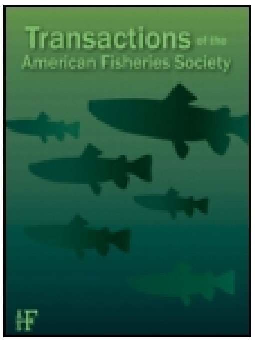

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Origin and Straying of Hatchery Winter Steelhead in Oregon Coastal Rivers

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Abstract.—We evaluated the origin and straying of hatchery steelhead *Oncorhynchus mykiss* among 16 rivers on the Oregon coast to examine rearing or release practices that might contribute to straying. Data were collected on the returning adults of three brood years that had been differentially marked and released as smolts in 1990–1992. The percentage of strays averaged 11% (range, 4–26%) of the samples of hatchery and wild fish in 11 streams where hatchery steelhead were released. Stray hatchery fish composed a mean of 22% (range, 9–43%) in 5 streams without hatchery releases. The two predominant factors that contributed to straying were releases of stocks transplanted from their natal basins and releases into adjacent basins. Releases of transplanted stocks into adjacent basins accounted for 41% of the strays, while releases of transplanted stocks into nonadjacent basins accounted for 29% of the strays. Local stocks of steelhead released into adjacent basins accounted for 16% of the strays. The incidence of straying by hatchery fish and its widespread occurrence in Oregon coastal rivers present genetic and ecological risks to wild populations of winter steelhead. Strategies to reduce straying may include using local brood stocks, rearing and releasing fish within their natal basins, reducing the numbers of hatchery fish released, and eliminating some hatchery releases altogether.

Homing of adult anadromous salmonids to their natal stream has been recognized as an important adaptation in establishing and maintaining distinct spawning populations through reproductive isolation (Ricker 1972; Horrall 1981). Mature fish that migrate to and spawn in a stream other than the one where they originated are considered strays (Quinn 1993). Straying is a natural behavior that enables salmonids to colonize new habitat (Milner and Bailey 1989), to avoid locally unfavorable conditions (Leider 1989), to maintain genetic diversity within stocks (Horrall 1981), and to perpetuate metapopulations (Hanski and Gilpin 1997). The genetically distinct structure of anadromous salmonid populations (e.g., Reisenbichler et al. 1992) suggests that the successful reproduction of strays naturally occurs at low levels. However, straying of hatchery fish concerns fish managers because of the potential negative impacts on wild populations of interbreeding between wild and hatchery fish (e.g., Waples 1991a). Defining the ''home'' of hatchery fish can be difficult because local stocks are often reared and released in different locations. In addition, stocks of hatchery fish are often transplanted to nonnatal streams.

Stray hatchery fish can have genetic and ecological effects on wild fish populations. Hatchery fish that stray and hybridize with wild fish can reduce the genetic diversity between populations and decrease the fitness of wild populations through the displacement or breakdown of locally adapted gene complexes (Emlen 1991; Waples 1991a). Gene flow increases between nonnative hatchery and wild populations when hatchery strays successfully spawn with wild fish, and it can result in the reduced frequency and subsequent loss of locally adapted alleles (Felsenstein 1997). Hatchery strays spawning in several rivers can also result in a genetically homogenous population (Adkison 1995; Felsenstein 1997). A potential ecological effect of stray hatchery fish on wild fish is competition in spawning and rearing areas (Fresh 1997). In addition, large numbers of strays can mask trends in the population abundance of wild fish and bias estimates of the survival and exploitation of wild and hatchery stocks (e.g., Labelle 1992).

Concerns about the genetic and ecological impacts of hatchery fish on wild fish have led to proposals for assessing and altering hatchery programs (e.g., NRC 1996) as well as to policy changes in fish management agencies. For example, a wild fish management policy adopted in Oregon sets guidelines for the percentage of hatchery fish allowed in a wild spawning population (ODFW 1992). The National Marine Fisheries Service (NMFS) is also developing guidelines for managing stray hatchery fish in its efforts to protect natural populations under the Endangered Species Act (McElhany et al. 2000). Strategies to reduce

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the number of hatchery fish in a river basin depend, in part, on knowing the number and origin of the strays that occur with natural spawners. In addition, knowledge of hatchery release practices that contribute to straying is important for modifying hatchery programs.

Studies of straying have examined hatchery practices such as release time (Unwin and Quinn 1993; Pascual et al. 1995) and release location (Pascual and Quinn 1994; Pascual et al. 1995). A few studies have examined straying of hatchery salmon *Oncorhynchus* spp. over large geographic areas (Labelle 1992; Unwin and Quinn 1993; Pascual and Quinn 1994). Studies of straying in steelhead *O. mykiss* have focused on small geographic scales (Shapovalov and Taft 1954; Leider 1989) or the effects of smolt transportation in the Columbia River basin (Slatick et al. 1988). We are aware of just one study that examined straying of steelhead over a large geographic area (Lirette and Hooton 1988). Our study was initiated to examine the origin and straying of hatchery winter steelhead among rivers on the Oregon coast, as well as to examine the factors influencing patterns of straying.

