Straying Patterns of Coho Salmon (*Oncorhynchus kisutch*) Stocks from Southeast Vancouver Island, British Columbia

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Fourteen coho salmon (*Oncorhynchus kisutch*) stocks of wild and hatchery origin were tagged from 1985 to 1988 in nine streams within a 150-km coastal section of Vancouver Island. Tag escapements to natal streams were estimated from fence counts, stream surveys, and mark–recapture operations. On average, adult (age 3+) strays accounted for ~4.7% of escapements, but for >40% of the adult escapements in some cases. Adult straying rate, averaged across all years and stocks, was <2%. Straying rates tended to be lower for hatchery fish and highest for stocks subjected to certain enhancement practices. Adult strays escaped to streams 2–159 km from their home stream (average 15.7 km); over 50% escaped to streams <7 km from their stream of release. Straying rates of jacks (age 2+) in a given year and that of their adult siblings during the following year were not related. Genetic makeup, age-at-return, run timing, and exposure to nonnatal water sources during the rearing stage did influence homing. Changes in natural straying patterns should be suspected where enhancement measures include flow controls, selective breeding, and exposure of fry to various water sources. Straying levels and stray contributions should be considered when estimating survival and exploitation rates

De 1985 à 1988, on a étiqueté des saumons cohos (*Oncorhynchus kisutch*) sauvages et d'élevage prélevés de 14 stocks de neuf cours d'eau répartis sur 150 km du littoral de l'île Vancouver. L'échappée de saumons étiquetés aux cours d'eau d'origine a été établie à partir de dénombrements effectués à des barrières de comptage des poissons, de relevés des cours d'eau et d'expériences de marquage et de recapture. En moyenne, les adultes (3+ ans) n'appartenant pas au stock local constituaient environ 4,7 % de l'échappée, mais ce pourcentage pouvait atteindre plus de 40 % dans certains cas. La moyenne du taux d'abandon du stock d'origine dans le cas des adultes, établie pour cette période et tous les stocks, était inférieure à 2 %. Ce taux avait tendance à être moins élevé chez les saumons d'élevage; il était le plus élevé chez les stocks faisant l'objet de mesures de mise en valeur. Les adultes n'appartenant pas au stock local concerné ont remonté des cours d'eau situés de 2 à 159 km de leur cours d'eau d'origine (distance moyenne : 15,7 km); ainsi, plus de 50 % ont remonté des cours d'eau situés à moins de 7 km du cours d'eau où ils ont été mis en liberté. Dans le cas des jeunes mâles précoces (2+ ans), le taux d'abandon du stock d'origine au cours d'une année donnée n'était pas lié à celui des adultes du même stock au cours de l'année suivante. Le patrimoine génétique, l'âge au moment de la remonte, le moment de la remonte et l'exposition à d'autres sources d'eau lors de l'élevage ont influé sur le retour vers les eaux natales. On doit s'attendre à des modifications du régime naturel d'abandon du stock d'origine lorsque les mesures de mise en valeur comprennent la régulation du débit, l'élevage sélectif et l'exposition des alevins à diverses sources d'eau. On devrait tenir compte du taux d'abandon du stock d'origine et de la contribution des saumons étrangers dans l'estimation des taux de survie et d'exploitation.

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One of the distinguishing features of the Pacific salmon life history is their ability to return back to their natal stream to spawn and die after a period of ocean residency. Various theories have been proposed to account for this "homing" ability (Smith 1985), which is generally assumed to be fairly accurate (see Brannon 1982). Larkin (1978) noted that there was no evidence to support the view that a measurable part of the natural mortality at sea could be accounted for by salmon becoming "lost". However, there are numerous well-documented cases of salmon "straying" to streams other than their natal one, which is essentially the process by which new habitats get colonized.

Information on the amount of straying for a given population is useful for stock assessment purposes, since it serves to clarify the relation between stock and recruitment, and improve estimates of total survival rates. Knowledge of the factors which affects straying can also be used to improve enhancement practices and assess the effects of environmental impacts. Various studies have already provided some evidence that straying is substantial for some populations (Shapavalov and Taft 1954) and that straying can be influenced by genetic factors and enhancement practices (Bams 1976), spawner age, and season (Quinn and Fresh 1984). However, a review of the existing information on straying led Quinn and Fresh to state that "reliable estimates of the proportion of salmon that home are virtually non-existent".

An investigation was conducted during 1984–89 in southern British Columbia to determine the similarity among coho salmon (*Oncorhynchus kisutch*) populations. One objective of the study was to quantify straying rates within a local assemblage of wild and hatchery salmon stocks. A secondary objective was to identify the population attributes, hatchery practices, and environmental variables that influence homing of

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coho salmon. Since all stocks were subject to coded-wire tagging and escapement enumeration, information was available on stream location, flow patterns, smolt size and time of ocean entry, run timing, adult size and age-at-return, year of return, exposure to enhancement activities, hatchery rearing practices, genetic differences, exploitation patterns, and survival rates. As a result, it was possible to provide estimates of straying among these stocks based on tag recovery patterns and assess the effects of the above factors on homing.

Materials and Methods

Nine streams on the east side of Vancouver Island were selected for this study on the basis of accessibility, geographical location, coho abundance levels, hydrological regimes, availability of logistic facilities, and exposure to enhancement activities. The streams were the Quinsam River, Black Creek, Puntledge River, Trent River, Rosewall Creek, Big Qualicum River, Little Qualicum River, French Creek, and the Millstone River (Fig. 1). Details on the biological and physical features of the streams and populations monitored during this study have been reported by Hancock and Marshall (1985), Reinhardt and MacKinnon (1979), Fraser et al. (1983), Hamilton (1978), Hurst and Blackman (1988), Lukyn et al. (1985), Bocking et al. (1988), and Labelle (1990a).

The various "types" of coho found in these streams were classified as follows: "wild" stocks consisting of coho that spawn and rear under natural conditions, "production" stocks consisting of coho reared entirely under hatchery conditions, "colonization" stocks consisting of coho reared under hatchery conditions for a few months and released as fry (<10 g) into the stream to complete their growth before smolting, and "enhanced" stocks consisting of a mixture of wild coho and unmarked hatchery coho from colonization releases. Some of the streams selected were occupied by several identifiable types of coho, so a total of 14 stocks were available for comparative purposes. For the present study, coho from different streams were considered to be genetically distinct, except when one stream population consisted of the progeny of spawners from another stream where brood stock was collected. In such cases, the progeny was considered to be genetically similar to the sibling population in the parent stream.

To generate reliable information on the life history traits of each stock, juvenile tagging and escapement enumeration were conducted in all streams. Coded-wire tags (CWT)(Jefferts et al. 1963; Jewell and Hager 1972) were used for this purpose, since this technology has been shown to be cost-effective for large-scale juvenile tagging programs and because Pacific salmon fisheries and escapements are systematically sampled for CWT

