NPAFC

Doc. 197

Rev. 1

Do steelhead trout school selectively in the North Pacific Ocean?

by

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submitted to the

North Pacific Anadromous Fish Commission

by

CANADA and THE UNITED STATES OF AMERICA

October 1996

THIS PAPER MAY BE CITED IN THE FOLLOWING MANNER:
McKinnell, S., J.J. Pella and M.L. Dahlberg. 1996. Population-specific aggregations of steelhead trout (*Oncorhynchus mykiss*) in the North Pacific Ocean (NPAFC Doc. No. 197, Rev. 1). 22 p. Dept. of Fisheries and Oceans, Ocean Science and Productivity Division, Pacific Biological Station, Nanaimo, BC, Canada V9R 5K6

Abstract

The distribution of North American hatchery origin steelhead trout (*Oncorhynchus mykiss*) in the North Pacific Ocean varied by age and hatchery location. Columbia River steelhead were more abundant south of the Aleutian Islands at an earlier age than steelhead from the Georgia Basin (Georgia Strait, Puget Sound and waters connecting with the open Pacific). Between 1984 and 1989 there were eight independent and coincident recoveries of coded-wire tagged steelhead trout, where individuals released from hatcheries as juveniles at similar times and locations were recovered together on the high seas up to three years later. A statistical test was developed to determine whether these coincident recoveries should be expected if individual steelhead trout within populations travelled in the North Pacific in an uncoordinated manner. The overall test suggested that some tagged steelhead trout populations travelled together in a significantly ($P<0.05$) coordinated manner on the high seas.

Introduction

The general distributions and origins of Pacific salmon *(Oncorhynchus sp.)* in the North Pacific Ocean were developed from high seas tagging programs during the 1950s and 1960s (French et al. 1976, Neave et al. 1976, Groot and Margolis 1991), although there is recent evidence that these distributions have changed (Ogura and Ito 1994). The general distribution and origin of steelhead trout (*Oncorhynchus mykiss*) in the North Pacific Ocean has only recently been reported (Burgner et al. 1992). The delay can likely be attributed to the lack of sufficient data. Beginning in the 1980s, North American steelhead trout were routinely tagged with coded-wire tags and subsequently recovered on the high seas. These new data, in combination with the accumulated historical data allowed Burgner et al. (1992) to propose a general model of ocean migration of North American steelhead trout.

Burgner et al. (1992) reported that most North American steelhead smolts entered the sea during the spring and moved offshore directly. By late summer of the first year, most North American juveniles were concentrated in the western Gulf of Alaska. By the second summer, they were distributed widely in the North Pacific with greatest abundance between 130°-165°W longitude and 44°-50°N latitude, and by late July of the second year, most steelhead trout moved north and west and were more abundant in the eastern Aleutian islands and the western Gulf of Alaska. Maturing fish separated from the immatures during the spring or summer of their second summer to return to North America. By the spring of their third summer, steelhead trout were again widely distributed in the North Pacific with the maturing component separating and returning to North America. Burgner et al. (1992) noticed that the genetically distinctive (Allendorf 1977, Parkinson 1984, Okazaki 1985) inland summer-run steelhead trout were relatively more abundant in the central North Pacific. In the northeastern Pacific their distribution was more restricted to the southern Gulf of Alaska.

Little is known about the behavior of individual populations of salmonids in the ocean. As juveniles, salmonids aggregate as they migrate to the ocean (Österdahl 1969, Wood et al. 1993). Aggregations appear in coastal waters of northern British Columbia and Southeast Alaska (Jaenicke and Celewycz 1994). Whether these inshore aggregations consist of individual populations or mixtures is unknown. For the most part, salmon and steelhead trout are not observed again until they reappear as adults in coastal fisheries.

The major purpose of this paper is to describe the co-incident recovery of tagged steelhead trout, released from hatcheries as juveniles at similar times and locations and recovered together on the high seas up to 3 years after release. The data suggest that some steelhead trout, within populations, travel in groups (or at least in restricted ranges) during the marine phase of their lives. The second purpose is to augment Burgner et al. (1992) by providing new information on age-specific distributions of steelhead trout in the North Pacific Ocean.