Methods

In this study we considered hatchery steelhead as strays if they returned to a river basin other than the one where they were released. Studies have demonstrated that hatchery steelhead tend to return to specific release sites within a river basin (Wagner 1969; Slaney et al. 1993). We examined the origin of stray steelhead and their spatial distribution in rivers along the Oregon coast over a distance of about 500 km (Figure 1).

Hatchery winter steelhead were differentially marked by excising fins or maxillary bones for three brood years at seven steelhead hatcheries on the Oregon coast (Figure 1) and were released as smolts in 1990–1992 (Table 1). We generally varied the marks within and among release groups over the 3-year study to reduce bias in estimates of straying attributed to particular groups. Because the number of distinct clip combinations is limited and because a few hatcheries that released steelhead into several basins were unable to rear separate groups of steelhead, some groups were released with duplicate marks (Table 1). However, in most cases we released steelhead with duplicate marks in geographically distant areas of the coast. The release locations of hatchery fish were those customarily used by the Oregon Department of Fish and Wildlife (ODFW) and were not altered for this study. We grouped the releases into two categories, namely, local stocks and transplanted stocks. Local stocks were steelhead released into their natal basins and included those reared within the natal basin and those reared outside but released within the natal basin. Transplanted stocks were steelhead taken from their natal basin and released into another basin. Some transplanted stocks were reared within the basin where they were released, but most were reared outside the release basin.

Release groups returned as adults in the 1991–1992 through the 1993–1994 run years. We collected data on stray hatchery fish in 12 streams by using trap catches and creel surveys. Seven of these streams were stocked with hatchery steelhead (the Nestucca, Siletz, Yaquina, Alsea, Siuslaw, Coquille, and Chetco rivers), and five streams received no hatchery fish (the Trask, Elk, Sixes, and Winchuck rivers, and Drift Creek) (Figure 1). In addition, we used data reported by anglers to examine the percentage of stray hatchery fish in four streams that were stocked with hatchery steelhead (the Necanicum, Nehalem, Umpqua, and Rogue rivers). Anglers voluntarily collected scales and reported clip information under an ODFW program to obtain information about the catch of steelhead.

We estimated straying within a surveyed basin as the percentage of the total sample of winter steelhead (hatchery and wild) that was of stray hatchery origin. We could not calculate a stray rate (i.e., the percentage of a release group that strayed) because we could not account for all adult returns of a given release. The hatchery portion of the return to a basin was divided into a homing component (those from releases into that basin) and a straying component (those from releases into other basins). In catch-and-release fisheries, we determined the catch of wild fish from angler interviews during creel surveys. We assigned returning adults to a release year by using circuli patterns on scales to determine age (Chapman 1958). Where no scales were available, we used fish length to estimate the age of adults.

Some steelhead had marks that could not be assigned to a particular release and were classed as ‘‘unknown’’ strays. We also included unmarked hatchery steelhead, as determined by scale analysis of freshwater growth patterns (Chapman 1958), in the ‘‘unknown’’ category for most rivers. However, we sampled a large number of unmarked hatchery steelhead in two southern Oregon rivers (Chetco and Winchuck) in years when all Oregon releases were marked. We assumed these fish were from unmarked releases of steelhead from northern California hatch-