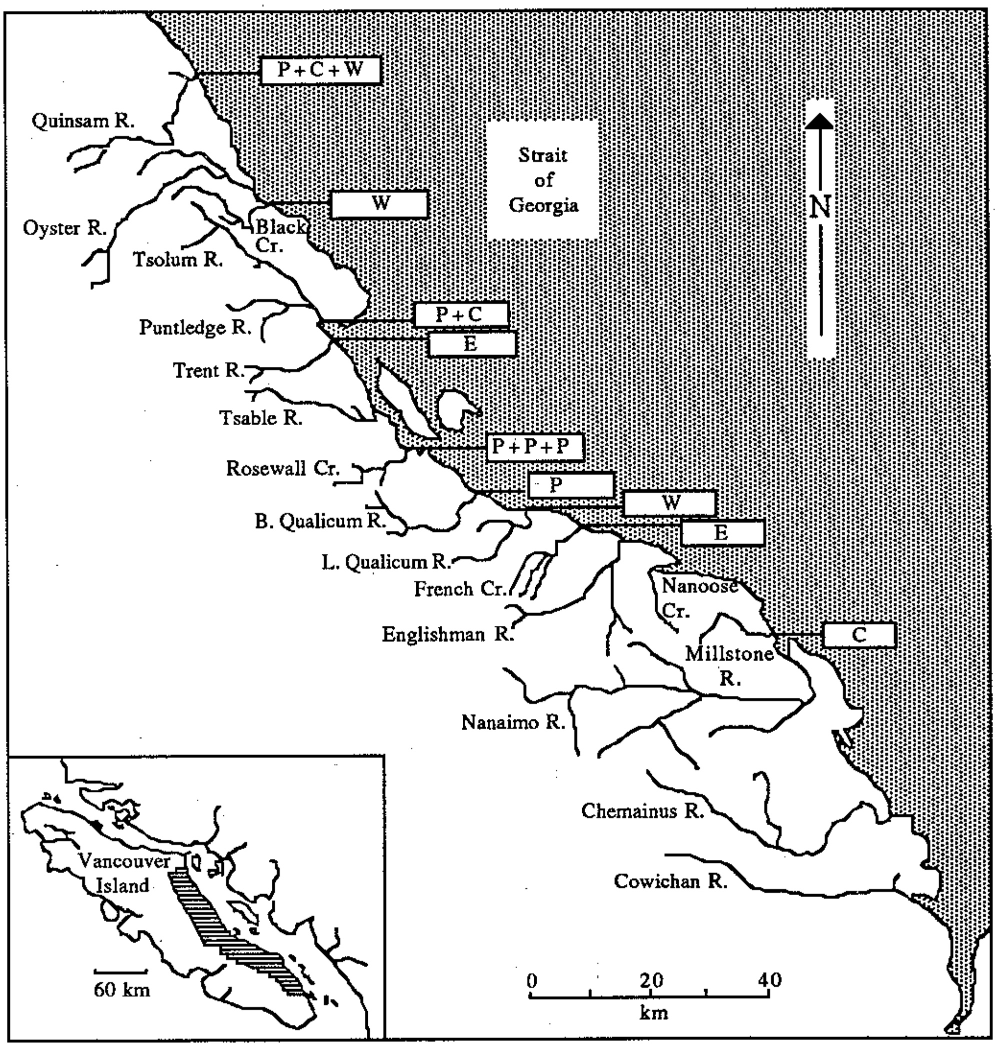

FIG. 1. Geographical location of study site. The abbreviations used to represent the stocks in each stream are as follows: P, production; C, colonization; E, enhanced; W, wild.

recovery. Juveniles from each stock were tagged and released during the springs of 1985, 1986, and 1987. Escapement enumeration and tag recovery were conducted at the release sites and in the adjacent systems during the 1985–88 period. Juvenile tagging, escapement estimation, and tag recovery operations differed substantially among streams, so a brief description of the procedures used at each location is presented here.

Juvenile Tagging

Large public hatcheries are located on the Quinsam, Puntlege, and Big Qualicum rivers. English et al. (1991) gave a detailed account of the hatchery production and sampling programs conducted at these locations by hatchery personnel. Coho were reared in the holding ponds and rearing channels located in areas adjacent to each river. Several weeks prior to release, a fraction of the fry population in each pond or channel was fin clipped and tagged. Total fry abundance was then determined by mark–recapture methods. Dead fry recovered subsequently were deducted from the mark–recapture estimates to determine the remaining fry populations. English et al. noted that these "book estimates" can be positively biased, since undetected losses due to predation and decomposition were not included. Samples were subsequently taken several weeks after tagging to estimate tag loss, which was theoretically a sufficient time to account for all tag loss (Blankenship 1990). Juveniles released from each facility as smolts after an 18-mo rearing period were considered to be individual production stocks. Some of the fry and smolts released from these facilities during 1984 and 1985 (1983 brood) were also given a characteristic mark (left ventral fin excised) to conduct detailed assessment of the 1986 fishery contributions.

Some of the coho reared at the Puntledge River and Quinsam River facilities were released in the headwaters of these systems as fry during their first summer after being fin clipped, tagged, and sampled for tag loss. These two groups were classified as colonization stocks. At Puntledge River, the number of tagged smolts that survived and migrated to sea each year was based on the number of fry released, and the average fry-to-smolt survival estimated from previous surveys conducted by hatchery personnel. At Quinsam River, smolt traps installed at the main fence upstream from the hatchery were used to determine the number of tagged smolts from colonization releases that migrated to sea each year. The traps were also used to capture and enumerate wild (unmarked) smolts leaving the river. Wild smolts exhibiting no visible injuries were fin clipped, tagged, and released within a 48-h period after samples were checked for tag loss. This latter group was classified as a wild stock.

At Little Qualicum River, a large spawning channel is used primarily for the production of chum salmon (*Oncorhynchus keta*). However, some adult coho also enter the channel each year and spawn. Since the progeny rear in the channel under seminatural conditions, this group was considered to be a wild stock. A sampling device was installed at the exit of the channel each year to determine the total coho smolt output. Smolts exhibiting no visible injuries were fin clipped, tagged, and released within a 48-h period after samples were checked for tag loss.

At the Millstone River, hatchery-reared coho were released as fry during their first summer in the headwaters. The brood stock used for this program was collected each fall in this river and transported to the nearby Nanaimo River hatchery for rearing. A few days prior to release, the fry were fin clipped, tagged, and checked for tag loss after a 48-h retention period. Smolt traps were used each year to determine the number of tagged smolts leaving the system. Details of the trapping and tagging operations were reported by Hurst and Blackman (1988), who also noted that the hatchery-reared coho accounted for the vast majority of the smolt output of this system. The tagged group was classified as a colonization stock.

At Black Creek, Trent River, and French Creek, downstream smolt traps (Conlin and Tutty 1979) were installed to tag smolts throughout the migration period each year. Fin clipping and tagging were conducted in areas adjacent to the trap, with the same procedures as used in neighboring hatcheries. Tags were applied exclusively to juvenile coho exhibiting smolting characteristics (Wedemeyer et al. 1980), lacking visible injuries, and exceeding 7 cm in fork length. All smolts were released within 48 h from the period of capture after samples were checked for tag loss. Tagged coho from Black Creek were classified as a wild stock, since the natural production was not supplemented with the addition of hatchery fry. At French Creek and Trent River, brood stock were collected each fall for enhancement purposes. The fry were reared separately in small artisanal hatcheries located nearby and released unmarked during the first summer in the respective streams. Given the lack of a characteristic fin clip, smolts from colonization releases were not clearly distinguishable from wild smolts during tagging, but Labelle (1990a) estimated that hatchery-reared coho accounted for >10% of the smolts from French Creek and 40–60% of the smolts from Trent River. The tagged groups from these two streams were classified as enhanced stocks.

During 1984 and 1985, brood stock were collected at Black Creek, Trent River, and the Little Qualicum River, and the progenies from each group were reared separately at the Rosewall Creek hatchery. A few weeks prior to release, the fry were fin clipped, tagged, and examined for tag loss after a 48-h retention period. All smolts were released simultaneously each year at times which corresponded as much as possible to the peak migration periods of their natural counterparts. These coho were classified as production stocks of different broods.

Escapement Estimation and CWT Recovery

At the Quinsam, Puntledge, Little Qualicum, and Big Qualicum rivers, permanent fences diverted most of the returning coho to holding channels. At Rosewall Creek, an electric fence (Burrows 1957) diverted most returning coho into concrete raceways. Most of the coho held at these sites were sexed, aged (jack/adult), measured, examined for missing fins, and processed for sales, brood stock acquisition, and tag recovery. Estimates of the number of adults and jacks that spawned and died in the stream were obtained through interviews with managers of each facility, who have surveys conducted for such purposes. These figures were combined with those from the hatchery to determine total escapement, sampling rates, and overall tagged proportions by age category for each system.

At Black Creek, Trent River, and French Creek, collapsible fences designed by engineers of the Salmon Enhancement Program (SEP) were used for escapement enumeration. Fish intercepted at the fence were identified, aged (jack/adult), examined for missing fins, and usually marked on the operculum prior to release. Stream surveys were then conducted periodically to determine trends in marked proportions throughout the season, estimate the proportion of each escapement lacking specific fins (fin-clipped proportions), and recover tagged heads from carcasses. Mark–recapture estimates of jack and adult escapements were generated separately based on fence counts and stream survey data. Details of the sampling regimes and the mark–recapture estimation procedures used were reported by Labelle (1990a).

To obtain additional information on movement patterns of coho in the Trent River, 43 adult coho were captured with seine nets in pools from the middle reaches, approximately 9 d after their entry into this river. Serially numbered tags were applied to the coho, which were released within 60 s from the time of capture (see Bocking et al. 1988 for details). To determine if hatchery strays (fin clipped) and nonhatchery coho spawned together, efforts were made to capture spawners paired together near redds, or in the process of spawning. All fish captured were examined, sexed, measured, and released within 60 s. No attempt was made to dig out the redds to determine the extent of egg fertilization.