Methods and materials

Since the 1980s, small numbers of coded-wire tagged steelhead trout have been recovered annually in high seas commercial and research fishing operations in the subarctic waters of the North Pacific Ocean. Release and recovery information for tagged North American steelhead trout were obtained from two data sources: (1) the Mark/Recovery Program (MRP) database (Kuhn, 1988), located at the Pacific Biological Station (Nanaimo, BC) and (2) a coded-wire tag recovery database compiled by staff of the U.S. National Marine Fisheries Service, Auke Bay Laboratory in Juneau, Alaska (Dahlberg 1981, 1982, Wertheimer and Dahlberg 1983, 1984, Dahlberg and Fowler 1985, Dahlberg et al. 1986, 1987, 1988, 1989, 1990, 1991, 1992, 1993, 1994). The Auke Bay database includes coded-wire tag recoveries from offshore or non-salmonid fisheries. Tags recovered offshore were mainly from Japanese, Canadian, or American offshore research operations or from observers on commercial fishing vessels (McKinnell et al. 1991). Fish ages were reported using the European system (Ward and Slaney 1988) of age designation (x,y); x=number of freshwater annuli and y=number of saltwater annuli.

Tags were recovered from steelhead trout caught in commercial salmon gillnet, commercial squid gillnet, research gillnet and floating longline operations. A fishing operation is defined as one gillnet or longline set. A *multiple* recovery is defined as the recovery of more than one coded-wire tagged steelhead trout in a single fishing operation, and a *match* is defined as the recovery of at least two tags in a single fishing operation from the same hatchery release group. Release groups are defined as tagged steelhead trout released from hatcheries at similar locations and dates in the same year. For many release groups the tag code was unique, but occasionally codes were sequential or nearly so, and a few release groups had quite different codes.

Detailed release data were carefully examined to insure that the grouping of tag codes was appropriate. For those release groups with different tag codes, release dates ranged from identical dates up to dates separated by approximately 1 month. Where release dates within a release group were separated by a month or so, it involved early outplanting of juveniles (late March or early April). Hatchery steelhead trout released into the Keogh R. (Vancouver Is., BC) before the migratory period delayed migration such that the pattern of time and size of downstream migration of hatchery smolts was similar to that of the wild smolt migration (B. Ward, Fisheries Research Branch, Ministry of Environment, Lands & Parks, Government of B.C., personal communication). Using the Auke Bay database, we determined the total number of fishing operations in which tagged steelhead trout were captured. For such operations, we recorded the number of tagged steelhead trout recovered and the numbers of matches.

The criterion for assessing whether recoveries were matching or not was stringent; tagged steelhead trout from release groups had to be caught in the same fishing operation to qualify. When more than one member of a release group was caught any time during a year, the temporal and spatial distribution of all such recoveries was examined. Release group members were recovered on temporal scales of days up to years apart so the ratio of the distance to the number of days between recovery of two release group members was examined.

The interaction between freshwater release location and North Pacific recovery location was examined by stratifying data into three major production regions (Columbia River; Georgia Basin including Georgia Strait, Puget Sound, Johnstone Strait and Juan de Fuca Strait; Outer Coastal portions of Washington State and BC). Finer scale geographic resolution based on smaller hatchery production areas (Kuhn et al. 1988) created too few recoveries within strata and compromised the contingency table statistical tests. We defined three geographic recovery regions in the North Pacific Ocean. The Aleutian region included all tags recovered west of 165°W longitude, the North Gulf of Alaska region included all tags recovered north of 50°N latitude and east of 165°W longitude, and the South Gulf of Alaska region included all tags recovered south of 50°N latitude and east of 165°W longitude.

Our objective was to quantify how unusual the observed number of matches would be if a null hypothesis was true that "all steelhead trout recovered from any release group migrated on the high seas with no more coordination with their recovered release members than with recovered members of other groups". The alternative hypothesis is that at least some of the recovered individuals from the release groups travelled in a coordinated manner. To quantify how unusual the observed numbers of matches were, we used the probability distribution for matches when the null hypothesis was true (the null distribution). In other words, how many matches might be expected if steelhead trout from these release groups were travelling in an uncoordinated manner? All tag recoveries were stratified by sea age, recovery year, and general recovery region. Stratification was necessary to develop an adequate spatial/temporal framework where the null hypothesis of uncoordinated movement could apply. For example, two release groups with release dates separated by a decade would not be travelling together so temporal stratification is needed. Geographic stratification is necessary because populations from different regions have been shown to have different general distribution patterns in the ocean (Burgner et al. 1992). Finally, because age at maturity varies among individuals within populations (Ward and Slaney 1988), some steelhead trout will be returning to the coast to spawn while others of the same brood year remain at sea for an additional year or two.

