



A comparison of the behavior and survival of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) in a small estuary system

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ABSTRACT

We used radio and acoustic telemetry to study the behavior and survival of wild steelhead trout (*Oncorhynchus mykiss*) and hatchery coho salmon (*Oncorhynchus kisutch*) and steelhead outmigrants in a small coastal estuary during two years. Survival was generally low for hatchery fish but more variable, both within and between years, for wild steelhead. The rate of downstream movement in the river varied both within and between species and was generally not correlated with flow. Both hatchery and wild steelhead tended to spend less than a day in the estuary, and tended to move downstream on outgoing tides. In contrast, hatchery coho salmon spent a longer period of time in the estuary (~8 d). On several occasions, coho salmon were observed moving both upstream and downstream between the upper (freshwater) and lower (saline) zones of the estuary. We also documented a high incidence of predation by avian and mammalian predators on coho outmigrants.

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1. Introduction

Several populations of salmonids have declined significantly in recent decades throughout the Pacific Northwest of the U.S. (National Marine Fisheries Service, 2000). The decline has been attributed to habitat degradation, over harvest, the damming of rivers, and the influence of hatchery fish (Knudsen, 2000; Levin et al., 2001; Noakes et al., 2000; Raymond, 1988; Williams et al., 2005). To date, the status of Columbia River stocks has received the most attention, however, stocks in some other coastal river systems are also threatened or in serious decline (Allendorf et al., 1997; Nehlsen et al., 1991). In Oregon, these include coho salmon and some steelhead populations. To restore the salmon runs to sustainable levels and maintain healthy anadromous salmonid populations, it is imperative that the factors leading to the mortality of all life history stages be identified and monitored.

Monitoring of salmonid numbers is essential for sound fishery management, recovery planning, and delisting of species. Accurate and precise quantification of ocean-related mortality is vital for setting harvest goals and the robustness of population viability models used in recovery planning by the National Marine Fisheries Service, State fish and wildlife agencies, and the U.S. Fish and Wildlife

Service. However, metrics to assess ocean mortality are currently based on data that reflect combined survival in the lower reaches of rivers, estuaries, and the ocean. This is because present monitoring is based on counts of out-migrant fish in traps which are often located many kilometers upriver from the ocean. Recent data from studies in the lower Columbia using biotelemetry have shown that the mortality of juvenile salmonids can be quite substantial (up to 80%) (Clemens et al., 2009; Schreck et al., 1993, 1996, 1997; Schreck et al., 2001a, 2001b; Schreck et al., 2002a, 2002b; Schreck and Stahl, 1998). This would have the obvious effect of biasing ocean survival estimates downward. Very importantly, it also means that a significant portion of habitat, that could be restored and/or managed, has not been adequately considered in viability models or recovery planning.

Aside from the Columbia River, we know very little about the relative losses of salmon in the lower river and estuary of most systems. There is some evidence that the relative strength of a year class is determined soon after entry to saltwater (Fisher and Percy, 1988; Ricker, 1976). Several researchers have shown that a variety of predators including piscine (Beamish et al., 1992; Hvidsten and Mokkalgjerd, 1987; Larsson, 1985), mammalian (Laake et al., 2002; Olesiuk et al., 1995; Yurk and Trites, 2000), and avian (Collis et al., 2001; Moring et al., 1998) predators may consume a significant number of migrants during their passage through the estuary. If our estimates of mortality in the lower Columbia can be applied to other estuaries, the total number of juvenile salmonids taken by predators, or otherwise lost in estuaries, may be sufficiently large to negatively influence adult returns, particularly during times when

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there are other natural (e.g. climatic) or anthropogenic (e.g. over harvest) bottlenecks to recruitment.

Our goal is to determine whether outmigration through the estuary represents a bottleneck to recruitment and understand whether the behavior of juvenile salmonids in this region influences their survival to the ocean. During 2001, and 2002 we conducted an assessment of the behavior and survival of hatchery coho and both hatchery and wild steelhead outmigrants in the Nehalem watershed on the northwest coast of Oregon (USA) (Fig. 1). We used radio and acoustic telemetry to: 1) measure the survival of outmigrating smolts between the smolt trap and the ocean, 2) determine if there are differences in behavior between species or between hatchery and wild fish that may result in differential mortality in the estuary, and 3) determine whether outmigrant smolts are depredated by avian, mammalian, or piscine predators in the estuary.