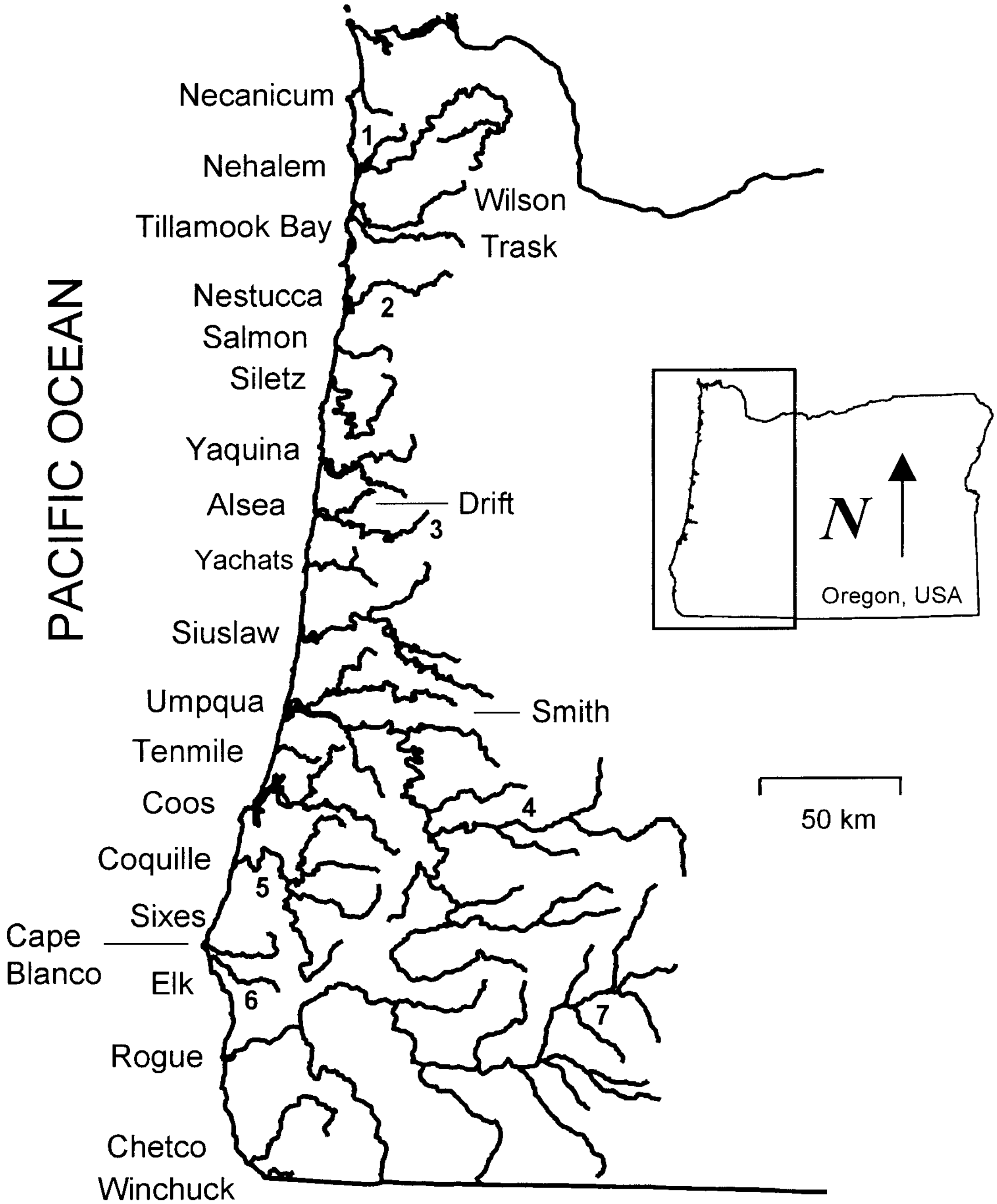

FIGURE 1.—Map showing Oregon coastal rivers where winter steelhead were sampled or where juvenile hatchery steelhead were released. Numbers indicate hatcheries that rear winter steelhead; 1 = Nehalem, 2 = Cedar Creek, 3 = Alsea, 4 = Rock Creek, 5 = Bandon, 6 = Elk River, and 7 = Cole Rivers.

eries (Busby et al. 1996). Hatchery summer steelhead from northern California hatcheries have been sampled in the Rogue River in southern Oregon (Everest 1973; Satterthwaite 1988). California hatcheries also released marked winter steelhead, which we recovered in Oregon rivers.

We used slightly different data to estimate the percentage of strays and to determine their origin.

TABLE 1.—Fin clips and numbers (thousands) of winter steelhead smolts released from hatcheries on the Oregon coast, 1990–1992. Clip abbreviations are as follows: Ad = adipose, Rp = right pectoral, Lp = left pectoral, Rv = right ventral, Lv = left ventral, Rm = right maxillary, and Lm = left maxillary. Clip designations separated by commas indicate more than one release; clip designations that are run together indicate multiple clips per fish. Stock abbreviations are as follows: AG = Applegate (Rogue basin), AL = Alsea, CO = Coos, CQ = Coquille, CT = Chetco, NC = Necanicum, NH = Nehalem, RO = Rogue, SI = Siuslaw, SU = South Umpqua, and TR = Three Rivers (Nestucca basin).