For each stratum, its unique null distribution, resulting from the number and size of successful fishing operations and their matching recoveries, was determined. If the null hypothesis was true, then the observed matches were taken from an unorganized mixture of release groups and could be viewed as one realization from all possible random shuffles of the recoveries among the successful operations without regard to release group identity. The numerical values for the probabilities of matches among operations, which compose each null distribution, were evaluated from 100,000 Monte Carlo simulations (Fig. 1). For each simulation, the stratum tag recoveries were shuffled randomly and independently, without reference to release group, among the total successful operations so that the observed numbers and sizes of operations were preserved. For each simulation, the numbers of matches and types of matches (doubles, triples) for every operation were recorded.

Outcomes from the 100,000 simulations were ordered by their numbers of matching tags, beginning with combinations that produced no matches, 2 matching tags, 3 matching tags, etc. of the possible combinations of matches among operations. The null distribution for matches was the histogram of probabilities with the outcomes so ordered. Monte Carlo error of estimation of the probabilities was small because of the large number of simulations: standard error for the probability of any outcome could not be greater than 0.00158 [$=\sqrt{(0.5)(0.5)/100000}$].

Compared to the null distribution, the nonspecific probability distribution of matches when the alternative hypothesis was true (the alternative distribution) would have its probability mass shifted toward outcomes with greater numbers of matches. Therefore, the probability (P) associated with the statistical test of the null hypothesis was computed from the null distribution as the sum of probabilities of outcomes with equal or more matching tags than the outcome actually observed. The probability of the test was called the tail probability because the sum included all outcomes in the right hand tail of the null distribution. The same hypothesis was tested from data of each stratum.

To combine findings across strata, we used Lancaster's (1949) modification of Fisher's (1948) method and verified the assessment by Monte Carlo simulation. Fisher noted that the transform, _^{2} = - 2 log(P), is distributed under the null hypothesis as a chi square random variable with 2 degrees of freedom (expected value equal to 2 and variance equal to 4), so a sum of k such _^{2} values from independent sources would be distributed as a chi square random variable with 2k degrees of freedom (expected value equal to 2k and variance equal to 4k) because of the additive property of the chi square distribution. Therefore, the joint evidence from a wide variety of experiments and data sources bearing on the same hypothesis can be appraised from this simple statistic.

The chi square distribution for _^{2} is exact for continuous data and a good approximation for discrete data with many possible outcomes. Our data are discrete and many of our samples have few possible outcomes, for which situation the chi square distributional approximation for $\chi^2 = -2 \log(P)$ is less satisfactory mainly because of bias, i.e., the expected value of χ^2 is far too low (Lancaster 1949). Lancaster (1949) recommended replacing the value of χ^2 by its mean value, χ_m^2, in each interval between adjacent discrete possible values for χ^2 with the calculation performed as though χ^2 was distributed as a chi square random variable with 2 degrees of freedom. Lancaster observed that although the distribution of χ_m^2 is still discrete, it does have the correct expected value of 2 but variance slightly under the correct value of 4. Therefore, Lancaster noted, the distribution of a sum of k independent χ_m^2 values would be only approximately rather than exactly distributed as a chi square random variable with 2k degrees of freedom, but the approximation would be better than for the corresponding sum of Fisher's χ^2 values.

A combined test over k strata was performed by summing χ_m^2 values for observed outcomes in the strata. The tail probability (P) of the combined test corresponding to this sum was evaluated in two ways. First, the tail probability was computed by assuming the sum of χ_m^2 values was distributed exactly as a chi square random variable with 2k degrees of freedom (Lancaster's approximation), using subroutine GAMMQ of Press et al. (1989). Second, the tail probability for the sum was evaluated by Monte Carlo simulation. A random value was drawn from the null distribution for χ_m^2 of each stratum and their sum was formed. The process was repeated 1000 times. The Monte Carlo null distribution for the sums was composed of the relative frequencies of these sums of χ_m^2 values and used to determine the tail probability of a sum as large or larger than that for the observed outcomes. The two approaches to evaluating tail probabilities for combined tests are called chi square and Monte Carlo methods.

Results

One hundred and fifty tag codes were recovered from 195 steelhead trout recovered with tags during 151 high seas research or commercial fishing operations (Fig. 2). Four of these tags had insufficient recovery information to be useful so they were not considered in the analysis. Eighty-eight percent of tagged steelhead trout recovered on the high seas were taken in June or July and the remainder in April, May, or August. Three tagged steelhead trout were recovered during their year of release (age 1.0), 117 during the second summer at sea (age 1.1), 69 during the third summer (1.2) and six during the fourth summer (age 1.3). Recoveries during the first and fourth summers after release were too infrequent to comment on distribution. Of three steelhead trout recovered during the summer of release, two were released at coastal sites and recovered in the Gulf of Alaska a few months later. The minimum rates of travel between release site and recovery location were 23.9 $km.day^{-1}$ and 19.9 $km.day^{--1}$. The true rate will be faster as the computed rates assumed straight line travel. The third individual was released from an inland hatchery. Its minimum rate of travel included a large freshwater component and therefore is not comparable with the other two.