2. Methods

2.1. Study site

The Nehalem estuary is located in Northwest Oregon (Fig. 1). The estuary is approximately 11.1 km² in area. The lower 4 km of the North Fork Nehalem River is tidally influenced. During all three years we did not observe any saltwater in the upper estuary (above the county boat ramp). In the mid-estuary (Paradise Cove), the salinity ranged from 8 to 20 ppt at the bottom (~4 m) to between 2

and 8 ppt at the surface. In the lower estuary (Jetty Fishery) the salinity at high tide was between 10 and 25 ppt near the bottom (~10 m) and between 5 and 20 ppt at the surface. Daily flow in the lower river varied throughout the outmigration in both years (Fig. 2). The period of peak outmigration of wild coho and steelhead was during the week of April 25 in 2001 (both species) and April 11 (coho) and May 1 (steelhead) in 2002.

2.2. Radio and acoustic tagging

2.2.1. Fish collection

In 2001 and 2002, we collected wild steelhead outmigrants using a 2.7 m rotary screw trap operated by ODFW on the North Fork Nehalem River (Fig. 1). The trap was cleared between 08:00 and 09:00 each day and wild steelhead smolts were transferred to a separate holding tank (125 L) and held for 15–20 min prior to tagging. Water in the holding tank was periodically replaced to maintain temperature and oxygen levels close to those in the river.

In 2002, we collected hatchery coho salmon and steelhead trout from the outlet of the raceway using a dipnet during the evenings of April 3, 7, and 15. All fish were transferred downstream in 125 L plastic containers (~3 min) and placed in holding cages. The fish were held overnight for between 12 and 20 h prior to tagging. Steelhead and coho salmon were held in separate cages at all times. The numbers of fish tagged and their mean length on each date are given in Tables 1 (Radio-tagged fish) and 2 (Acoustic-tagged fish).

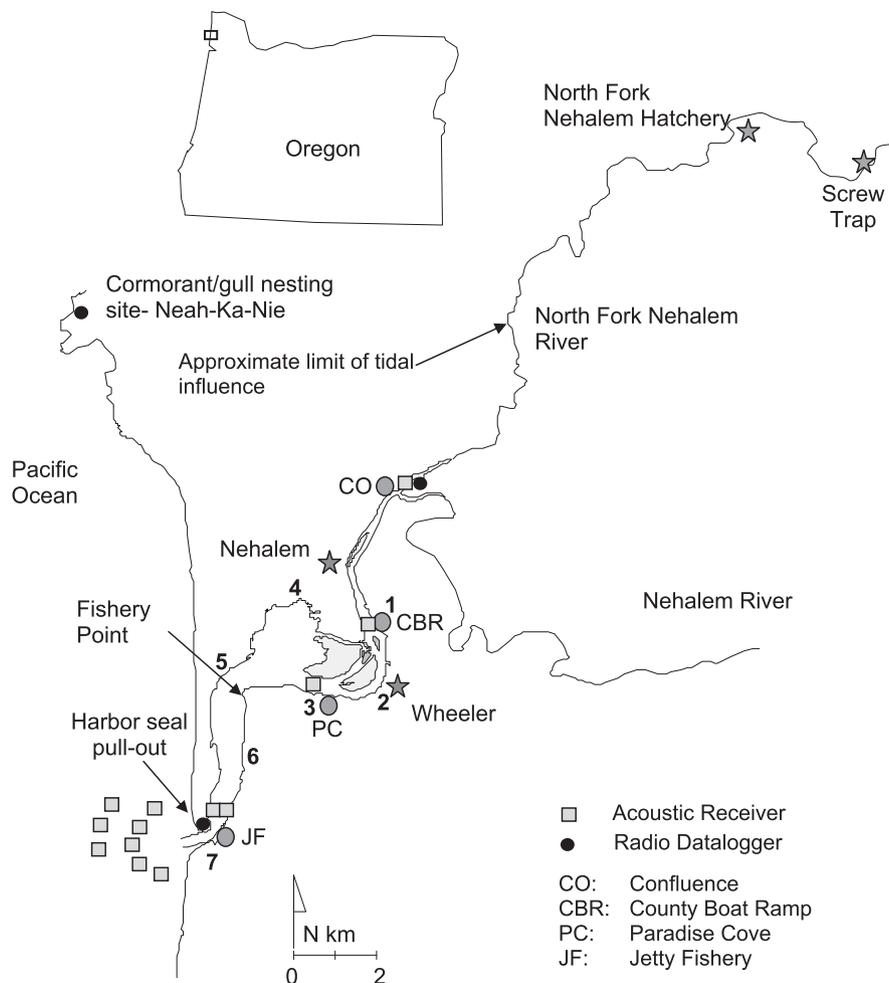


Fig. 1. Nehalem River and estuary study area. Fish were captured, tagged, and released from the screw trap (wild steelhead, 2001 and 2002) or from the North Fork Nehalem Hatchery (hatchery coho and steelhead, 2002). Numbers (1–7) refer to the predator survey sites.