		1990 release		1991 release		1992 release	
Hatchery (Stock)	Release location	Fin clip(s)	Number (1,000s)	Fin clip(s)	Number (1,000s)	Fin clip(s)	Number (1,000s)
Local stocks reared and released in natal basin							
Nehalem (NH)	Nehalem	Rv, Lv	157	Ad, AdRv, AdLv	154	Lp, AdRv, AdLv	160
Cedar Creek (TR)	Nestucca			Ad	130	Ad	130
Alsea (AL)	Alsea	AdRm, AdLm	116	AdRp, AdLp	120	AdRp, AdLp	120
Rock Creek (SU)[a]	South Umpqua			RvLm	19	AdRv, LvLm	70
Bandon (CQ)[b]	Coquille	AdRv	116	Lp, RvRm	184	RvLm, RvRm	120
Cole Rivers (RO)[c]	Rogue	Ad, AdRp, AdLp	150	Ad, AdRv, AdLv	150	Ad, AdLvRm, AdLvLm	150
Cole Rivers (AG)[c]	Applegate	Ad, AdRvRm, AdRvLm	150	Ad, AdRpRm, AdRpLm	150	Ad, AdRvRm, AdRvLm	150
Local stocks reared outside and released in natal basin							
Nehalem (NC)	Necanicum					Rv	2
Alsea (SI)	Siuslaw			LpLm	35		
Alsea (CO)	Coos					AdLv	120
Alsea (CQ)	Coquille	LvLm	25				
Bandon (CO)[b]	Coos			Ad	10	Rm	10
Elk River (CT)	Chetco	Lv	52	AdLm	42	AdLm, AdRm	50
Transplanted stocks reared in release basin							
Rock Creek (AL)[a]	South Umpqua	AdLv	46	LvRm	35		
Transplanted stocks reared outside release basin							
Nehalem (NH)	Necanicum	Lv	40	Ad	40	Lp	40
Cedar Creek (TR)	Tillamook[d]			Ad	25	Ad	25
	Wilson[d]			Ad	120	Ad	120
	Kilchis[d]			Ad	40	Ad	40
	Miami[d]			Ad	10	Ad	10
Alsea (AL)	Salmon	Lp	37	Rp	35	Lv	35
	Siletz	Lp	108	Rp	100	Lv	100
	Yaquina	Lp	30	Rp	30	Lv	20
	Siuslaw	Lp	178	RpRm, RpLm, LpRm	127	RpRm RpLm, LpLm, LpRm	166
	Smith	Lp	65	Rp	65	Lv	65
	Coos	Lp	40	Rp	65		
	Tenmile	Lp	30				
Alsea (CO)	Tenmile			Rv	30	AdLv	25
Alsea (CQ)	Coos	LvLm	79	RvRm	54		

[a] North Umpqua basin.
[b] Coquille basin.
[c] Rogue basin.
[d] Rivers entering Tillamook Bay.

We estimated the percentage of strays by using all data where steelhead could be classified as either wild, homing hatchery, or straying hatchery fish (including unknown strays). We included information voluntarily reported by anglers when we received 20 or more samples for a specific stream in a given year or where angling regulations allowed the harvest of wild steelhead. In contrast, we evaluated the origin of strays by using data only where we could assign hatchery steelhead to a particular release group. In this case, we included information reported by anglers for all streams, including those where fewer than 20 samples were received and those where wild steelhead were released under catch-and-release regulations.

We statistically analyzed differences in straying between six releases (five local stocks and one transplanted stock) for which we had sufficient recoveries. Local stocks were further divided into groups reared within and outside their natal basins (both were released within their natal basin). We used an arcsine and square-root transformation of data and a one-way analysis of variance (ANOVA) to test for differences in the percentage of strays. Equality of variances was tested with Bartlett's test. We chose $P = 0.10$ as our level of significance to increase the ability to detect differences.

We examined the effects of run size and stream flow on straying within the Siletz, Alsea, and Siuslaw rivers, where data were consistently collected during the 3 years of the study. We used the total counts of wild and homing hatchery steelhead as an index of run size, along with the average November−May stream flow from U.S. Geological Survey records. We did not compare straying and run size among basins because sampling intensity differed from basin to basin. To estimate the distance that hatchery fish strayed from their release basins, we used the shortest distance by ocean between the mouths of river basins. We considered fish to be long-distance strays if they were sampled more than 100 km from their release basin (Hard and Heard 1999).

On a larger spatial scale, we examined straying between Oregon coastal basins to the north of Cape Blanco and those to the south (Figure 1). Cape Blanco was used by NMFS as the geographic delineation between two evolutionarily significant units (ESUs; Waples 1991b) of coastal steelhead (Busby et al. 1996). The delineation of these ESUs was based, in part, on the genetic distinctiveness of their populations, which assumes little straying between ESUs. We calculated the percentage strays that originated from the neighboring ESU in steelhead populations to the north and south of Cape Blanco.

Results

In Oregon coastal rivers where hatchery steelhead were released, the incidence of straying was 4–26% of the total sample (Table 2). Stray hatchery steelhead composed 9–43% of winter steelhead in five streams where no hatchery fish were released (Table 2). The Alsea River, Drift Creek (a tidewater tributary of the Alsea River), and the Trask River (a tidewater tributary of Tillamook Bay) had the highest percentage of strays. Stray hatchery fish in these streams predominantly originated from large releases of transplanted stocks into nearby rivers. The Winchuck River also had a high percentage of strays, most of which were from releases of a local stock into the Chetco River and from releases into northern California basins.

TABLE 2.—Number of wild, homing hatchery, and straying hatchery winter steelhead recovered in Oregon coastal rivers, 1991–1994 run years. Data are from creel surveys, traps, and voluntary angler reports. Angler reports were used only where wild steelhead could be kept.