Steelhead trout distributions based on coded-wire tag recoveries were evaluated within general recovery regions (Aleutian, North, and South Gulf of Alaska) because fishing effort varied among regions (Table 1). Chi-square contingency table analysis indicated that there was a significant (P=0.00) interaction between sea age and release region for steelhead trout recovered in the Aleutian region but not for recoveries in either the North (P=0.21) or South (P=0.71) Gulf of Alaska regions. Age 1.1 steelhead trout from Columbia River hatcheries accounted for 85.5 percent of recoveries of age 1.1 steelhead in the Aleutian region, whereas they accounted for only 22.2 percent of age 1.2 recoveries. Age 1.1 steelhead trout from Georgia Basin hatcheries accounted for only 1.8% of age 1.1 steelhead in the Aleutian region, whereas they accounted for 40.7% of age 1.2 recoveries. Steelhead trout from outer coastal hatcheries were intermediate; age 1.1 steelhead trout accounted for 12.7 percent of Aleutian recoveries and 31.5 percent of age 1.2 recoveries. In summary, this suggests that Columbia River steelhead trout take a more direct route to the Aleutian region because they tend to be caught at a younger age in that region than steelhead trout from other coastal areas.

The maximum number of tagged steelhead trout recovered in one fishing operation was 6 (Table 2). Multiple tag recoveries occurred in 27 of 151 fishing operations (17.9 percent) in which tagged steelhead trout were recovered (Table 2). Matching recoveries (Table 3, Fig. 2) were observed in 8 (5.3 percent of the total) fishing operations. Matching recoveries of tag code 12-17-53 (Somass River, B.C.) were repeated 1 year apart. The first pair was recovered (with 4 other tagged steelhead) at 53°N 155°W on 19 July 1984, and the second pair at 50°N 155°W on 9 July 1985. A single recovery of this tag code also occurred in the Gulf of Alaska in 1983.

Not all strata were adequate for testing the null hypothesis. For example, if only single tag recoveries occurred in fishing operations in a stratum, that stratum contains no useful information about the mixing of release groups. To be informative of release group mixing, matches had to be possible within a stratum even though actual matches may not have occurred. The minimum requirements for including a stratum were that at least one fishing operation had a multiple recovery, and at least two fish in the stratum were from the same release group (Table 4). Within the strata meeting these criteria, the random shuffling experiments provided the basis for judging the plausibility of the null hypothesis. As an example, 13 distinct outcomes occurred during the 100,000 shuffles of the 1987 southern Gulf of Alaska sea age 1 recoveries with relative frequencies ranging between 0.00001 and 0.33451 (Table 5). The cumulative probabilities for all outcomes are provided. The probability for the observed outcome, two double matches (fourth outcome coded 20), was 0.67453 (the tail probability of the test).

When discrete random variables are analyzed, values of Fisher's χ^2 are always biased low compared to Lancaster's χ_m^2 or that of a chi square random variable with 2 degrees of freedom: in the present instance, the expected value of Fisher's χ^2 is only 1.47147 (weighted sum over χ^2 values of outcomes with relative frequencies as weights) but that for Lancaster's χ_m^2 is 2 (as is always the case). The probability (P) associated with a test from Fisher's χ^2 will always be biased and greater (less significant) than that from Lancaster's χ_m^2 if the chi square method of evaluating the probability is used.

The tail probabilities for tests of the null hypothesis among the individual strata ranged from 0.056 to 1 (Table 6). Numbers of outcomes among strata ranged from only two to 13, with nine strata having three or less outcomes, so Fisher's transform of the tail probabilities, $\chi^2 = -2 \log(P)$, would be seriously biased for combining probabilities if the chi square method were used. Lancaster's χ_m^2 for observed outcomes in the strata were also computed (Table 6) for use in combined tests.

Combined tests of hypothesis by sea age and by region were performed using sums of Lancaster's χ_m^2 for observed outcomes in the sea age strata: (1) sea age 1 recoveries for seven strata, (2) sea age 2 and 3 recoveries for four years, and (3) all three sea ages for all strata. The tail probabilities for outcomes under the null hypothesis were consistent between evaluation methods (Table 7). Depending on the evaluation method, the tail probabilities were 0.30 (both methods) for sea age 1, 0.00-0.03 for sea ages 2 and three combined, and 0.034-0.065 for all sea ages combined. By region, the tail probabilities were 0.30-0.35 for the Aleutian Region, 0.45-0.70 in the northern Gulf of Alaska, and 0.01-0.02 in the southern Gulf of Alaska. Unless a change in migration behavior is postulated among sea ages, the combined test for all ages would be appropriate to judge whether the null hypothesis of uncoordinated migration among members of steelhead releases could account for observed matches. If no behaviourial change occurred, at least some recovered members of the steelhead releases seem to have traveled in closer association with members of their own group than of other groups.