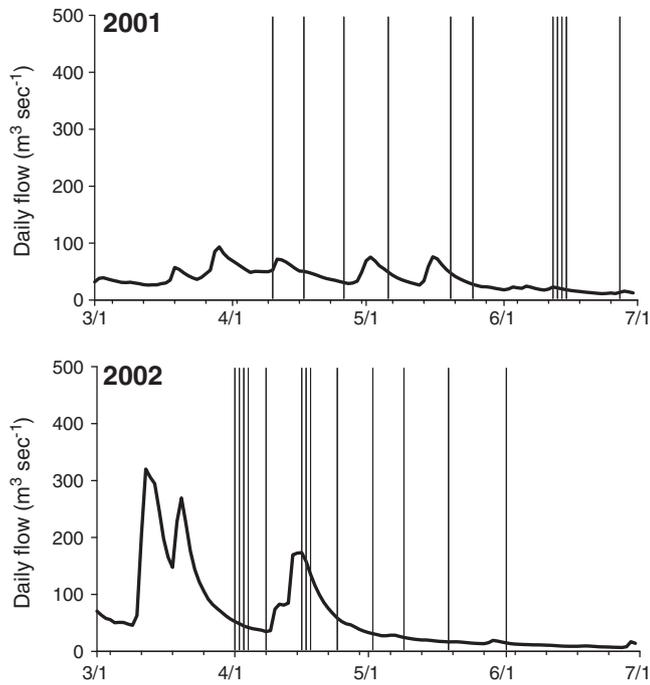


Fig. 2. Mean daily flow ($\text{m}^3 \text{s}^{-1}$) at the Foss Gauging station on the mainstem Nehalem River (USGS station number 14301000) in 2001 and 2002. Solid vertical lines represent dates on which tagged fish were released.

2.2.2. Tag implantation

The fish were anesthetized in 50 mg/L tricaine methanesulfonate (MS-222, buffered with 125 mg/L NaHCO_3), measured (length and weight), and any external abnormalities noted. Only fish in apparently healthy condition were used, although this did include fish with mild (<10%) descaling and fin abrasion (in hatchery fish). Both radio and acoustic transmitters were implanted surgically into the peritoneal cavity (surgical implant) using the methods described in Clements et al. (2009). The fish were transferred to a recovery area following tagging.

The radio transmitters (0.8 g, minimum life 18 d) were purchased from Lotek Wireless (Newmarket, Ontario, Canada). The antenna of each transmitter was trimmed to 20 cm to minimize interference with swimming. We found no effect on the range of detection when the antenna was trimmed in a preliminary trial. The acoustic transmitters (V9: 3.4 g in air, 69 KHz, power output 149 dB re 1 μPa at 1 m, 7–21 s pulse interval, >54 d battery life) were purchased from Vemco (Halifax, Nova Scotia, Canada). Prior to implantation all tags were tested for proper function.

2.2.3. Recovery and release

In 2001 and 2002 both the hatchery and wild fish were transferred to a net enclosure (2.5 m long \times 1.2 m wide \times 1 m deep) following

surgery. The enclosure was placed in-river in close proximity to the site of tagging (North fork fish hatchery for hatchery coho and steelhead and the screw strap for wild steelhead). The fish were held in the enclosure for 5–8 h after surgery at which time they were liberated. The hatchery coho and steelhead were held in separate enclosures. We typically liberated fish close to sunset to minimize the likelihood of predation. Survival during this period was 100%.