Streams sampled (number of years)	Origin: Wild	Origin: Homing hatchery	Origin: Straying hatchery	Percent strays (SE)
Streams with hatchery releases				
Necanicum (1)	13	32	5	10 (4.2)
Nehalem (1)	11	62	12	14 (3.8)
Nestucca (3)	182	255	39	8 (1.3)
Siletz (3)	148	141	56	16 (2.0)
Yaquina (3)	121	106	26	10 (1.9)
Alsea (3)	287	508	283	26 (1.3)
Siuslaw (3)	927	1482	104	4 (0.4)
Umpqua (3)	283	52	48	13 (1.7)
Coquille (3)	760	1191	100	5 (0.5)
Rogue (1)	38	31	7	9 (3.3)
Chetco (3)	832	273	71	6 (0.7)
Streams without hatchery releases				
Trask (3)	130		39	23 (3.2)
Drift[a] (3)	107		82	43 (3.6)
Sixes (1)	61		8	12 (3.8)
Elk (1)	48		5	9 (4.0)
Winchuck (3)	196		52	21 (2.6)

[a] Tributary of the Alsea River that enters Alsea Bay.

Based on all streams sampled, transplanted stocks of hatchery steelhead accounted for a higher proportion of strays than local stocks. Strays from releases of steelhead transplanted outside their natal basins accounted for 70% of strays reported in Oregon coastal basins, with releases of transplanted stocks into adjacent basins accounting for 41% of the strays. Releases of transplanted stocks composed 42% of the annual smolt releases in Oregon coastal basins. Strays from transplanted releases were predominant in 6 of 16 streams we sampled. Local stocks reared and released in their natal basins accounted for 18% of all strays from 51% of smolt releases and composed the majority of strays in 4 of 16 sampled streams. Local stocks reared outside but released in their natal basins accounted for another 12% of the strays from 7% of the smolt releases and composed the majority of strays in two streams. The composition of strays in the remaining four streams was not predominated by a release type.

Paired releases into the Siuslaw and Umpqua rivers further suggested that transplanted stocks contributed more to straying than local stocks (Table 3). In the Siuslaw River, fewer local Siuslaw than transplanted Alsea steelhead strayed, al-

TABLE 3.—Percentage of the stray hatchery steelhead recovered in Oregon coastal rivers from releases of local and transplanted stocks into the Siuslaw and Umpqua rivers. Numbers of recoveries were adjusted to account for unequal release numbers.

Location of strays	Location of release			
	Siuslaw River[a]		Umpqua River[b]	
	Siuslaw stock	Alsea stock	Umpqua stock	Alsea stock
Alsea River	1	6	<1	4
Other rivers[c]	0	1 (1)	1 (1)	10[d] (7)

[a] Reared in the Alsea basin.
[b] Reared in the Umpqua basin; Alsea stock eggs were incubated at Alsea Hatchery and transferred as eyed eggs.
[c] Number of basins is given in parentheses.
[d] Mean value.

though both were reared in the Alsea basin before their release into the Siuslaw. In the Umpqua River, more Alsea than Umpqua steelhead strayed, although both stocks were reared and released in the Umpqua basin (Table 3). Because Alsea steelhead were incubated to the eyed egg stage at Alsea Hatchery prior to their transfer to the Umpqua River, straying of adults back to the Alsea suggested some fish imprinted during egg incubation. A genetic component to homing could also have been a factor. Few Umpqua steelhead strayed to the Alsea River.

However, we found no significant difference (*P* = 0.41) among the mean percentages of strays from releases of a transplanted stock and two types of local stocks (Figure 2) for six releases that could be statistically compared. The composition of strays from these transplanted and local releases was highly variable in the recovery basins and generally ranged from 1 to 50%, with the exception of one basin where the transplanted stock composed almost 80% of strays (Figure 2).

Transplanted and local releases of steelhead that returned to their rearing basins instead of their release basins accounted for 39% of all the strays reported in the surveyed rivers. However, most of these strays were from releases of Alsea steelhead into the Siuslaw River that returned to the Alsea basin. Excluding these fish, 9% of all strays were fish returning to their rearing basin. Steelhead returning to their natal or incubation basins rather than to their release basin composed less than 1% of all reported strays, although these types of releases were limited.

