</td>
<td>11 002 (s)</td>
<td>1.5</td>
<td>3.6</td>
<td>Densities based on 3870 live fish on survey date.</td>
</tr>
<tr>
<td>1993</td>
<td>Gluskie</td>
<td>19 556 *</td>
<td>10.0</td>
<td>5.1</td>
<td>Densities based on strip-counts near peak of spawning in each stream. Significant portions of the total population inhabited section 2 upstream.</td>
</tr>
<tr>
<td></td>
<td>Forfar</td>
<td>15 990 *</td>
<td>4.6</td>
<td>2.7</td>
<td>Densities based on strip-counts near peak of spawning in each stream. Significant portions of the total population inhabited section 2 upstream.</td>
</tr>
<tr>
<td></td>
<td>O’Ne-ell</td>
<td>26 225 *</td>
<td>6.5</td>
<td>3.6</td>
<td>Densities based on strip-counts near peak of spawning in each stream. Significant portions of the total population inhabited section 2 upstream.</td>
</tr>
<tr>
<td>1994</td>
<td>Gluskie</td>
<td>3 919 (s)</td>
<td>2.7</td>
<td>4.5</td>
<td>Almost entire seasonal migration for each stream was present and alive on spawning grounds on date of survey.</td>
</tr>
<tr>
<td></td>
<td>Forfar</td>
<td>4 902 (s)</td>
<td>2.9</td>
<td>3.4</td>
<td>Densities based on strip-counts near peak of spawning in each stream. Significant portions of the total population inhabited section 2 upstream.</td>
</tr>
<tr>
<td></td>
<td>O’Ne-ell</td>
<td>4 371 (s)</td>
<td>1.8</td>
<td>1.7</td>
<td>Densities based on strip-counts near peak of spawning in each stream. Significant portions of the total population inhabited section 2 upstream.</td>
</tr>
<tr>
<td>1995</td>
<td>Early season Gluskie</td>
<td>13 689</td>
<td>8.4</td>
<td>8.8</td>
<td>Numbers of live fish for each survey period in 1995 were determined from daily fence counts plus DFO stream surveys.</td>
</tr>
<tr>
<td></td>
<td>Early season Forfar</td>
<td>14 859</td>
<td>6.8</td>
<td>2.6</td>
<td>Numbers of live fish for each survey period in 1995 were determined from daily fence counts plus DFO stream surveys.</td>
</tr>
<tr>
<td>1995</td>
<td>Near peak of spawning Gluskie</td>
<td>9 510</td>
<td>7.4</td>
<td>8.8</td>
<td>Numbers of live fish for each survey period in 1995 were determined from daily fence counts plus DFO stream surveys.</td>
</tr>
<tr>
<td></td>
<td>Near peak of spawning Forfar</td>
<td>10 804</td>
<td>4.4</td>
<td>2.6</td>
<td>Numbers of live fish for each survey period in 1995 were determined from daily fence counts plus DFO stream surveys.</td>
</tr>
<tr>
<td></td>
<td>Near peak of spawning O’Ne-ell</td>
<td>18 063</td>
<td>6.1</td>
<td>4.3</td>
<td>Numbers of live fish for each survey period in 1995 were determined from daily fence counts plus DFO stream surveys.</td>
</tr>
</tbody>
</table>

Strip counts have provided estimates of population abundance that closely approximated those generated from adjusted fence counts for all streams in most years. In 1995, strip-count expansions were within 16.3 and 12.9% of the equivalent fence counts for the same survey date for early-season and mid-season population assessments respectively (Table 2). In 1992, the numbers of live sockeye estimated from expansions of strip counts were within 5.6–13.3% of estimates based upon adjusted fence counts (Tschaplinski 1994).

The accuracy of fence counts decreased in 1993 because floods damaged the fish fences and allowed many spawners to migrate upstream without being enumerated. Given the relatively consistent correspondence between strip-count expansions and adjusted fence counts in our study streams, strip counts provided useful alternate estimates of population abundance for specific survey dates in 1993 (Table 1).