At the Millstone River, trained technicians from the Nanaimo River hatchery conducted foot surveys and sampling activities during the period of peak spawner abundance to determine escapement levels, acquire brood stock, and recover tagged heads from carcasses. Estimates of escapements by age category and the corresponding fin-clipped proportions were obtained form hatchery records. Additional surveys were also conducted periodically by Department of Fisheries and Oceans (DFO) personnel each fall to determine escapements to other streams in the same region. The rivers surveyed included the Quatsese, Oyster, Little Oyster, Tsable, and Chase. The creeks surveyed included Granite Bay, Coal, Waterloo, and Chef. Estimates of escapements, fin-clipped proportions, and sample sizes were obtained directly from the surveyors. In the rare cases where sample sizes or escapement estimates were not available, the number of tagged coho recovered (''select recoveries'') (Kuhn et al. 1988) was used as the total number of tagged coho of a given code that escaped to the stream.

Statistical Treatments and Analytical Methods

Heads collected each season from escapement samples were sent to DFO's Head Recovery Laboratory for identification or processed at the hatcheries by experienced tag readers. Data on tag identities and sampling rates are stored in the Mark–Recapture Database (MRP) along with pertinent statistics on juvenile attributes, tagging procedures, and rearing conditions. This database is maintained by personnel from DFO at the Pacific Biological Station in Nanaimo, British Columbia. All statistics used in the following analysis were extracted from this database according to the procedures described by Kuhn (1988).

Not all coho lacking an adipose fin in a sample are successfully dissected and positively associated with a given code. These ''nontags'' (Kuhn et al. 1988) include coho that were not dissected (no data; ND), those that were dissected but the tag was lost (lost pin; LP), and those that lacked a tag (no pin; NP). Specific methods were used to account for these nontags based on the recovery source and the availability of ancillary information. The methods used were similar to those proposed by Kuhn et al. Sample statistics were first corrected for sampling deficiencies and the reported emigration of marked coho from some streams. Nontags were then associated with certain codes to estimate the expected number of tags of a given code in a sample (adjusted recoveries). These were then expanded according to the sampling rate to estimate the expected number of tags in the escapement (estimated recoveries). It should be emphasized that these estimates are generated for each age class (jacks/adults) separately. The major steps in this estimation process are described here, but further details can be obtained from Labelle (1990b).

For escapement samples from Rosewall Creek and the Quinsam, Puntledge, and big Qualicum rivers (hatchery systems), the frequencies in the various nontag categories were first corrected to account for the misidentification of 1% of the unclipped coho, which was hypothesized to occur during the sorting stage at the last three locations (DFO unpublished internal report). The adjusted recoveries in escapement samples were then estimated as follows:

$$(1)\quad T_{\mathrm{corr},c} = T_{\mathrm{obs},c} \cdot \left(1 + \frac{\mathrm{LP}}{K}\right) \cdot \left(1 + \frac{\text{tag loss}_c}{1 - \text{tag loss}_c}\right)$$

$$(2)\quad K_{\mathrm{corr}} = \sum_c T_{\mathrm{corr},c}$$

$$(3)\quad T_{\mathrm{adj},c} = T_{\mathrm{corr},c} \cdot \left(1 + \frac{\mathrm{ND}}{K_{\mathrm{corr}}}\right)$$

where $T_{\mathrm{obs},c}$ = number of observed recoveries of code c in the sample, $T_{\mathrm{adj},c}$ = estimate of adjusted recoveries of code c in the sample, tag loss_c = estimate of tag loss associated with code c, and K = number of identified tags in the sample (Σ observed recoveries).

The number of estimated recoveries for each code ($T_{\mathrm{tot},c}$) in the escapement (esc) was obtained after accounting for the sampling rate and the nondetection of adipose-clipped coho (8%) which was assumed to occur during the sorting stage (DFO unpublished internal report):

$$(4)\quad T_{\mathrm{tot},c} = \frac{T_{\mathrm{adj},c}}{0.92} \cdot \frac{\mathrm{esc}}{\mathrm{sample}} .$$

Sampling error was considered to be negligible in all other streams monitored. The number of NP associated with all tagged fish of stray origin (nearly always from hatchery systems) in an escapement sample was estimated by multiplying the contributing stray tag codes by their corresponding tag loss estimates. This estimate was then deducted from the total number of NP in the escapement sample to obtain the number of NP associated with tag codes of nonstray origin escaping back to their stream of release. The ratio NP/(K + NP) based on nonstray statistics was considered as the tag loss estimate for nonstray tagged groups in the sample, since these were not held long enough before release to account for all tag loss. This tag loss estimate was assumed to apply to all codes of nonstray origin in the sample, since roughly equal numbers of coho were usually tagged with each code at release. This tag loss estimate was also used to determine (by Eq. 1–3) the number of adjusted recoveries for the associated tag codes, in hatchery systems and other streams where strays were detected. For streams where no strays were detected, there was simply no need to allocate nontags based on code-specific estimates of tag loss, so nontags were allocated in proportion to the contribution of each code in the escapement samples:

$$(5)\quad T_{\mathrm{adj},c} = T_{\mathrm{obs},c} \cdot \left(1 + \frac{\mathrm{NP} + \mathrm{LP} + \mathrm{ND}}{K}\right)$$

$$(6)\quad T_{\mathrm{tot},c} = \frac{T_{\mathrm{adj},c} \cdot \mathrm{esc}}{\mathrm{sample}} .$$

Estimates obtained by Eq. 4 and 6 represent the number of tagged coho of a given stock, release year, age class, and code that escaped to a given stream and year. The tag escapement for a given group (combination of stock, release year, and age class) to one stream and year was obtained by pooling the estimated recoveries across all tag codes associated with the group. The total tag escapement for each group was estimated by further pooling across all streams:

$$(7)\quad \text{tag esc}_g = \sum_{st} \sum_{c} T_{\text{tot},st,c}$$

where tag esc_g = total tag escapement for a given group (g) and $T_{\text{tot},st,c}$ = estimated recoveries with code (c) in a stream (st).

For each group, homing proportions were obtained from the ratio of the tag escapement in the stream of release to the total tag escapement. Straying rates were defined as 1.0 minus the homing proportion, or the fraction of the group that escaped to streams other than the stream of release.

The contribution of strays from hatchery systems to each escapement was obtained by expanding the estimated recoveries of each stray tag code to account for the associated untagged smolts released. For each of these codes, the corresponding tagged proportions at release ($p(\text{tagged})_{\text{rel}}$) were estimated from

$$(8)\quad p\,(\text{tagged})_{\text{rel},c} = \frac{\text{tag rel}_c}{\text{total rel}_c}$$

where tag rel_c = total number of smolts released that were tagged with code c, adjusted for mortalities and tag loss prior to release, and total rel_c = estimate of total smolt output represented by code c, adjusted for mortalities prior to release.

The total number of coho associated with each code (c) that strayed to a given stream (stray_c) and the contribution of strays associated with all foreign tag codes ($C = \Sigma c$) to each escapement (expressed as the proportion: $p(\text{stray})_{\text{esc}}$) were estimated as

$$(9)\quad \text{stray}_c = \frac{T_{\text{tot},c}}{p(\text{tagged})_{\text{rel},c}}$$

$$(10)\quad p(\text{stray})_{\text{esc}} = \frac{\sum_{C} \text{stray}_c}{\text{esc}}.$$

Note that the above estimation procedure does not account for the contribution of strays from unassociated releases: groups of fry released from a hatchery, or transplanted to neighboring streams, that do not contain tagged individuals and that cannot be readily associated with another tagged group. However, such groups represented a relatively minor portion of the total production of public hatcheries during the 1984–88 period (MRP database records).

To determine the contribution of strays from nonhatchery systems, the above estimation procedure was slightly modified. Trapping and tagging operations conducted by means of smolt traps did not provide accurate estimates of total smolt output, so tagged proportions were based on escapement statistics. Escapements to nonhatchery systems were first adjusted to account for stray contributions to estimate escapements of coho returning to their stream of release. Estimated recoveries for these nonstray groups were expanded by a factor of 1.19 to account for the hypothesized differential mortality of tagged and untagged smolts at release that is induced by trapping and tagging operations (see Blankenship and Hanratty 1990). This expanded figure divided by the corrected escapement was used as the tagged proportion estimate for each group returning to their stream of release. The contribution of strays from these groups to other streams was then estimated from Eq. 9 and 10.