Hatchery releases into adjacent basins (defined as the nearest basin with hatchery releases north and south of the subject basin) accounted for 57%

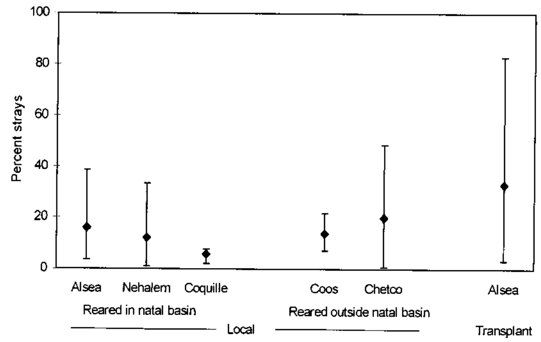

FIGURE 2.—Mean percentage of stray hatchery steelhead recovered in Oregon coastal rivers from six release groups. The groups consisted of (1) five local broodstocks that were reared either within or outside of their natal basins and then released into those basins and (2) one stock that was transplanted into several basins. The vertical lines represent the ranges for percent strays.

of the strays reported in coastal basins (Figure 3) and composed the majority of strays in 10 of 16 streams. Alsea stock steelhead transplanted into the Siuslaw River but returning to the Alsea River accounted for over 50% of the fish that strayed to an adjacent basin. If these fish are excluded, releases into adjacent basins accounted for 38% of all strays (Figure 3). The median distance between adjacent basins where hatchery steelhead were released was 37 km, whereas the median distance that steelhead strayed from their release basin was 54 km (range, 5–456 km). Long-distance strays (>100 km from their release basins) composed 24% of the strays. Strays from hatchery releases into northern California rivers were most frequent, reported in 11 of the 16 Oregon streams we surveyed (Table 4). Of the hatchery releases into

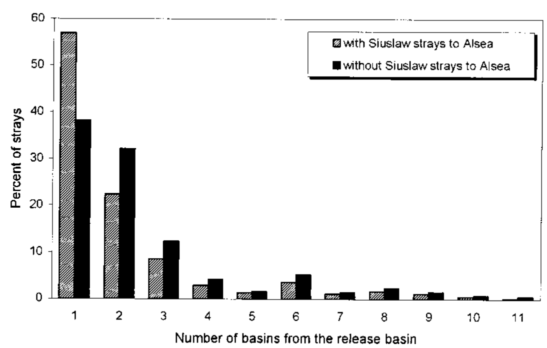

FIGURE 3.—Frequency distribution of stray hatchery steelhead in Oregon coastal basins by proximity to their release basin, 1991–1994 run years. Data are shown with and without transplanted Alsea Hatchery releases into the Siuslaw River that strayed to the Alsea basin.

TABLE 4.—Number and origin of hatchery winter steelhead in Oregon coastal rivers with and without hatchery releases, 1991–1994 run years (except Elk and Sixes rivers, which are 1991–1992 run year only). Homing hatchery returns are indicated by numbers in bold italics. Sampled streams and release groups are listed from north to south from top left.

	Release group													
Streams sampled	Necanicum	Nehalem	Cedar Creek Hatchery[a]	Alsea transplant[b]	Alsea local	Siuslaw[c]	Umpqua	Tenmile	Coos[d]	Coquille	Rogue	Chetco	California	Unknown strays
Streams with hatchery releases														
Necanicum	***56***	3	6											2
Nehalem		***63***	4		1									9
Nestucca		5	***255***	29			1							4
Siletz		1		***141***	3		2	2	1			3	5	39
Yaquina				***106***	1								10	15
Alsea[e]		4		49	***567***	221	4		9	6	4	3	4	24
Siuslaw		4		29	45	***2,205***	13		11	9			5	18
Umpqua					1		***52***			2		2	22	21
Coquille				20[f]		3	8	10	11	***1,191***	8	25	12	3
Rogue					1		1		1		***44***		11	0
Chetco							3				10	***273***	29	29
Streams without hatchery releases														
Trask		9	49	2										1
Drift				10	1	37	4		7	2			4	17
Sixes											4			4
Elk				1									2	2
Winchuck											1	22	22	7

[a] Released into the Nestucca and Tillamook Bay rivers.
[b] Includes hatchery steelhead released into Salmon, Siletz, Yaquina, Smith, and Coos rivers; does not include releases into the Siuslaw River.
[c] Released from Alsea Hatchery into the Siuslaw River.
[d] Includes some fish that may have been released into nearby Tenmile Creek.
[e] Two steelhead released from hatcheries in the lower Columbia River were also recovered in the Alsea River.
[f] Probably from releases into the nearby Coos River.

Oregon basins, strays from Umpqua River releases were most frequent, reported in 8 of 16 streams (Table 4). Eighty-nine percent of these strays were from releases of Alsea stock steelhead into the Umpqua basin.

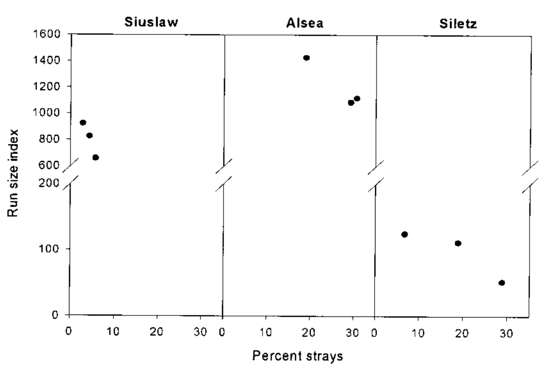

FIGURE 4.—Relationship between percentage of stray hatchery steelhead and an index of run size within three Oregon coastal rivers, 1991–1994 run years. The run size index was derived from counts of wild and homing hatchery fish. Because sampling intensity differed among rivers, indices of run size are not comparable.