To date, strip counts have shown strong deviation from fence counts only in 1994 for O’Ne-ell Creek. On 5 August, strip counts generated a population estimate for live sockeye (5095) that exceeded the adjusted fence count (3583) by about 42% (Table 2). This departure between methods occurred when populations were low. When few fish are on the spawning grounds, strip-count estimates are sensitive to (a) small errors in visual counts made at the strips, and (b) any bias occurring in the distribution of habitat types sampled by the strip-count stations. In 1994, strip-count stations appear to have been slightly biased toward habitats such as glides that contained above-average densities of spawners (for a discussion of errors, see Tschaplinski and Hyatt 1990, 1991). This bias appears to be consistent for O’Ne-ell Creek in 1994 and 1995, because populations estimated from strip counts were high relative to adjusted fence counts in every instance (Table 2). However, the effect of this bias was minor in 1995.
Table 2. Comparison of population estimates for live sockeye spawners in O'Ne-ell Creek in 1994 and 1995 by strip counts, total-stream surveys by interval counts, and DFO fence counts. For interval counts, live sockeye were summed by 30-m intervals in 1995 and 120-m intervals in 1994. Fence counts were the cumulative number of live sockeye that had migrated through the fence up to the survey date adjusted by adding the number of live sockeye counted downstream of the fence on the same survey date, then subtracting the cumulative number of sockeye carcasses enumerated seasonally up to that same time. Adjustments were based upon DFO stream surveys conducted on alternate days.

<table>
<thead>
<tr>
<th>Year</th>
<th>Stream</th>
<th>Survey date</th>
<th>Strip-count expansion</th>
<th>Total-stream survey by interval counts</th>
<th>Adjusted fence counts</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994</td>
<td>O'Ne-ell Creek</td>
<td>5 August</td>
<td>5,095</td>
<td>3,068</td>
<td>3,583</td>
</tr>
<tr>
<td>1995 Early season</td>
<td>O'Ne-ell Creek</td>
<td>4 August</td>
<td>27,755</td>
<td>21,206</td>
<td>23,857</td>
</tr>
<tr>
<td>1995 Near peak of spawning</td>
<td>O'Ne-ell Creek</td>
<td>11 August</td>
<td>20,402</td>
<td>12,875</td>
<td>18,063</td>
</tr>
</tbody>
</table>

when sockeye returns were high: the population estimates obtained from the two methods were similar.

The degree of correspondence usually observed in this study between population estimates generated from fence and strip counts is relatively unusual, and indicates that strip-count estimates are relatively accurate. The accuracy of the strip-count technique increases when (a) conditions for visual counts of spawners are good, and (b) the full range of habitats throughout the spawning grounds are well represented by the strip-count stations (Tschaplinski and Hyatt 1990, 1991). These conditions were satisfied within the present study. Conditions for visual counts (relatively shallow and clear water plus bright daylight) were almost always ideal. Additionally, population surveys were based upon large numbers of stations: as many as 81, 115, and 161 stations were used to sample Gluskie, Forfar, and O'Ne-ell creeks, respectively.

The strip-count procedure also generated sockeye abundance estimates that were on average at least as accurate or better than those derived from labor-intensive, total-stream surveys (Table 2). In 1994 and 1995, total-stream surveys (interval counts) underestimated the true population size in every case (Table 2). Furthermore, the total-count procedure seriously underestimated the abundance of sockeye relative to adjusted fence counts by about 40% near the peak of spawning in 1995 (Table 2; 11 August). Total-area surveys of spawners often underestimate the true size of the population because of the difficulty in obtaining accurate counts when spawners occur in dense aggregations frequently encountered in pools and glides, especially in years of high fish abundance (Tschaplinski and Hyatt 1990, 1991).