Effects of Various Factors on Homing

A linear logistic model (Fienberg 1980) was used to describe the structural relationship between the tag recovery patterns and various factors monitored during this study. The objective was to predict the probability of homing for different types of coho characterized by particular combinations of population attributes and environmental factors. The logistic model describing this relationship is

$$(11)\quad E\left(\frac{r_1}{r_2}\right) = \frac{\exp^{(b_0 + b_1x_1 + b_2x_2 + \ldots)}}{1 + \exp^{(b_0 + b_1x_1 + b_2x_2 + \ldots)}}$$

where r_1 = estimated number of tagged coho of a group that escaped to its home stream, r_2 = estimated number of tagged coho of a group that escaped to all streams, b_n = parameters to be estimated, and x_n = population attribute (x_1 = year of return, x_2 = smolt size, etc.).

The relative frequencies in each category (r_1, r_2) was considered to be the response variable of interest. The population attributes tested for their effects were x_1 = calendar year of escapement (1–4, representing 1985–88), x_2 = genotype (parental stock) of the group released (the eight categories used were Quinsam (1), Black Cr. (2), Puntledge (3), Tent (4), B. Qualicum (5), L. Qualicum (6), French Cr. (7), and Millstone (8); wild, colonization, and production coho residing in the same sream were considered to be members of the same category; Rosewall Creek releases from different brood stocks were categorized according to the parent stock used (2, 4, and 6), x_3 = duration of the hatchery rearing period in months (the estimates used were wild = 0, enhanced ≈ 3, colonization ≈ 6, production ≈ 18), x_4 = smolt weight at release (in grams), x_5 = median date of smolt migration (calendar date), x_6 = release location, expressed as the latitudinal distance (in kilometres) from Nanaimo, x_7 = starting date of the upstream spawner migration, x_8 = median date of the upstream spawner migration, or run timing (calendar date), x_9 = age of the spawners, in terms of ocean residency period (jacks = 1, adults = 2), x_{10} = exposure to nonnatal (foreign) water sources during the rearing stage (Y/N), x_{11} = total number of escapement recoveries, and x_{12} = existence of mechanical flow control in the stream of release (Y/N).

The stepwise logistic regression program (LR) of the BMDP statistical package (Dixon et al. 1988) was used to fit the logistic model to the data. Given the relatively low number of distinct observations (stock/year combinations) in relation to the large number of factors that could be incorporated into the model, it was necessary to impose limits on the number and type of interactions tested simultaneously. Main factors related to each other ($r^2 > 0.50$) were identified by means of correlation matrices, and only one factor from each correlated pair was allowed into the model. From the remaining set, only the main factors and their first-order interactions were tested. The first-order interactions tested were those hypothesized to have an influence on the trait of interest through some plausible mechanism.

The objective of the model fitting process was to determine which source contributed most to an improvement in fit, which was accomplished by examining the reduction in "deviance" obtained by the inclusion of additional factors in the model (as suggested by Green and Macdonald 1987). For the present study, additional factors were incorporated into the model until the reduction in deviance associated with the additional factors was ≤5% of the largest reduction in deviance obtained during previous inclusions. As a result, factors which had a relatively small contribution to the improvement in fit were not incorporated in the model, even if their contribution was "statistically" significant. By omitting factors with marginal contributions, the resulting model was more parsimonious, yet could still be used for "predictive" purposes, since it accounted for the effects of the main factors.

Once a suitable model was identified, a sensitivity analysis was performed by conducting goodness-of-fit tests with different versions of the model characterized by the presence or absence of each factor. Further insight into the direction of changes in homing resulting from variation in the levels of each factor was obtained by incorporating the regression coefficient estimates generated by the BMDP program into the logistic model and then predicting homing proportions associated with particular combinations of parameter values arbitrarily selected within a realistic range.

Results

Stray Contributions and Straying Rates

Information on tag identities revealed that the majority of the tagged adults recovered in the Trent River during 1986 were of Puntledge River origin (Tables 1 and 2) and that adult strays contributed about 44.8% of the total escapement to this river (Table 3). However, such high stray contributions were not typical, since in the majority of cases, strays contributed less than 1% of the escapements of adults and jacks. Stray contributions, averaged across all streams, accounted for ~3% of the jack escapements and ~4.7% of the adult escapements. Such high average contribution estimates were mainly induced by the relatively large contribution of strays to the Trent River, which accounted for more than half of the coho escaping to this river in 1987. Adults and jacks tended to stray more to the Puntledge River than to other large hatchery systems such as the Big Qualicum and Quinsam rivers. Strays in the Puntledge River consisted mainly of coho reared at the Puntledge River hatchery and released in the headwaters of the adjacent river (Tsolum River) for colonization purposes.

The accuracy of hatchery stray contributions based on expansion of tag recoveries was assessed based on the proportions of fin-clipped coho observed in the 1986 escapements to nonhatchery systems. The proportion of adults lacking a left ventral fin in the 1986 escapement at Trent River was estimated to be about 40.1%. Given that about 82% of the smolts released from the Puntledge River hatchery were fin clipped, the number of fin-clipped adults in the Trent River should be expanded by 1.22 to account for the unclipped smolts released. Based on this expanded figure, it was estimated that adults from the Puntledge River hatchery accounted for ~48.9% of the 1986 Tent River escapement, which is similar to the estimate based on expansion of tag recoveries (44.8%). At French Creek, fin-clipped adults accounted for less than 0.8% of the escapement, which is comparable with the figure obtained by expansion of tag recoveries (0%). Such results indicate that the contribution of strays can be reliably estimated by expansion of tag recovery data.

Straying rates among adults ranged from 0 to 54.1%, but for most groups, a high proportion of the tagged coho escaped to their home stream (Tables 1 and 2). Among adults, straying was lowest for production releases (Table 4). On average, adults from colonization releases strayed slightly more than those from production releases. Adults from wild populations strayed slightly more than the two former types, and adults from enhanced populations strayed more than those of wild populations. Adults from experimental releases conducted at the Rosewall Creek hatchery exhibited unusually high levels of straying during 1987, but straying in 1988 was only slightly greater than average. Chi-square tests of the stray:nonstray frequencies revealed significant differences among stock types each year, but no clear pattern was consistent across all years. On average, adults exhibited more straying in 1987 than in other years. On an overall basis, adult straying averaged 1.5%, but if the experimental releases from Rosewall Creek were omitted, the average was 1.0%. Adult strays escaped to streams located 2–159 km from their home stream, but the average straying distance was 15.7 km, and over 50% of the strays escaped to streams located less than 7 km from their home stream.

Straying rates among jacks ranged from 0 to 50%. As for adults, production and colonization releases from large hatchery systems exhibited very little straying. Those from experimental releases at Rosewall, and colonization releases at the Millstone River, strayed the most. On average, straying appeared to be greatest during 1988 and 1986. No significant correlation was detected between the level of straying among jacks in a given year and their adult siblings during the following year. On an overall basis, jack straying averaged 0.43%, and if the experimental releases from Rosewall Creek were omitted, the average was 0.38%, which is substantially less than was observed for adults. Jack strays escaped to streams located 2–91 km from their home stream, but the average straying distance was 26.3 km, and over 50% of the strays escaped to streams located less than 7 km from their home stream.

Some of the Trent River strays were recovered in the Puntledge River, which serves as the water source for the artisanal hatchery used to rear the colonization fry. In addition, some adults of Trent River brood stock released from the Rosewall Creek facility were recovered at the Trent River. However, in the majority of cases where adults and jacks strayed from their location of release, they were recovered in streams which were neither their ancestral stream nor the stream where they reared for a portion of their presmolt life.

Effects of Various Factors on Homing

Not all variables tested contributed to a substantial improvement in fit (Table 5). The duration of the hatchery rearing period per se (x_3) was not required in any of the models, indicating that this factor had relatively little influence on homing. All remaining variables were useful in predicting homing proportions, with some of them being incorporated into the model only as interaction factors. Model 9 was judged to be an appropriate model for describing homing proportions. The predicted values were highly correlated with the observations, and no pattern was detected in the residuals. More complex models incorporated mainly interactions of factors already included in model 9 and failed to provide a substantial improvement in fit as judged by the trajectory of the reduction in deviance. This indicates that information on return year, rearing conditions, genetic makeup, run timing, and flow control was sufficient for predicting homing proportions. Factors related to the juvenile migration (smolt migration date, smolt size, release location) had a relatively minor influence.