When two release group members were caught in different locations on different dates, we considered the potential that they may be from the same migrating group. Figure 3 shows the distance and distance.day^{-1} between all possible pairwise recoveries of release group members for all release groups with two or more recoveries within a calendar year. Approximately 64 percent of release group members were caught within distances (and dates) that could theoretically be achieved (at the maximum observed swimming speed of 62 km per day, Burgner et al. 1992). The percentage is reduced to 33.6 if average migrating speeds are used.

Discussion

Burgner et al. (1992) described a general model of steelhead trout distribution at age in the North Pacific Ocean. Our analyses suggested that some refinement of the summer distributions is warranted. Columbia River populations dominated the recoveries of age 1.1 steelhead trout in the

Aleutian region, whereas Georgia Basin populations of this age in the Aleutian region were rare. Outer coastal populations were of intermediate abundance in the Aleutian region. This pattern was reversed for age 1.2 steelhead trout. Georgia Basin populations represented the largest fraction of age 1.2 fish and the Columbia River, the least. Again, outer coastal hatcheries were intermediate. Alaskan populations were represented by only three age 1.2 tagged fish that were recovered in the Aleutian region. It appears that Georgia Basin populations tended to remain within the Gulf of Alaska during the first two summers at sea and thereafter, some migrated or were advected by westward moving currents to a region south of the Aleutian archipelago near 180° longitude. In contrast, Columbia River populations were the least abundant in the northern Gulf of Alaska at age 1.1. There were only six age 1.2 tags recovered in the northern Gulf of Alaska. Columbia River populations were more abundant than other groups in the southern Gulf of Alaska. Georgia Basin populations were least abundant and outer coastal populations intermediate.

Pink salmon (*O. gorbuscha*), sockeye salmon (*O. nerka*) and chum salmon (*O. keta*) populations from around the Pacific Rim intermingle extensively in the North Pacific (Neave 1964). Sockeye salmon tagged in a single fishing operation in the central Gulf of Alaska in 1962 migrated to a variety of locations from the Fraser River in southern British Columbia to Bristol Bay in western Alaska (Neave 1964). Pink salmon tagged on or near the same date in various locations throughout the Gulf of Alaska converged and were caught in fisheries near Kodiak Island, Alaska (Neave 1964). Neither observation is inconsistent with population-specific aggregations by at least some members of populations comprising the North Pacific mix, but it was these kinds of observations of pink, chum and sockeye salmon that prompted the null hypothesis of uncoordinated movement of tagged steelhead trout. The steelhead trout results suggested that as they transit the North Pacific Ocean, some do so in a manner that maintains population-specific aggregations on at least the temporal and spatial scales covered by high seas fishing gear.

Although there is shown evidence that steelhead trout aggregated by population to some degree, sampling has been insufficient to determine the size, structure, or stability of these aggregations. Various models could be hypothesized in which individuals of a population might form one aggregation or they may form several geographically isolated aggregations or some variant thereof. What is certain is that the North Pacific Ocean is sufficiently large and steelhead can swim sufficiently fast that individuals within populations are theoretically capable of being quite distant from one another. That some individuals of a population are known to be very distant from one another on or near the same date quickly eliminates the hypothesis of one aggregation per population. Nonetheless, aggregations of steelhead from individual populations are expected to vary with time. The combined effects of variation in age at maturity and the cues to begin spawning migrations will, by definition, expand spatial distributions of populations.

The degree to which population-specific aggregation extends to other species is unknown at this time. Pearcy (1984) reported 19 tagged coho salmon (*O. kisutch*) from the Columbia River caught in a single seine haul 140 km and 31 days after release. The Auke Bay tag database also contains some matching coho salmon tags recovered in coastal trawls. Some related evidence occurs from sockeye salmon. In assessing the Japanese mothership salmon fishery, Fukuhara (1975) reported that the daily age composition of sockeye salmon was homogeneous within 10 by 10-1.50 latitude.longitude statistical blocks, but not within 20 by 50 latitude.longitude blocks. He concluded that sockeye salmon are distributed in a systematic manner with discrete populations identifiable by age composition. In themselves, these examples are insufficient to conclude that salmon are schooling on the high seas, but they are sufficient to establish testable hypotheses. These hypotheses are becoming testable because of the developments of our ability to identify salmon populations using biological characteristics such as DNA and allozyme variation. If applicable to other salmonids, our finding will influence salmon assessment models through their assumptions about how fisheries and salmon populations interact.