Strip counts and complete (interval) counts generated population abundance estimates that differed substantially in magnitude (Table 2). However, the spatial distribution of spawners described by each technique corresponded closely. The longitudinal range inhabited by adult sockeye, and the mode and tails of the population distribution determined from strip-count samples were reflected by the same parameters determined from the spatially-continuous interval counts (compare Fig. 3 with 4, 5 with 6, and 7 with 8 respectively for O'Ne-ell Creek). This correspondence was maintained regardless of whether populations levels were low as in 1994 (Figs. 3, 4) or several fold greater as in 1995 (Figs. 5 to 8). [Visual comparisons between techniques are more difficult for 1994 because complete counts in that year were made over 120-m intervals instead of the 30-m interval generally employed in this study.]

Interval counts were superior to strip counts for illustrating the distribution of tagged sockeye (Figs. 3 to 8). The numbers of tagged fish were relatively small, especially when spawner returns were high (e.g., ca. 500 yellow-tagged sockeye in O'Ne-ell Creek among nearly 24,000 untagged fish early in 1995). Counts made at 1-m wide strips spaced 30-m apart did not efficiently sample tagged fish sparsely dispersed over several kilometres of stream. By contrast,
Figure 3. Longitudinal distribution of adult sockeye in O’Ne-ell Creek in 1994 by the strip-count method near the peak of spawning activity. Counts of live sockeye at each station also represent densities of fish per lineal meter. Strip-count stations were numbered consecutively within two study sections. Section 1 was located from strip 0 near the stream mouth to strip 85 (>2.6 km upstream). Section 2, located immediately upstream from section 1, had strips consecutively numbered 0-70. The historical limit of sockeye spawners was about 4.7 km upstream measured from strip 0, section 1.

Figure 4. Longitudinal distribution of adult sockeye in O’Ne-ell Creek in 1994 by the total-count method near the peak of spawning activity. In 1994, counts of fish were summed usually by 120-m interval along the stream (a 30-m interval was used in other years).
Figure 5. Longitudinal distribution of adult sockeye in O'Ne-ell Creek by the strip-count method early in the spawning season in 1995.

Figure 6. Longitudinal distribution of adult sockeye in O'Ne-ell Creek by the total-count method early in the spawning season in 1995. Counts of fish were summed by 30-m interval along the stream.
Table 3. Sockeye density (number of live fish per lineal metre) correlated with microhabitat variables for selected strips when population abundance was low. Linear correlation coefficients (r) are provided. No significant correlations were observed between spawner density and any measured microhabitat variable in 1994 (all p > 0.05). All strip-count stations selected were located in the lowermost reaches of each stream (section 1) where nearly all spawners resided when mean densities were low. The number of strips sampled in each stream is shown (n).

<table>
<thead>
<tr>
<th>Stream</th>
<th>Year</th>
<th>Population abundance on survey date</th>
<th>Linear correlation coefficients (r) (spawner density vs. physical variables)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gluskie Creek</td>
<td>1994</td>
<td>3 197(4 August)</td>
<td>Stream width (m): -0.05  Water depth (m): 0.24  Strip volume (m³): 0.30  Velocity (m/s): -0.40</td>
</tr>
<tr>
<td>(n = 11)</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Forfar Creek</td>
<td>1994</td>
<td>4 462(5 August)</td>
<td></td>
</tr>
<tr>
<td>(n = 9)</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>O'Ne-ell Creek</td>
<td>1994</td>
<td>3 583(5 August)</td>
<td></td>
</tr>
<tr>
<td>(n = 11)</td>
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</table>

a majority of tagged individuals were enumerated by the spatially continuous interval-count procedure. However, the accuracy of interval counts was also limited. Even fish marked with brightly colored tags were difficult to see when tags were obscured within dense groups of untagged spawners. Counting efficiency was so reduced by this effect that only about 61-65% of tagged, live sockeye could be detected in the stream 3 days after tags were applied early in the spawning season (e.g., Figs. 4, 6). Because these percentages were determined early in the spawning season, mortality of tagged fish was insignificant. Reductions in counting efficiency can seriously reduce the accuracy of any abundance estimates based upon recovery of tagged spawners (Tschaplinski and Hyatt 1991). [Abundance estimates based upon counts of tagged sockeye are not presented here.]