The percentage of strays in 11 basins where data were collected for 3 years was highly variable (the mean coefficient of variation, $100 \times$ SD/mean, = 37%). However, we saw no clear effect of run size or stream flow on straying in the Siletz, Alsea, or Siuslaw rivers, where data were sufficient to examine these relationships. We saw some evidence within basins that the percentage of stray hatchery steelhead was higher in years when run size was low (Figure 4), but sample sizes were small.

The incidence of straying was lower when examined at the scale of an ESU than at the smaller scale of individual basins. Of hatchery steelhead from known release groups, those straying from the neighboring ESU composed 2% of all hatchery fish in the northern ESU and 4% of hatchery fish in the southern ESU. The average number of hatchery steelhead smolts released into northern ESU basins was twice the average number released into southern ESU basins (including California). If wild steelhead are included (assuming all wild fish accurately homed), steelhead straying from the neighboring ESU composed 1% of all fish sampled in each ESU. The percentage of steelhead from a neighboring ESU was highest in basins closest to the ESU boundary. About 15% of all strays sampled within an ESU were from the neighboring ESU.

Discussion

The percentage of stray hatchery steelhead in rivers where hatchery fish were released was generally higher in Oregon rivers (4–26% of the total catch) than that reported for six rivers (0–9% of the total catch) in British Columbia (Lirette and Hooton 1988). Hatchery steelhead also strayed to basins where no hatchery fish were released in five Oregon streams (9–43% of the total catch) and in two British Columbia streams (3% and 41% of the total catch). Hatchery fish transplanted to other basins, which accounted for the majority of strays in both studies, composed a larger percentage of the marked release in Oregon (42%) than in British Columbia (21%). However, the percentage of strays is probably underestimated in Oregon rivers because we removed various fins or maxillary bones to identify hatchery steelhead, which may cause higher mortality than the removal of adipose fins (Vincent-Lang 1993) in the British Columbia study. Stray steelhead composed 1% and 6% of the wild steelhead counted in two adjacent coastal California streams (Shapovalov and Taft 1954).

In Oregon coastal basins the mean percentage of strays from transplanted stocks was about twice that from local stocks, although a statistical difference could not be demonstrated. The incidence of straying in Vancouver Island streams increased an average of eight times when steelhead were transplanted to other streams rather than locally released (Lirette and Hooton 1988). Other studies also report that locally adapted populations stray less than transplanted populations in the case of chinook salmon *O. tshawytscha* (McIsaac and Quinn 1988; Pascual et al. 1995), coho salmon *O. kisutch* (Labelle 1992), and pink salmon *O. gorbuscha* (Bams 1976). Pascual and Quinn (1994) reported accurate homing of Rogue River salmon transplanted to the Columbia River but considerable straying within the Columbia. In addition, a study of chinook salmon in Alaska indicated that transplanted hatchery fish did not stray at high rates when the gametes of adults were transported to the release stream and were cultured to smolts (Hard and Heard 1999). High levels of straying in some transplanted releases may be because the sequence and timing of imprinting is disrupted or because an inherited olfactory response to the release site is absent (McIsaac and Quinn 1988; Pascual et al. 1995).

The straying patterns of hatchery steelhead among Oregon coastal basins suggest that the potential for gene flow between hatchery and wild fish is greatest in basins that are geographically proximate to the basin where the hatchery fish are released. These observations are consistent with a study of winter steelhead in Vancouver Island streams (Lirette and Hooton 1988) and other studies of salmon (Labelle 1992; Pascual and Quinn 1994; Hard and Heard 1999). However, proximity to a release site alone did not explain the occurrence of strays in all rivers. For example, we found that the percentage of strays in the Siuslaw and Coquille basins was low despite their proximity to basins with large releases of hatchery steelhead. Factors such as watershed geology, flow, temperature, and stream order may influence straying (Lirette and Hooton 1988; Labelle 1992; Pascual and Quinn 1994).

In addition to the effects on nearby populations, the occurrence of long-distance straying in our study (24% of the strays) indicates that hatchery releases can potentially influence wild fish populations over a large geographic area. Even a low rate of gene flow from distant hatchery populations can reduce the genetic diversity of wild populations (Adkison 1995; Felsenstein 1997). Long-distance straying can greatly increase the migration of hatchery alleles into distant wild populations because the hatchery alleles can reach the distant population without having to migrate through a string of populations (Felsenstein 1997).