Acknowledgments

This work would not have been possible without the years of assistance and cooperation of research staff and vessel officers and crews from Canada, Japan and the United States. Comments from B.R. Ward, two anonymous reviewers and the consulting editor improved the manuscript considerably and we are grateful for their efforts.

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Table 1. Numbers of age 1.1 and age 1.2 steelhead trout coded wire tag recoveries by hatchery production region/area and North Pacific recovery region. The Aleutian region was defined as west of 165°W longitude, North and South Gulf of Alaska (east of 165°W) were divided at 50°N latitude.

Age 1.1

Production Region	Production Area[a]	Aleutian	North Gulf of Alaska	South Gulf of Alaska	Total
Columbia R.	HEAD	3	0	6	9
	SNAK	42	4	27	73
	BRGT	0	0	2	2
	LOCO	2	0	0	2
Outer coast	UPWA	6	2	4	12
	SWVI	1	6	1	8
Georgia Strait & Puget Sound	WA04	0	3	1	4
	WA06	1	0	1	2
	GSMS	0	0	1	1
	GSVI	0	2	0	2
	JNST	0	1	0	1
	LWFR	0	1	0	1
Total		55	19	43	117

Age 1.2

Production Region	Production Area[a]	Aleutian	North Gulf of Alaska	South Gulf of Alaska	Total
Columbia R.	SNAK	8	0	6	14
	LOCO	4	2	0	6
Outer coast	GRAY	3	0	0	3
	UPWA	7	0	0	7
	SWVI	7	3	3	13
Georgia Strait & Puget Sound	WA04	1	1	0	2
	GSMN	2	0	0	2
	GSVI	7	0	0	7
	LWFR	9	0	0	9
	JNST	3	0	0	3
Alaska	SIAK	2	0	0	2
	WEAK	1	0	0	1
Total		54	6	9	69

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[a] BRGT=Brights (Columbia R.), GRAY=Grays Harbor, GSMN= Georgia Strait (Mainland North), GSMS= Georgia Strait (Mainland South), GSVI=Georgia Strait (Vancouver Island), HEAD=Headwaters (Columbia R.), JNST=Johnstone Strait, LOCO=Lower Columbia R., LWFR=Lower Fraser R., SIAK=Southern inside Alaska, SWVI=Southwest Vancouver Island, UPWA=Upper Washington, SNAK=Snake R., WA04=Washington Management area 4, WA06=Washington Management area 6, WEAK=Western Alaska. Production area codes obtained from Kuhn, Lapi & Hamer (1988).

Table 2. Up to 6 coded-wire tagged steelhead trout were recovered in individual fishing operations. This table reports the frequencies of different observed outcomes (variable numbers of coded-wire tags recovered in individual fishing operations).

Number of tags recovered	Number of fishing operations
1	124
2	20
3	4
4	1
5	1
6	1
Total	151

Table 3. All observations of matching recoveries of coded-wire tagged steelhead trout tagged and released at similar times and locations.

Release group	Release location	Release date	Recovery location	Recovery date	Number recovered
051461	Hoh R.,WA	May, 1984	49°N 155°W	July 19, 1985	2
051846 051852	Clearwater R., ID	March, 1988 May, 1988	44.9°N 178.5°E	July 8, 1989	3
121753 122027	Somass R., BC	April, 1983	53°N 155°W	July 19, 1984	3
121753	Somass R., BC	April, 1983	50°N 155°W	July 9, 1985	2
121904 121905	Coquihalla R., BC	April, 1982 March, 1982	47.6°N 127.6°W	July 7, 1985	2
122122 122126	Tamihi Cr. Chilliwack R., BC	May, 1984	44.5°N 171.5°E	June 25, 1986	2
633837 633838	Snake R., WA	April, 1986	48.5°N 130.3°W	July 20, 1987	2
633837	Snake R., WA	April, 1986	48.5°N 129.7°W	July 25, 1987	2

Table 4. Release group composition of informative recovery samples by recovery year, sea age, and region. Release groups are identified by letters, and letters enclosed by back slashes represent tagged fish recovered in a single operation.