In spite of some limitations, the overall performance of the strip-count method was good. Because strip-count surveys can be completed in less than one-half the time required for complete counts (Tschaplinski and Hyatt 1990, 1991), strip counts were clearly an appropriate and convenient technique to sample and study the distribution of sockeye spawners and stream habitats.

Macrohabitat-Level Assessment

Two basic patterns of spawner distribution have become clear at the macrohabitat or stream-reach level, and each pattern is associated with a different level of spawner abundance. In 1992 and 1994 when relatively low numbers of sockeye returned to the spawning grounds (Table 1), the longitudinal distribution of spawners was limited primarily to the lowermost portion of each stream (Figs. 3, 4). Seasonal estimates of spawner abundance for Gluskie, Forfar, and O'Ne-ell creeks in 1994 were only 3919, 4902, and 4371, respectively (DFO fence counts adjusted by stream surveys of spawners downstream of the fences). Mean spawner densities in 1994 were < 3 fish/lineal m in any stream, and <2 fish/lineal m in O'Ne-ell Creek (Table 1).

Because of these low numbers, sockeye occupied only part of their potential range in each creek that year. For example, spawners in O'Ne-ell Creek occupied approximately the lowest 5 km of stream (Figs. 3, 4) where gradients varied sequentially from 0.7 to 2.0%, and sediment textures changed from gravel with sand to primarily gravel with cobbles, and finally to cobbles with gravel. Within this lowermost stream area, channel morphology was controlled by LWD, featured gravel bars, and consisted of repeating sequences of riffles, pools, and glides. These characteristics of the lowermost part of O'Ne-ell Creek were repeated in the other two study streams (see Hogan et al. 1998).

Sockeye distribution in Gluskie and Forfar creeks in 1994 was similarly limited to the lowermost part of each stream, where the basic reach characteristics described for O'Ne-ell Creek were repeated. The same general patterns of sockeye distribution had
Table 4. Sockeye density (number of live fish per lineal metre) correlated with microhabitat variables for selected strips when population abundance was high. Linear correlation coefficients (r) are provided. Each significant correlation (p < 0.05) is shown with an asterisk, and provided with the r-square value (proportion of observed variance explained). All strip-count stations selected were located in the lowermost reaches of each stream where gradients were 2% or less and most (about 80-93%) spawners resided even in years when mean densities were high. The number of strips sampled in each stream is shown (n).

<table>
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<td></td>
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<td>Stream width (m)</td>
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<tr>
<td>Gluskie Creek</td>
<td>1993</td>
<td>19 556</td>
<td>0.78 * (r$^2$: 0.61)</td>
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<tr>
<td>Forfar Creek</td>
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<td>15 990</td>
<td>0.76 * (r$^2$: 0.58)</td>
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<td>(n = 10)</td>
<td>(10 August)</td>
<td></td>
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<td>1993</td>
<td>26 225</td>
<td>0.52</td>
</tr>
<tr>
<td>(n = 11)</td>
<td>(11 August)</td>
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<td>9 510</td>
<td>0.21</td>
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<tr>
<td>(n = 14)</td>
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<td></td>
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</tr>
<tr>
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<td>10 804</td>
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</tr>
<tr>
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<td>1995</td>
<td>18 063</td>
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</tr>
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<td>(11 August)</td>
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</table>

been observed in 1992 when seasonal population abundances estimated by DFO were 3 749, 12 904, and 11 002 for Gluskie, Forfar, and O'Ne-ell creeks, respectively (Table 1). Populations in both Forfar and O'Ne-ell creeks were more than twice as abundant in that year when compared with 1994; however, sufficient spawning habitat was apparently available in the lowermost area of each stream because only small numbers of sockeye moved upstream to spawn in the steeper-gradient sites (Tschaplinski 1994). [Spawner densities shown for Forfar and O'Ne-ell creeks in 1992 were only about 40 and 60% of their respective seasonal maxima because the strip-count surveys were conducted about 3 days after the peak of live spawner abundance. However, stream surveys by DFO staff confirmed the limited distribution of fish in both streams.]