2.3. Migration rate

We used acoustic telemetry to evaluate the rate of migration into and through the estuary. We placed hydroacoustic receivers (VR2, Vemco) throughout the estuary prior to the first release of fish (see Fig. 1 for place names and location of receivers). All receivers were left in place until the batteries of all acoustic tags would have failed (>54 d). The location of the receivers was similar between years, with the exception of the receivers placed immediately downriver of the county boat ramp, which were not present in 2001. The receivers were positioned in lines across the estuary to ensure that there was a high probability that fish could not pass a particular site without being recorded, based on range testing data. In practice, the spacing between the receivers varied from 10 m (confluence: Co) to 100 m (county boat ramp: CBR). Similarly, the receivers in the ocean were deployed at \sim 300 m intervals. For the purposes of the discussion the estuary is split into four zones: the upper estuary (Co–CBR); the mid estuary (CBR–Paradise Cove [PC]); the lower estuary (PC–Jetty Fishery [JF]); and the estuary mouth (JF–Ocean).

2.4. Predation

In 2002, we used radio telemetry to determine whether juvenile salmon were subject to predation by avian, piscine, and mammalian predators. We documented incidences of predation using both autonomous datalogging sites (SRX 400, Lotek Wireless) and manual tracking. The autonomous dataloggers were located near the cormorant nesting colony (*Phalacrocorax auritus*, *P. penicillatus*, *P. pelagicus*) on Neah-Ka-Nie Mountain and the seal (*Phoca vitulina*) haul-out opposite at the mouth of the estuary. Predation was confirmed either by triangulating the location of a transmitter to an individual predator or by the final resting location of the radio tag being associated with a specific predator (i.e., in air at the double-crested cormorant colony or at known roosting sites in the estuary). When the final location of a tag was not associated with a specific predator, the fate of the fish was considered unknown.

2.5. Predator evaluation

We documented the distribution of salmonid predators, specifically double-crested cormorants and harbor seals, in the Nehalem estuary during both years of the study. We also monitored known

Table 1

Summary of the numbers and mean length (SE) of fish (implanted with radio transmitters) released on each day and the fate of those fish in 2002. Numbers in the columns represent the number of fish that were released, heard at the automated listening sites at the confluence, the bird colony, or the seal haulout site, or detected in a bird during estuarine surveys. H = hatchery, W = wild, st = steelhead trout, co = coho salmon.

	1–4 Apr			16–18 Apr			24 Apr	2 May	19 May
	H-st	H-co	W-st	H-co	H-st	W-st	W-st	W-st	W-st
Mean length (mm)	155.40 (3.79)	198.10 (2.87)	180.00 (13.23)	152.30 (2.25)	192.70 (6.14)	177.67 (6.21)	176.40 (4.68)	163.60 (4.01)	173.00 (7.03)
Released	10	10	3	10	8	6	10	10	9
Confluence	9	5	1	5	0	4	2	9	6
Cormorant	5	0	0	3	0	1	0	1	0
Other avian	1	0	0	0	0	0	0	0	0
Seal	0	0	1 ^a	0	0	0	0	0	0

^a This fish is not the same one that was detected entering the estuary.

Table 2
Estimated mean (SE) survival probabilities (S) for juvenile wild steelhead trout in 2001 (A) and coho salmon and steelhead in 2002 (B). Fish were implanted with an acoustic tag. The probability of detection for all estuarine arrays was 1.00 unless included (bold numbers). The survival probabilities are calculated between successive arrays. Overall S equals the total survival from release to the lower estuary (Jetty Fishery). Estuarine survival is the proportion of fish that migrated into the estuary and were later detected at the mouth of the estuary. The estimate of survival from release to the ocean was adjusted for the estimated efficiency of the ocean array (83%) and is calculated as a simple point estimate. N/A: we did not include these estimates as no fish migrated into the estuary. H = hatchery, W = wild, st = steelhead trout, co = coho salmon.