Results of the sensitivity analysis indicated that the genetic × exposure interaction factor was a major determinant of homing proportions (Table 6) and suggest that certain stocks are more susceptible than others to straying when exposed to for-

TABLE 1. Estimates of the number of tagged jacks from each population that escaped to selected streams (recovery locations) from 1985 to 1988. Numbers accompanied by a ">" sign are minimum estimates of tag escapements obtained from select samples. % homing indicates the proportion of the total tag escapement that escaped to their stream of release.

		Recovery locations (km from Chase, Nanaimo)																			
Year	Release site and stock[a]	Quatsese 300	Granite 143	B. Quins. 141	Oyster 120	Black 118	Little 101	Puntl. 99	Trent 93	Tsable 80	Coal 75	Waterloo 74	Rosewall 73	Chef 71	B. Qual. 59	L. Qual. 50	French 41	Millst. 8	Chase 0	Sum	% homing
1985	Quins. (p)		>4	1687											2					1693	99.6
	Quins. (c)		>2	305																307	99.3
	Black Cr.					88														88	100.0
	Puntl. (p)		>2					3109	1											3112	99.9
	Puntl. (c)							15												15	100.0
	Trent R.																			0	—
	B. Qual.														203					203	100.0
	L. Qual.								1							56				57	98.2
1986	Quins. (p)			1128					2											1130	99.8
	Quins. (c)			213																213	100.0
	Quins. (w)			1																1	100.0
	Black Cr.					268														268	100.0
	Puntl. (p)							88												88	100.0
	Puntl. (c)							3												3	100.0
	Trent R.								6						1					7	85.7
	Rosew. (b.c)												66							66	100.0
	Rosew. (t.r)												30							30	100.0
	Rosew. (l.q)												27							27	100.0
	B. Qual.														80					80	100.0
	L. Qual.															52				52	100.0
	French Cr.																7			7	100.0
	Millstone							1										7	6*	14	50.0
1987	Quins. (p)			1018																1018	100.0
	Quins. (w)			19																19	100.0
	Black Cr.					417									1					418	99.8
	Puntl. (p)							218												218	100.0
	Puntl. (c)							5												5	100.0
	Trent R.							2	39						1					42	92.9
	Rosew. (b.c)												25							25	100.0
	Rosew. (t.r)												13		5					18	72.2
	Rosew. (l.q)												64		3					67	95.5
	B. Qual.														494					494	100.0
	L. Qual.														1	261				262	99.6
	French Cr.												1		9	1	184			195	94.4
	Millstone																	12		12	100.0
1988	Quins. (p)			3072											2					3074	99.9
	Black Cr.					266									6					272	97.8
	Puntl. (p)							207												207	100.0
	Puntl. (c)							17												17	100.0
	Trent R.							2	144											146	98.6
	B. Qual.														284					284	100.0
	French Cr.														4		168			172	97.7
	Millstone																	>2	>1	3	66.7

[a]Letters in parentheses are stock type or origin if different from release site: p, production; c, colonization; w, wild; bc, Black Creek; tr, Trent River; lq, Little Qualicum River. See text for further explanation.

eign water sources during the rearing stages. Run timing and flow controls were also necessary for predicting homing, and their influence upon homing varied from year to year (because of the interaction). Run timing was also found to influence the homing of various age classes and stocks to a different extent.

Predictions of homing proportions made with the logistic models indicated that homing was negatively affected by the exposure to nonnatal water sources during rearing stages. For all stocks, a reduction in the age-at-return (adult to jack) caused the predicted homing rate to increase by a few percentage points, which supports the previous observation that jacks strayed less than adults.

Predicted homing proportions also improved in the presence of flow control, but the magnitude of the improvement differed from stock to stock. Accordingly, delays in run timing caused the predicted homing proportions to decrease. A 1-wk delay caused a 6 percentage point reduction in homing proportions (88–82%) for adults returning to the Trent River in 1986, but only a 0.5 percentage point reduction in the predicted homing proportions of Trent River jacks returning that year. The difference is attributed to the influence of the age × run time interaction and suggests that jacks are less likely to stray than adults due to delays in fall freshets. The magnitude of the reduction in the predicted homing proportions of Trent River adults was found to differ slightly in other years for comparable delays in run timing. This was expected, since the year × run time interaction was a factor in the model and a determinant of homing. Of particular interest is the finding that delays in run timing led to a slight increase in the predicted homing proportions of stocks returning to streams characterized by flow controls. During this study, the starting and median date of upstream migration in large systems with flow controls (Quinsam, Puntledge, Big Qualicum, and Little Qualicum rivers) generally occurred several weeks earlier than in the other streams. These results suggest that early runs are more likely to stray than later runs.

The influence of genetic factors on homing proportions can be assessed by contrasting the three groups released from the Rosewall Creek hatchery. None of the brood stocks used exhibited consistently greater or lesser adult homing proportions during 1987 and 1988. By contrast, adults returning to the Trent River exhibited consistently lesser homing than those returning to Black Creek and Little Qualicum River. Thus, in the absence

TABLE 2. Estimates of the number of tagged adults from each population that escaped to selected streams (recovery locations) from 1985 to 1988. Numbers accompanied by a "<" sign are minimum estimates of tag escapements obtained from select samples. % homing indicates the proportion of the total tag escapement that escaped to their stream of release.

Year	Release site and stock[a]	Quatsese 300	Granite 143	B. Quins. 141	Oyster 120	Black 118	Little 101	Puntl. 99	Trent 93	Tsable 80	Coal 75	Waterloo 74	Rosewall 73	Chef 71	B. Qual. 59	L. Qual. 50	French 41	Millst. 8	Chase 0	Sum	% homing
		Recovery locations (km from Chase, Nanaimo)																			
1985	Quins. (p)			7472																7472	100.0
	Quins. (c)			614																614	100.0
	Puntl. (p)							3079	19											3098	99.4
	Puntl. (c)							144												144	100.0
	B. Qual.														414					414	100.0
1986	Quins. (p)			5388				2	4											5394	99.9
	Quins. (c)			1301				4												1305	99.7
	Black Cr.			2		824	>2													828	99.5
	Puntl. (p)							2152	128					>3	7					2290	94.0
	Puntl. (c)							164												164	100.0
	Trent R.							6	64						2					72	88.9
	B. Qual.														307					307	100.0
	L. Qual.															99				99	100.0
1987	Quins. (p)			1715										>2						1717	99.0
	Quins. (c)			996																996	100.0
	Quins. (w)	>10		118																128	92.2
	Black Cr.				>19	558														577	96.7
	Puntl. (p)							175	16											191	91.6
	Puntl. (c)							113												113	100.0
	Trent R.							6	158						9					173	91.3
	Rosew. (b.c)							2	16				58	>2	21					99	58.6
	Rosew. (t.r)								64				79	>2	25	2				172	45.9
	Rosew. (l.q)										>1		34		4					39	87.2
	B. Qual.														165					165	100.0
	L. Qual. R.														4	245				249	98.4
	French Cr.														7		51			58	87.9
	Millstone														2			27		29	93.1
1988	Quins. (p)			892																892	100.0
	Quins. (w)			95																95	100.0
	Black Cr.					1541														1541	100.0
	Puntl. (p)							382	7				1							390	97.9
	Puntl. (c)							104												104	100.0
	Trent R.							45	384				1							430	89.3
	Rosew (b.c)											>1	139		4	5				149	93.3
	Rosew. (t.r)												152		2					154	98.7
	Rosew. (l.q)							1					176		6					183	96.2
	B. Qual.														276	3				279	98.9
	L. Qual.															628				628	100.0
	French Cr.															3	623			626	99.5
	Millstone																	172		172	100.0

[a]Letters in parentheses are stock type or origin if different from release site: p, production; c, colonization; w, wild; bc, Black Creek; tr, Trent River; lq, Little Qualicum River. See text for further explanation.

TABLE 3. Estimates of the contribution of strays to each escapement based on expansion of CWT recoveries. The contributions are expressed as a fraction of the total escapement × 100.