In contrast with 1994, adult sockeye returns to all streams were markedly higher in 1993 and 1995 (Table 1). Populations in both Gluskie and O'Ne-ell creeks also increased by about two- to three-fold in 1993 and 1995 relative to 1992. Compared with returns in 1992, modest increases were also observed in sockeye abundance in Forfar Creek (about 24% higher in 1993, and 15% in 1995). In 1993 and 1995, mean densities of sockeye increased in the lowermost study section of each stream to between 4.4 and 10.0 fish/lineal m depending upon stream and year.

With these increases in density, sockeye spawners in all streams extended their ranges upstream into narrower, faster-flowing, higher-gradient reaches (>2-6%) where channel morphology was controlled more by boulders, large cobbles, and bedrock than by LWD. Substrates suitable for spawning frequently occurred as patches of gravel and cobbles located among the boulders. For example, sockeye mean density in the lowermost part of O'Ne-ell Creek increased from 1.8 fish/lineal m in 1994 (Fig. 3) to 6.1 fish/lineal m in 1995 (Fig. 5). Accordingly, spawners extended their range by >1 km to occupy about 4.3 km of the stream measured from strip-zero located 240 m downstream of the fish fence (Figs. 5, 6). In 1993, when peak numbers of live fish exceeded 26 000, sockeye occupied their maximum range in O'Ne-ell Creek which extends about 4.7 km upstream from strip 0 (see strip 70, section 2; Fig. 5).
Physical barriers to migration limit the distribution of sockeye spawners in all streams. In Forfar Creek, this barrier is a waterfall located only about 750 m upstream from the lowermost study section, which contains almost all sockeye in years of relatively low spawner abundance. In both O’Ne-ell and Gluskie Creeks, the barriers are located within canyons containing stepped-pool, boulder cascades. Sockeye in both streams usually are limited to the lower parts of the canyon where gradients are <8%. In Gluskie Creek, the upstream limit of sockeye distribution is only about 2.5 km upstream from the stream mouth.

**Mesohabitat-Level Assessment**

Analyses of sockeye habitat preferences at the mesohabitat level are yet in progress. Therefore, the results of the categorical data analyses, including logistic regressions of spawner density versus the habitat type surveyed at each strip are not currently available. However, some general trends are apparent. Unusually high sockeye counts were frequently obtained from major pools where large aggregations of sockeye occurred. These schools were especially common early in the spawning season and consisted primarily of individuals that recently arrived on the spawning grounds (as shown by the abundance of recently tagged fish), which are not yet fully mature. Previously, these sockeye were in holding pools prior to moving out from them to spawn.

Holding pools were important habitats both in years of low and high spawner abundance. For example, in 1994 when relatively few sockeye returned, the highest spawner densities occurred in pools at strips 35 and 51 at the peak of spawning in O’Ne-ell Creek (8 fish/lineal m; Fig. 3). In 1995 when sockeye returns were over five-fold higher, peaks associated with pools occurred at strips 28, 31, and 50 early in the spawning season (section 1 downstream, 24–34 fish/lineal m; Fig. 5). Peak counts also occurred later near the height of spawning activity at some of the same strips in 1995 (e.g., 28, 50, and 51; Fig. 7).