Year	Sea age	Region	Release groups and operations
1984	2	Aleutian	A/B/C/D/B/EF/G/H/E/I/I/I/J/C/K/F/L/E
1986	2	Aleutian	A/BB/C/D/D
1988	1	Aleutian	A/B/AC/D
1989	1	Aleutian	A/B/AAA/AC/A/A/A/A/D
1991	1	Aleutian	A/BC/D/E/D/FG/H/I/F
1992	1	Aleutian	A/AB/C
1984	1	North GOA	A/BCAADA/EF
1985	3	South GOA	AA/B
1985	2	South GOA	A/B/CC/C/A
1985	1	South GOA	A/B/C/D/E/FF/G/A
1987	1	South GOA	ABC/D/C/D/ECC/EF/E/C/F/C/EG/EC/CC/E/H/C

Table 5. Outcomes[a], numbers of matching tags in outcomes, their Monte Carlo probabilities under the null hypothesis, cumulative probabilities (P), Fisher's $\chi^2=-2\log(P)$, and Lancaster's χ_m^2: sample from 1987 South GOA region, sea age 1.

Outcome[a] (xy)	matching tags	relative frequency	cumulative probability (P)	Fisher's $\chi^2=-2\log(P)$	Lancaster's χ_m^2
00	0	0.05572	1.00000	0.00000	0.05678
10	2	0.24090	0.94428	0.11467	0.39475
01	3	0.02885	0.70338	0.70372	0.74530
20	4	0.33451	0.67453	0.78748	1.39489
11	5	0.05801	0.34002	2.15750	2.33874
30, 02	6	0.18470	0.28201	2.53163	3.41044
21	7	0.03628	0.09731	4.65971	5.09010
40, 12	8	0.04627	0.06103	5.59278	6.68718
31	9	0.00886	0.01476	8.43167	9.21042
50, 22	10	0.00489	0.00590	10.26561	11.53650
41	11	0.00081	0.00101	13.79561	14.99591
60, 32	12	0.00019	0.00020	17.03439	18.71905
51	13	0.00001	0.00001	23.02585	25.02585

Expected value of Fisher $\chi^2=1.47147$ Variance of Fisher $\chi^2=3.10829$

Expected value of Lancaster $\chi_m^2=2.00000$ Variance of Lancaster $\chi_m^2=3.83668$

χ_m^2 of observed outcome=1.39489

[a] xy=number of matching pairs (x) and triples (y).

Table 6. Value of Lancaster's χ_m^2 for the observed outcome, numbers of distinct outcomes[a] and tail probabilities (P) of outcomes that were as or less probable than that observed, by recovery year, sea age, and region.

Year	Sea age	Region	Observed χ_m^2	Number of Outcomes	Tail Prob (P)
1984	2	Aleutian	1.671	2	1.000
1986	2	Aleutian	6.028	2	0.133
1988	1	Aleutian	1.492	2	1.000
1989	1	Aleutian	1.179	5	0.669
1991	1	Aleutian	1.590	3	1.000
1992	1	Aleutian	1.287	2	1.000
1984	1	North GOA	1.584	3	0.712
1985	1	South GOA	7.753	2	0.056
1985	2	South GOA	4.638	2	0.267
1985	3	South GOA	4.192	2	0.334
1987	1	South GOA	1.395	13	0.674

[a] from 100,000 Monte Carlo shuffles of the sample.

Table 7. Comparison of combined probabilities of stratum outcomes by the chi square[a] and Monte Carlo[b] methods.

Strata	samples combined (k)	Sum of observed χ_m^2	Number of outcomes[c]	Probability	
				Chi Square	Monte Carlo
Sea ages					
1	7	16.280	314	0.297	0.295
2-3	4	16.529	14	0.035	0.004
1-3	11	32.809	617	0.065	0.034
Regions					
Aleutian	6	13.247	66	0.351	0.295
North GOA	1	1.584	3	0.453	0.702
South GOA	4	17.978	54	0.021	0.009

[a] Computed as probability that a chi square random variable with 2k degrees of freedom equals or exceeds the sum of observed χ_m^2 values.

[b] Determined from the distribution of 1000 sums of χ_m^2 values randomly sampled from the null distributions of the component strata.

[c] Number of distinct values of Monte Carlo sums of χ_m^2 among the 1000 sampled values.

Fig. 1. Diagrammatic representation of the resampling process used to develop the null distribution for matching recoveries within a stratum. The upper portion represents an observed distribution of tag release groups in six fishing operations. One fishing operation resulted in a matching recovery. Tags were randomly reshuffled among the six fishing operations 100 000 times. The probability of getting a random match was 0.1926, which agrees closely with the exact value (easily evaluated for this case) of 8 ÷ 42 = 0.19047. Far more frequently, there were no random matches in this hypothetical stratum.