Stream	Jacks 1985	Jacks 1986	Jacks 1987	Jacks 1988	Adults 1985	Adults 1986	Adults 1987	Adults 1988
Quins. R.	0	0.03	0	0	0.03	0.02	0	0
Black Cr.	0	0	0	0	0	0	0	0
Puntl. R.	0	2.6	0.3	0.1	0	7.6	8.6	9.1
Trent R.	29.2	69.1	0	0	25.3	44.8	50.2	4.6
Rosew. Cr.	—	0	1.5	0	—	0	0	1.6
B. Qual. R.	1.0	0	0.3	0.3	0	0.9	1.6	0.2
L. Qual. R.	0	0	0.4	0	0	0	0.2	5.9
French Cr.	0	0	0	0	0	0	0	0
Millstone. R.	—	0	0	0	—	0	0	0

of experimental releases from the Rosewall Creek hatchery, it might have been hypothesized that genetic factors were responsible for the differences in homing observed among stocks from the three streams. As suggested by the structure of model 9, genetic factors affect homing, but this effect is influenced by hatchery rearing practices (genetic × exposure). Adult homing proportions for 1987 were predicted for these three stocks under the assumption of no differences in fry rearing regimes and run timing. The predicted homing of Black Creek adults decreased by less than 1 percentage point, but that of Trent River adults increased to levels comparable with the two other stocks. This suggests that the lower homing proportion of adults escaping to the Trent River occurred because some juveniles were exposed to nonnatal water sources during rearing.

Hatchery rearing effects can also be assessed by comparing the homing proportions of coho released from the same loca-

TABLE 4. Proportion (× 100) of total tag escapement of each population that strayed to other streams and average straying distances (km). Q.R., Quinsam River; B.C., Black Creek; P.R., Puntledge River; T.R., Trent River; R.C., Rosewall Creek; B.Q., Big Qualicum River; L.Q., Little Qualicum River; F.C., French Creek; M.R., Millstone River. Groups: p, production; c, colonization; w, wild; e, enhanced. Abbreviations for Rosewall Creek production releases refer to the broodstocks used: bc, Black Creek; tr, Trent River; lq, Little Qualicum River. BY figures represent differences in straying between the two corresponding age classes (jacks and adults).

	Q.R. (p)	Q.R. (c)	Q.R. (w)	B.C. (w)	P.R. (p)	P.R. (c)	T.R. (e)	R.C. (bc)	R.C. (tr)	R.C. (lq)	B.Q. (p)	L.Q. (w)	F.C. (e)	M.R. (c)	Mean
Proportion (× 100) of total tag escapement															
Adults															
1985	0	0			0.6	0					0				0.1
1986	0.1	0.3		0.5	6	0	11.1				0	0			2.2
1987	0.1	0	7.8	3.3	8.4	0	8.7	41.4	54.1	12.8	0	1.6	12.1	6.9	11.2
1988	0		0	0	2.1	0	10.7	6.7	1.3	3.8	1.1	0	0.5	0	2.0
Mean	0.0	0.1	3.9	1.3	4.3	0.0	10.2	24.1	27.7	8.3	0.3	0.5	6.3	3.5	6.5
Jacks															
1985	0.4	0.7		0	0.1	0					0	1.8			0.4
1986	0.2	0	0	0	0	0	14.3	0	0	0	0	0	0	50	4.6
1987	0		0	0.2	0	0	7.1	0	27.8	4.5	0	0.4	5.6	0	3.5
1988	0.1			2.2	0	0	1.4				0		2.3	33.3	4.9
Mean	0.2	0.4	0.0	0.6	0.0	0.0	7.6	0.0	13.9	2.3	0.0	0.7	2.6	27.8	
BY															
1985 rel.	0.3	0.4		−0.5	−5.9	0					0	1.8			−0.6
1986 rel.	0.1	0	−7.8	−3.3	−8.4	0	5.6	−41.4	−54.1	−12.8	0	−1.6	−12.1	5.6	−9.3
1987 rel.	0		0	0.2	−2.1	0	−3.6	−6.7	26.5	0.7	−1.1	0.4	5.1	0	1.5
Mean	0.1	0.2	−3.9	−1.2	−5.5	0.0	1.0	−24.1	−13.8	−6.0	−0.4	0.2	−3.5	2.8	
Average straying distances (km)															
Adults															
1985					6										6.0
1986	46	42		20	8		13								25.8
1987	70		159	2	6		23	16	18	12		9	18	51	34.9
1988					9		6	17	14	16	9		9		11.4
Mean	58	42	159	11	7.25		14	16.5	16	14	9	9	13.5	51	
Jacks															
1985	29	2			31							43			26.3
1986	48						34							19.9	34.0
1987				59			15		14	14		4	19		20.8
1988	82			59			6						19	8	34.8
Mean	53.0	2.0		59.0	31.0		18.3		14.0	14.0		23.5	19.0	14.0	

TABLE 5. Composition of various logistic models describing the homing proportion of all stocks during the 1985–88 period. The main factor and interactions included in each model are listed with the corresponding degrees of freedom (df) and deviance (G). The factors are year (x_1), genetic (x_2), hatchery rearing period (x_3), smolt weight (x_4), smolt migration date (x_5), stream location (x_6), run timing (x_8), spawner age (x_9), exposure to foreign water sources (x_{10}), total number of escapement recoveries (x_{11}), and flow control (x_{12}).

Model	Main factors	Interactions	df	G
0	Constant (k)	—	81	2202
1	k, x_{10}	—	80	1317
2	k, x_{10}, x_{11}	—	79	1212
3	k, x_{10}, x_{11}	$x_8 \times x_9$	78	1077
4	k, x_{10}, x_{11}	$x_8 \times x_9, x_1 \times x_{12}$	75	832
5	k, x_{10}, x_{11}	$x_8 \times x_9, x_1 \times x_{12}, x_2 \times x_8$	68	503
6	k, x_{10}, x_{11}, x_9	$x_8 \times x_9, x_1 \times x_{12}, x_2 \times x_8$	67	463
7	k, x_9	$x_8 \times x_9, x_1 \times x_{12}, x_2 \times x_8, x_2 \times x_{10}$	62	392
8	k, x_9	$x_8 \times x_9, x_1 \times x_{12}, x_2 \times x_8, x_2 \times x_{10}, x_1 \times x_8$	59	369
9	k, x_9, x_1	$x_8 \times x_9, x_1 \times x_{12}, x_2 \times x_8, x_2 \times x_{10}, x_1 \times x_8$	56	321
10	k, x_9, x_1	$x_8 \times x_9, x_1 \times x_{12}, x_2 \times x_8, x_2 \times x_{10}, x_1 \times x_8, x_6 \times x_8$	55	302
11	k, x_9, x_1	$x_8 \times x_9, x_1 \times x_{12}, x_2 \times x_8, x_2 \times x_{10}, x_1 \times x_8, x_6 \times x_8, x_9 \times x_{12}$	54	290
12	k, x_9, x_1	$x_8 \times x_9, x_1 \times x_{12}, x_2 \times x_8, x_2 \times x_{10}, x_1 \times x_8, x_6 \times x_8, x_9 \times x_{12}, x_9 \times x_{10}$	53	274
13	k, x_9, x_1	$x_8 \times x_9, x_1 \times x_{12}, x_2 \times x_8, x_2 \times x_{10}, x_1 \times x_8, x_6 \times x_8, x_9 \times x_{12}, x_9 \times x_{10}, x_{10} \times x_{11}$	52	263
14	k, x_9, x_1	$x_8 \times x_9, x_1 \times x_{12}, x_2 \times x_8, x_2 \times x_{10}, x_1 \times x_8, x_6 \times x_8, x_9 \times x_{12}, x_9 \times x_{10},$ $x_{10} \times x_{11}, x_5 \times x_6$	51	252

TABLE 6. Relative influence of various factors on homing proportions predicted from model 9. Goodness-of-fit tests were performed in the presence and absence of each factor. The factor removed precedes the minus sign. The difference in chi-square obtained after the removal of the factor is given under the Difference column. Parenthetical df are df of factor omitted.