Many of the strips located in these pools also contained complex habitats, which included lamina- nating glides, especially if the strips were situated at the downstream margins of the pools (e.g., O’Ne-ell Creek, strips 50 and 51; Figs. 5, 7). Although some sockeye spawned within the pools, the highest densities of fish that were actually spawning were most often found at strips that contained these pool-and-glide elements, or that were located entirely within gravel glides. Most of the secondary peaks in abundance (as well as some of the primary ones) occurred at strips located in glide habitats. Examples of these glide-associated peaks are strips 12 and 42 in 1994 (Fig. 3; section 1), and strips 11, 12, 57, 58, 66 in 1995 (Fig. 5; section 1).
Despite these general observations, variations occurred both within and between years. For example, several glide sites contained only average numbers of spawners in any year. Additionally, the relative importance of some sites changed radically at different times during the season. Densities at strip 25 (section 1) in O’Neill Creek fell from 26 fish/lineal m on 4 August (Fig. 5) to only 4 fish/lineal m 1 week later near the peak of spawning activity (Fig. 7). High densities of spawners also occurred in sites other than glides and the tails of pools. Sockeye were sometimes abundant in gravel-and-cobble riffles (e.g., strip 75, Figs. 3, 5). Additional observations and continued analyses of sockeye densities and habitat categories are required to clarify spatial and temporal variations in spawner distribution.

Although some strips were associated with unusually high numbers of sockeye, spawner densities at most strips were near average for each stream (Figs. 3, 5, 7; Table 1; Tschaplinski 1994). Despite local peaks in abundance, adult sockeye were relatively evenly distributed throughout the spawning grounds. The even distribution of sockeye within each stream reach partly explains the relatively high accuracy of spawner abundance estimates generated from strip counts which sample the population from evenly spaced enumeration stations (Tschaplinski and Hyatt 1990, 1991). More significantly, the observed distribution of adult sockeye also suggests that high-quality spawning habitat was available virtually everywhere, at least in the lowermost reaches of each stream. When habitats in the lower parts of each stream contained the maximum densities of fish they could support, spawners moved into areas upstream (Figs. 5, 6, 7, 8). The only sites that sockeye appeared to avoid were areas flooded by beavers (e.g., strips 15–16, section 1; Figs. 7, 8) and steep, fast-flowing, riffles and rapids in sites upstream (section 2, strips 46–47, 50–51; Figs. 7, 8).

**Microhabitat-Level Assessment**

In 1994, when sockeye abundance was low, spawner densities were not correlated significantly with any measured microhabitat variable including water depth, velocity, or indices of habitat space such as stream width and strip volume (Table 3; all p > 0.05). These observations confirm similar results obtained in 1992 when spawner abundance was again relatively low (Tschaplinski 1994). When relatively few adult sockeye return to the study streams, mean densities of fish are low, and spawner distribution is not limited by available space. Sockeye are free to select prime spawning sites from less favorable ones. However, the observed range of spawner densities was also low in the same years. This relatively even distribution of fish indicates that habitat...
space in the lowermost stream reaches was plentiful, active site selection was limited, and the full range of depths, velocities, and spawning substrates were acceptable to the spawners. The results of surface-substrate texture analyses are not yet available; however, analyses of gravel samples collected by the frozen-core method confirms the high quality of spawning and egg-incubation substrates throughout the lower reaches of the study streams (Scrivener 1994). Furthermore, studies have shown that egg-to-fry survival is exceptionally high throughout the lowermost reaches of all study streams, and is the equivalent of survivals obtained in the best artificial spawning channels (Cope and Macdonald 1998).

In years when spawner abundance is high, some statistically significant correlations between sockeye densities and spatial indices were observed (Table 4). For example, spawner densities and stream width were significantly and positively correlated in Gluskie and Forfar creeks in 1993, and in Forfar and O'Ne-ell creeks in 1995 (Table 4; all \( p < 0.05 \)). Spawner distribution (density) was thus a function of available habitat space when population levels were high. These results confirm observations of spawner distribution at the mesohabitat and macrohabitat levels; that is, when sockeye are abundant, available habitats in the lowermost portion of each stream are fully occupied, and spawners then expand their distribution upstream into steeper-gradient areas.

One significant, positive correlation has been observed between spawner density and habitat volume (Gluskie Creek, 1993; \( p < 0.05 \)), and spawner density and velocity (O'Ne-ell Creek, 1993; \( p < 0.05 \); Table 4). Because of variation among years and streams, interpretation of these isolated results is difficult. However, the significant correlation between velocity and sockeye densities in O'Ne-ell Creek in 1993 likely resulted from spawners avoiding extensive stretches in the lowermost part of that stream where velocities were low because of beaver dams.