Homing of anadromous salmonids is more accurate when it is measured at large spatial scales than at small ones (Unwin and Quinn 1993; Quinn 1997). The incidence of stray steelhead in our study was lower at the geographic scale of ESUs than at the scale of individual basins. Designation of two ESUs for steelhead in Oregon coastal basins was partially based on the genetic differentiation among populations (Busby et al. 1996). The proportion of an ESU that consists of successfully spawning strays has been estimated at much less than 1% based on genetic data on Pacific salmonids (McElhany et al. 2000). We estimated that hatchery steelhead straying between neighboring ESUs composed 2–4% of the catch of hatchery fish and 1% of the catch if wild fish were included. However, we could not determine whether these strays successfully spawned.

The ESUs for coastal steelhead were also based on assumed patterns of ocean migration. Steelhead from rivers north of Cape Blanco are believed to migrate north into the Gulf of Alaska, while those from rivers south of Cape Blanco are believed to stay offshore of southern Oregon and northern California (Everest 1973; Pearcy et al. 1990). However, data on steelhead distribution in the ocean are based on a few recoveries of juveniles or adults in limited areas. In our study, about 15% of the strays in each ESU were from the neighboring ESU. Our data suggest two possibilities: (1) some steelhead overshoot their release basin on their spawning migration and enter a basin in the neighboring ESU; (2) ocean migration patterns are more variable than previously thought, and some southern ESU steelhead migrate north in the ocean as juveniles and enter the northern ESU basins as they return south on their spawning migrations, and vice versa. Because some steelhead have been transplanted beyond the ESU boundary in the past (e.g., Alsea River steelhead into the Chetco River), our observations could be partially influenced by interbreeding of local and transplanted stocks. However, most of the reported strays were from releases that have no history of stock transfers between ESU basins.

Our estimates of straying may have included fish that were transitory and would not have spawned in basins where they were sampled. Some fish exhibit exploratory behavior and may ascend nonnatal rivers before returning to their natal stream to spawn (Ricker 1972; Labelle 1992). The genetic effects of stray fish on a local population depend on interbreeding between the two groups, not just the physical migration of fish (Tallman and Healey 1994; Felsenstein 1997). Although some steelhead captured in this study could have been transients, traps used to capture steelhead were generally located in small spawning tributaries distant from the ocean where transitory strays might be less prevalent. For example, the traps operated in five river basins were an average of 62 km from the ocean and 35 km upstream of tidal reaches. Some stray steelhead caught in sport fisheries may not have remained in the basin, although steelhead fisheries in Oregon coastal rivers generally occur upstream of tidal waters. Even if stray hatchery fish spawn in nonnatal rivers, strays may differ from native fish in their spatial and temporal distribution on the spawning grounds or they may encounter barriers in mate choice (Tallman and Healey 1994; Quinn 1997). Some studies of salmon have estimated that gene flow between populations was less than would be suggested by stray rates (Labelle 1992; Tallman and Healey 1994).

Marking reduces the survival of fish (Vincent-Lang 1993) and can affect estimates of straying. In this study, almost all hatchery fish were marked with a combination of fin and maxillary clips, which would have reduced their survival. This probably decreased our estimates of the percentage of strays in the total run in most basins. Comparisons of straying within the hatchery component of the run were not affected because marking varied among and within release groups.

Although straying is a natural phenomenon in anadromous salmonids, the level of straying by hatchery steelhead and its widespread occurrence in Oregon coastal rivers raises concern about the long-term genetic impacts on local wild populations of winter steelhead. In addition, large numbers of strays to a hatchery pose a risk to the genetic integrity of local stocks of hatchery fish. If straying hatchery fish cannot be identified, they could be incorporated into the local hatchery stock. The genetic integrity of locally adapted populations can decrease with rates of gene flow from stray hatchery fish as low as 5–10% (Emlen 1991; Felsenstein 1997). Stray hatchery steelhead composed 10% or more of the steelhead sampled in 10 of 16 Oregon coastal streams. Of particular concern is the high percentage of strays (9–43%) in streams where no hatchery fish were released.

Our study indicates that using local brood stocks, rearing and releasing hatchery fish within their natal basins, or a combination of these strategies could reduce the straying of hatchery fish. Hatchery fish reared in a location distant from their release basin may more accurately home to that release basin than fish reared in a nearby basin (Lirette and Hooton 1988; Quinn 1993). However, Labelle (1992) reported that certain stocks of coho salmon were more susceptible to straying when exposed to foreign water sources during rearing. Because hatchery steelhead tend to return to their release locations (Wagner 1969; Slaney et al. 1993), releases into tributaries rather than into the main stem may increase homing within and among basins, but the residualism of hatchery smolts should be evaluated (Viola and Schuck 1995). Reducing the numbers of hatchery fish released or eliminating some hatchery releases altogether would also decrease the numbers of strays.

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