Model	Factor omitted	Log-likelihood	Chi-square	Difference	df	*P*
Main + interaction (M + I)	None	−1992.80	320.911	—	56	0.0000
$M + I - x_1$	Year	−2016.96	369.231	48.32	(3)	0.0000
$M + I - x_9$	Age	−2001.77	338.851	17.94	(1)	0.0000
$M + I - x_2 \times x_{10}$	Genetic × exposure	−2088.74	512.801	191.89	(7)	0.0000
$M + I - x_1 \times x_8$	Year × run time	−2017.56	370.441	49.53	(3)	0.0000
$M + I - x_2 \times x_8$	Genetic × run time	−2015.38	366.071	45.16	(7)	0.0000
$M + I - x_1 \times x_{12}$	Year × flow control	−2006.19	347.701	26.79	(3)	0.0000
$M + I - x_8 \times x_9$	Run time × age	−2002.98	341.271	20.36	(1)	0.0000

tion, but exposed to different hatchery rearing periods. For the Quinsam and Puntledge rivers, homing of adults from colonization releases tended to be slightly greater than that of the production release (Table 2), but chi-square tests of the stray:nonstray frequencies failed to detect significant differences in most cases. In addition, no significant differences were detected between the stray:nonstray frequencies of adults of wild and production origin returning to the Quinsam River in 1987 and 1988. This supports the finding that hatchery rearing period was not a major determinant of homing. However, the same test revealed significant differences between the three Rosewall Creek groups and their counterparts returning to Black Creek and Trent and Little Qualicum rivers in all cases for both years (all P's < 0.01). Adult homing proportions of the three Rosewall Creek groups were nearly always lower than those of their jack counterparts. Since the duration of hatchery rearing was not found to be a major determinant of homing, the lower homing of the Rosewall Creek groups was most likely induced by their later run times and differences in rearing conditions.

Additional Observations on Coho Behavior

Most of the coho with serially numbered tags were subsequently recovered in areas adjacent to the location of tagging. However, one tagged adult was recovered 2 wk after release in the headwaters of the Tsolum River, ~15 km from the tagging location. Such facts indicate that adult coho can move upriver for several kilometres before leaving the stream.

Field observations also revealed that several coho left the Trent River during the first flood each year, and coho with opercular marks were found in neighboring streams after the floods. Most of these emigrants went to the nearby Puntledge River hatchery, but their stream of origin could not be determined with certainty because the tags were not identified. After accounting for the sampling regime at the hatchery, the number of marked adult coho that emigrated from the Trent River during the 1986, 1987, and 1988 seasons was estimated to be 181, 8, and 12 adults, respectively. This represented 16.8, 4.1, and 3.3% of the adults counted at the Trent River fence and provides some information on the magnitude of the emigration that can occur after the initial upstream migration. Based on the time of recovery and the occurrence of floods on the Trent River, it was assumed that the marked coho left the stream on November 18, 1986, November 11, 1987, and November 1, 1988. None of the marked coho released at the other fences were ever recovered in adjacent streams, even though floods occurred each year in those systems.

Significant differences in the relative abundance of fin-clipped adults were detected between the upper and lower sections of the river during the 1986 season ($\chi^2 = 5.5, P = 0.02$). Samples from the upper sections (beyond the China Creek junction) contained proportionally fewer fin-clipped adults than samples from lower sections, indicating that hatchery strays tended to remain in the lower reaches of the river. There was also a reduction in the relative abundance of fin-clipped adults in samples taken before and after the flood, which is to be expected from the departure of fin-clipped hatchery coho returning to the Puntledge River hatchery. However, this reduction was not statistically significant ($P = 0.175$) because only a small proportion of the fin-clipped coho left the stream after the floods.

Examination of the coho captured on the spawning grounds revealed that hatchery strays were paired with fin-clipped and unclipped coho. Assuming that some unclipped coho were of nonhatchery origin, and that such pairing occasionally lead to successful spawning, then some hybridization of hatchery and nonhatchery fish occurred in the Trent River.

Discussion

Based on recovery patterns of coded-wire tagged coho, Quinn and Tolson (1986) estimated that stray contributions to the Quinsam River jack and adult escapements during 1980 were 0.08 and 0.33%, respectively, and were nonexistent for the 1981–83 period. Average stray contributions to the 1978–83 Big Qualicum River jack and adult escapements were 0.07 and 0.06%, respectively, and no strays were found in escapement samples from the Puntledge River (Quinn and Tolson 1986). Only one of the tagged strays in escapement samples had been released from the Big Qualicum River hatchery, and none of these had been released from the other two hatcheries (Quinn and Tolson 1986). Such figures suggest that straying among these hatchery populations was negligible during the 1978–83 period.

The results of the present study are in agreement with those of Quinn and Tolson (1986) and with circumstantial evidence from field surveys and inferences from genetic studies. None of the tagged jacks or adults sampled from the Quinsam River escapements were of Puntledge River and Big Qualicum River origin (Tables 1 and 2). None of the tagged jacks in the Puntledge River escapement samples were from the Big Qualicum or Quinsam River, and only two of the tagged adults were of Quinsam River origin. The number of tagged jacks from the Quinsam and Puntledge rivers found in the Big Qualicum River escapement samples were less than two per year, and only during 1986 were tagged adults from the Puntledge River detected in the Big Qualicum River escapement samples. Estimates of straying among hatcheries for the 1986–88 period were slightly greater than reported by Quinn and Tolson, but this is undoubtedly due in part to the corresponding increase in tagging effort and escapement sampling rates. If this is true, additional tagging of juveniles in adjacent streams should also induce higher stray contributions than reported by Quinn and Tolson. Accordingly, the stray contributions to the hatchery escapements of jacks, averaged across the 1985–88 period (from Table 3), ranged from 0.01% for the Quinsam River to 0.75% for the Puntledge River. Stray contributions to adult escapements ranged from 0.01% for the Quinsam River to 6.3% for the Puntledge River.

Shapavalov and Taft (1954) reported that 14.9% of the adult coho returning to Waddell Creek in California strayed to Scott Creek, a coastal stream located 8 km north of it. During their study, some of the hatchery-reared coho released at Scott Creek also strayed to Waddell Creek. Jacobs (1988) reported the results of an escapement survey of Oregon coastal streams aimed at determining straying levels of hatchery coho subjected to accelerated growth and released as preyearlings after a brief exposure to salt water. Based on the tag recovery patterns, Jacobs estimated that adult coho strayed considerably (range 1–30% of escapement) and strayed predominantly to basins located within a 40-km radius from their point of release. Hatchery-reared coho transported offshore prior to release were twice as likely to stray as those released from onshore facilities. The results of these investigations support the findings of the present study that straying rates of natural and enhanced coho stocks can be considerable and that rearing practices can affect straying patterns.

Bams (1976) conducted a series of experimental releases of pink salmon (*Oncorhynchus gorbuscha*) fry in the Tsolum River, using the progeny of a hybrid stock (Tsolum River × Kakweiken River cross). Differences in treatment effects between the various groups released were minimal. Based on the return rates observed, Bams concluded that adults from the transplanted hybrid stock homed less than those of the other stock. Note that Bams estimated homing rates based on the relative number of recoveries in the stream of release and not on the basis of tag recovery patterns across several streams. Further examination of the figures reported by Bams shows that the only marked adults recovered in adjacent streams were of Tsolum River stock. Bams might have therefore reached the opposite conclusion if his data had been analyzed in accordance with the procedure used in the present study. The results of his study could be viewed as support for the notion that homing is affected by the genetic factors. An alternative interpretation is that homing accuracy is affected by human manipulaton. The results of the present study indicate that the interaction of both of these factors can influence homing, and efforts should be made to account for their separate effects in further studies. Evidence of an hereditary component to the homing behavior of chinook salmon (*Oncorhynchus tshawytscha*) was given by McIsaac and Quinn (1988).

Using information on patterns of genetic variation among coho populations from southern Vancouver Island and the lower coastal mainland, Wehrhahn and Powell (1987) inferred that straying rates from each breeding population were about six successful spawning individuals per generation. For populations with about 1000 breeding adults, this translates into straying rates of approximately 0.5%. Adult straying rates among the five wild and enhanced stocks monitored during this study, with at least 1000 breeding adults, ranged from 0 to 11.1% and averaged 3.7%. This average rate was largely influenced by the relatively high straying rates of Trent River adults. The possibility exists that straying rates for this stock are abnormally high and are not representative of other stocks. Omitting this stock from the calculations leads to an average straying of 1.3%. This figure could represent a maximum straying rate, since it is not known if all strays recovered in various streams would have remained there to spawn successfully. This figure is still higher than the estimate of Wehrhahn and Powell, but the straying rates observed in the present study apply to local populations and are expected to be higher than those based across all stocks covering a wide geographical area. Wehrhahn and Powell estimated that the straying between the lower coastal mainland and southern Vancouver Island populations averaged 50 coho per year. During the present study, only two strays were detected from the mainland, but the area monitored was a small portion of southern Vancouver Island, so the straying estimates of Wehrhahn and Powell cannot be rejected based on the present study.