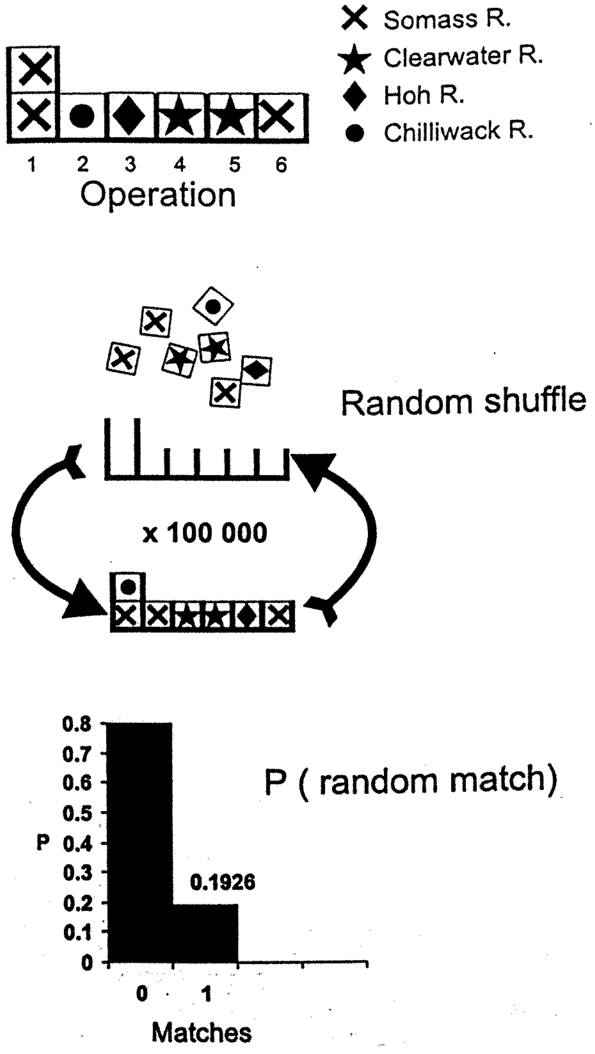

Fig. 2. Plotted points indicate recovery locations of coded-wire-tagged steelhead trout in the North Pacific Ocean from 1981 to 1994. Uncircled numerals appearing in the ocean indicate the locations where two tags (circled numerals = three tags) from the same release group were caught in the same fishing operation. To identify the hatchery origin of matching recoveries, the numerals can be matched to the hatchery locations on land. Release locations are reported in Table 3.

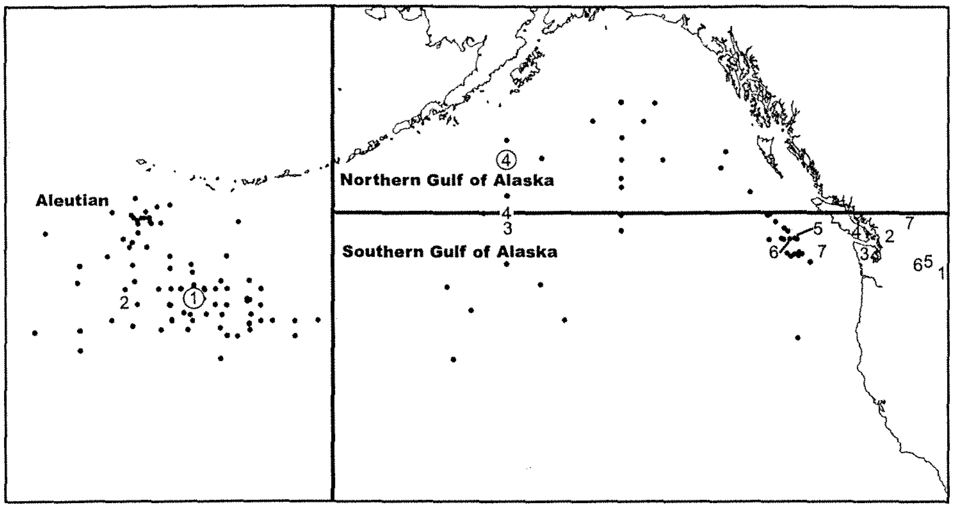

Fig. 3. Frequency distributions of distance (left panel) and distance per day (right panel) for all pairwise recoveries of all release group members with more than one tag recovered in a calendar year. Distance (kilometres) between two tags from the same release group is computed following the method of Robinson et al. (1978). Days are computed as the number of elapsed calendar days between the recoveries of two tags from the same release group.