### Distribution of Tagged Sockeye and Competition for Space

Observations on spawner distribution and habitat use, the high quality of the streambed substrates, and high egg-to-fry survival rates within the Stuart-Takla study (Cope and Macdonald 1998) clearly illustrate that the three principal study streams are exceptionally productive for sockeye salmon. However, results of tagging studies suggest that spawners can limit their own production within these streams.
Sockeye tagged early in the spawning season in 1995 quickly migrated and dispersed upstream as far as the untagged individuals. Three days after tagging, the distribution of tagged fish was equal to that of the untagged ones (Fig. 9). One week later, the distribution of the same tagged fish had not changed (Fig. 10; yellow-tagged sockeye). They were less abundant due to mortality among those that had already spawned. However, the fish that remained alive were actively spawning on top of redds belonging to fish that had spawned first. Superimposition of redds was confirmed through observation of large numbers of dead salmon eggs excavated by later spawners. Dead eggs drifting downstream with the current are especially common in years of high spawner abundance.

Furthermore, sockeye that arrived 1 week after the first sample of fish was tagged also spawned on top of redds belonging to the earlier arrivals (Fig. 10; red-tagged sockeye in O’Ne-ell Creek). Tagged samples of fish arriving in mid-season (or later) did not migrate as far upstream as the earliest arrivals. The distribution of fish arriving in mid-season was almost entirely towards the lowermost stream reaches (Fig. 10). In years of high spawner abundance, these low-gradient portions of the stream usually contain 84–94% of all spawners. Competition for space by superimposition of redds appears to be common in sites downstream although more area of high-quality habitat is available in that part of the stream compared to those reaches found upstream (e.g., section 2 upstream; Figs. 9, 10).

Sites upstream are occupied primarily by sockeye arriving prior to mid-season. Although suitable spawning substrate in the higher-gradient reaches is limited and frequently occurs in patches among boulders, egg-to-fry survivals in these areas are as high as those observed in sites downstream (Cope and Macdonald 1998). The upper reaches of the spawning grounds support at most only about 6–16% of all sockeye. However, fry production from these sites might be disproportionately large compared to the proportion of adults spawning in the same areas assuming redd superposition causes high mortality in the principal spawning sites downstream.
Summary

The results of studies on adult sockeye distribution and habitat preferences prior to forest harvesting have shown that:

1) The strip-count method can be employed to determine the abundance and longitudinal distribution of adult sockeye salmon in Gluskie, Forfar, and O'Ne-ell (Kynoch) creeks.

2) Large numbers of sockeye aggregate in deep pools in all streams prior to spawning.

3) The highest densities of spawners during the peak of spawning activity are found most frequently in gravel glides and at the downstream tails of pools.

4) Of the three study streams, the only areas sockeye consistently avoid are sites flooded by beavers, and high-velocity riffles and rapids found in the steep-gradient reaches upstream.

5) The length of stream occupied by adult sockeye depends directly upon overall levels of spawner abundance.

6) Linear correlations between spawner densities and stream microhabitat variables indicate that the entire range of depths, velocities, and (by extension) substrate textures occurring in the lowest stream reaches are suitable for sockeye spawners.

7) Substrate analyses and high egg-to-fry survival in all sites sampled by other observers confirm the abundance of high-quality spawning sites throughout the lower reaches of each stream accessible to sockeye.

8) Sockeye arriving later in the spawning season do not migrate as far upstream as the earliest arrivals: these fish may limit the survival of eggs deposited by early spawners by superimposition of redds.

Population and habitat assessments will continue in the future to determine (a) during-harvest and postharvest changes in habitat type, stream channel structure and stability, and the spatial distribution of adult sockeye, and (b) the consequences of these changes upon sockeye egg-to-fry survival and fry production from the study streams.

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