Quinn and Fresh (1984) estimated straying rates among chinook salmon released from the Cowlitz River hatchery in the Lower Columbia, based on CWT recovery patterns. They found that the adults did not stray substantially (<1.5%) and strays were generally recovered in streams within 30 km of the Cowlitz River. They reported a fourfold difference in the amount of straying between successive year classes, indicating that there can be pronounced year to year changes in straying. Quinn and Fresh found that older age classes tended to stray more than younger ones. Quinn et al. (1991) reported that older chinook salmon (ages 3–5) from the Columbia River also strayed more than younger ones (age 2) and found variation in straying among return years. Lower straying of younger coho was also observed in the present study, indicating that age can have similar influences on straying in different species of Pacific salmon. Quinn et al. speculated that differences in straying rates among age groups might be due to changes in the chemical characteristics of the stream over the years, or to loss of memory as the fish get older.

Quinn and Fresh (1984) noted that high homing proportions were associated with large returns and speculated that social factors strengthen the motivation to home. During the present study, no significant correlation was detected between homing proportions and the number of recoveries to a given stream, but perhaps this is a consequence of the relatively narrow range of recoveries observed during the study. However, insight into the nature of the factor(s) which affect the ability of coho to recognize their home stream can be gained from further examination of the rearing conditions of stocks exhibiting the greatest straying. Rosewall Creek releases consisted of the progeny from distant populations, which were hatchery reared and released from a stream which was not their parental one. This hatchery uses mainly surface water from Rosewall Creek for rearing purposes, but relies heavily on groundwater during June to September when surface flows are insufficient (R. Humphreys, pers. comm.). Fry released in the Millstone and Trent rivers for enhancement purposes were also reared at hatcheries located at some distance from their stream of origin, using nonnatal water sources. Thus, it is hypothesized that the process of exposing fry to groundwater or foreign (nonnatal) water sources for a prolonged period during the rearing stage increases the amount of straying exhibited upon return. In support of this hypothesis, the large fraction of the strays detected in the Puntledge River consisted of coho reared at the hatchery and released in the headwaters of the adjacent river (Tsolum River) for colonization purposes.

It seems reasonable to suspect that some of the year to year variation in straying observed within a small region must be attributed to changes in the tagging and production regimes at various hatcheries and in the streams themselves. However, biological and physical factors should play important roles as well. The relative abundance of strays among the Trent River adult population was highest in 1986 and 1987 when a prolonged drought period affected the upstream migration in all streams in the region lacking flow controls. Insufficient flows may inhibit the ability of early maturing coho to move upstream and may force them to seek alternative refuges and spawning locations. Run timing in streams lacking flow controls is largely influenced by the level of precipitation early in the season. This suggests a mechanism by which delays in run timing could be related to increases in straying. Trends in predicted homing proportions reported earlier also suggested that early runs were more likely to stray than later runs, which could be an adaptation of early runs to cope with the greater probability of insufficient flows early in the season.

It is puzzling that Trent River differs markedly from other streams in terms of its "attractiveness" to strays. Presumably, the proximity of the Trent and Puntledge rivers is partly responsible for the large number of Puntledge River strays found in the Trent River. However, the geographical location of the Trent River does not explain the relatively large number of strays from distant locations, such as from across the Strait of Georgia (Porpoise Bay) and the Lower Fraser (Capilano River). The Trent River does have a larger and more continuous discharge than other small streams and a relatively large estuary. Strays might be attracted more readily to larger rivers than to small streams. In support of this hypothesis, hatchery strays were observed to account for ~30% of the Tsable River escapement in 1986 (R. Hurst, pers. comm.), which is physically similar to the Trent River and located just 10 km south of it. Large numbers of strays were also detected in larger streams such as the Big Qualicum River and the Puntledge River. The number of strays found in the Quinsam River was negligible, but the river location (at the edge of the study area) and the absence of tagging in an adjacent stream could have played a role here.

The emigration of coho observed at the Trent River following a period of stream residency has been observed in other coastal streams where mark–recapture operations were conducted (N. Schubert, pers. comm.). The large emigration of adults from the Trent River in 1986, coupled with their return to the Puntledge River hatchery, suggests that many of the coho entering the Trent River are simply exhibiting "proving" behavior (Ricker 1972) and may not be committed to spawning there. Whether or not the number of coho proving a stream is related to particular attributes of the stream or the size of the stray populations is not known. No strays were ever detected at French Creek, Black Creek, and Millstone River, although they are located in the proximity of public hatcheries (at Big Qualicum, Quinsam, and Nanaimo rivers) which had substantial runs. The Trent River fence is the only one located in intertidal waters, and the number of strays detected might have been lower if the fence had been placed further upstream. Alternatively, it may be that smaller streams have a more characteristic odor (Hasler and Scholz 1983) which allows coho to distinguish them more easily than the Trent River, which has unusually clear water and comparatively little organic debris. Perhaps this type of water does not provide strong olfactory cues, which may mislead coho that enter this stream. Increases in discharge rates may provide stronger cues, allowing coho to distinguish this system from their own and induce them to move out, as was observed during this study when floods occurred.

The lack of significant numbers of hatchery strays in the escapements of French and Black creeks indicates that the level of interbreeding with hatchery coho from neighboring public hatcheries is not large in all natural systems located in proximity to these facilities. However, the extent of the contribution of hatchery strays to the Trent River escapement, coupled with the apparent hybridization, suggests that there may be considerable year to year variability in the stock composition of its spawning population. The magnitude of the genetic introgression could not be quantified during the present study, but the evidence presented suggests that it could be considerable and should be taken into account for a proper evaluation of the genetic consequences of releasing artificially propagated fish into the wild (Waples et al. 1990).

Although the overall level of straying observed during the present study tended to be small, some stocks exhibited a considerable amount of straying in some years. In such cases, not accounting for the strays would lead to erroneous estimates of exploitation and survival rates. Assume for instance that 20 000 coho smolts are tagged during their migration. Of these 2000 tagged adults survive and are intercepted in the fishery. Half of the 800 coho that escaped to the stream are tagged and lack an adipose fin. Assume that all 400 tagged coho in the escapement originated from that stream and that another 80 tagged coho from this stock escaped to other streams. The exploitation rate for this stock, usually estimated from the ratio of catch to catch plus escapement, would be 80.6% if all strays were accounted for and 83.3% if strays were not accounted for. So not accounting for the 20% stray rate would have resulted in positively biased estimates of exploitation rate. Additional simulations conducted with the same level of straying indicated that the magnitude of the bias increases with decreasing exploitation rates. Further simulations also indicated that the bias increases with increasing straying rates for a given exploitation rate.

The contribution of hatchery strays to a given population must also be taken into account. For the above case, assume that 100 of the 400 tagged coho in the stream were of hatchery (foreign) origin, so the actual exploitation rate becomes 84.3%. If the investigator cannot account for the contribution of hatchery strays in the tagged coho escapement (in this case, 25%), then the estimated exploitation rate would be negatively biased. Of course, sampling deficiencies could further compound the problem and increase the amount of bias. Additional simulations revealed that under realistic conditions such as encountered during this study, the discrepancy between the actual and the biased estimates of exploitation can exceed 10% if straying or stray contributions are not accounted for.

Estimates of survival rates, obtained from the ratio of total recoveries (catch plus escapement) to total release, can also be biased if strays are not accounted for. For the case described above, the actual survival rate would be 12.4% if straying to other streams is accounted for and 12.0% if such straying is unaccounted for. Thus, not accounting for straying (or stray contributions) has a relatively greater influence on exploitation estimates than on survival estimates. However, coho smolt to adult survival rates are usually not as variable as exploitation rates, so the small bias in survival rate estimates can still be relatively important. For these reasons, it is recommended that surveys be designed to account for straying when coho populations are subject to coded-wire tagging and escapement enumeration for stock assessment purposes.

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