A 2001 W-st	10 Apr	17 Apr	26 Apr	6 May	20 May	25 May	12–15 Jun	27 Jun				
Number released	9 ^a	10	9 ^a	10	7 ^a	2 ^a	6 ^a	3 ^a				
Mean length (mm)	191.60 (4.40)	202.60 (2.90)	190.40 (2.50)	186.30 (3.80)	155.90 (1.80)	153.80 (3.70)	148.80 (4.30)	191.60 (4.40)				
Confluence	0.78 (0.14)	0.80 (0.13)	1.00 (0.00)	0.6 (0.15)	0.56 (0.17)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)				
Paradise Cove	0.86 (0.13)	0.88 (0.12)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	N/A	N/A	N/A				
Jetty Fishery	0.83 (0.15)	0.86 (0.13)	0.89 (0.1)	0.67 (0.19)	1.00 (0.00)	N/A	N/A	N/A				
Overall	0.56 (0.17)	0.60 (0.15)	0.89 (0.1)	0.40 (0.15)	0.56 (0.17)	N/A	N/A	N/A				
Estuarine survival	0.71 (0.17)	0.75 (0.15)	0.89 (0.10)	0.67 (0.19)	1.00 (0.00)	N/A	N/A	N/A				
Ocean	0.54	0.24	0.54	0.36	0.52	N/A	N/A	N/A				
B 2002	1–4 Apr			8 Apr		16–18 Apr			24 Apr	2 May	9 May	1 Jun
	H-co	H-st	W-st	H-co	H-st	H-co	H-st	W-st	W-st	W-st	W-st	W-st
Number released	10	10	4 ^a	10	10	10	10	8 ^a	10	10	10	3 ^a
Mean length (mm)	155.70 (1.92)	212.30 (3.46)	195.00 (14.86)	159.10 (2.71)	213.20 (1.89)	159.30 (2.34)	192.50 (5.57)	177.38 (4.15)	172.25 (5.41)	182.90 (6.95)	170.00 (4.79)	160.33 (7.97)
Confluence	0.7 (0.14)	0.5 (0.16)	1.00 (0.00)	0.8 (0.13)	0.6 (0.15)	0.4 (0.15)	0.1 (0.095)	0.63 (0.17)	0.8 (0.13)	0.9 (0.095)	1 (0)	0.67 (0.27)
County boat ramp	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	0.67 (0.19)	0.75 (0.22)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)
Paradise Cove	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	0.75 (0.22)	1.00 (0.00)	1.00 (0.00)	1.1 (0.097)	0.88 (0.12)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)
Jetty Fishery	1.00 (0.00)	0.6 (0.22)	1.00 (0.00)	0.88 (0.12)	1.00 (0.00)	0.67 (0.27)	0.00 (0.00)	0.75 (0.22)	0.89 (0.15)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)
								0.75 (0.22)	0.8 (0.18)			
Overall	0.700 (0.1449)	0.3 (0.14)	1.00 (0.00)	0.7 (0.14)	0.3 (0.14)	0.2 (0.13)	0.00 (0.00)	0.5 (0.18)	0.63 (0.17)	0.9 (0.095)	1.00 (0.00)	0.67 (0.27)
Estuarine survival	1.00 (0.00)	0.6 (0.22)	1.00 (0.00)	0.88 (0.12)	0.5 (0.2)	0.5 (0.25)	0.00 (0.00)	0.8 (0.18)	0.78 (0.17)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)
Ocean	0.24	0.24	0.60	0.36	0.24	0.12	0.00	0.30	0.60	0.84	1.00	0.80

^a On these dates and for this fish type we were unable to implant the intended number of tags due to insufficient numbers of wild steelhead smolts in the screw trap, high water, or mechanical problems with the trap.

avian nesting sites near the Nehalem estuary to determine whether tagged fish were present. These sites were ~7 miles from freshwater (the estuary) so the presence of tagged fish at the nesting site is assumed to represent predation.

The surveys consisted of timed periods of observation at several sites throughout the estuary (Fig. 1). Generally, the estuary was surveyed once daily throughout the entire season. Surveys were typically conducted in the morning (09:00–10:00). For each survey, we spent 10 min at each site to standardize sampling and limit the total survey time to lower the chance of recounting the same predators at two sites. Predators were counted using both 10×50 binoculars and a tripod-mounted, variable-magnification (15–45×60) spotting scope. Only birds that might possibly prey upon smolts were identified and recorded (number and activity). These included double-crested cormorants (*P. auritus*), Brandt's cormorants (*P. penicillatus*), pelagic cormorants (*P. pelagicus*), Caspian terns (*Sterna caspia*), gulls (*Larus* spp.) and great blue herons (*Ardea herodias*). We also recorded the number and location of harbor seals. Because the distribution of birds is likely to be influenced by the tidal cycle we only used the data that was collected during the 3 h period either side of high tide during the analysis of predator distribution throughout the outmigration period. We made no attempt to correct for birds or seals that were feeding below the surface during a survey, although in practice we were generally able to record most of these animals during the 10 min survey period.

2.6. Survival

2.6.1. Acoustic line efficiency

We estimated the probability of detection (capture probabilities) for each acoustically tagged release group at all receiver lines using SURPH 3.0.9 (<http://www.cbr.washington.edu/paramest/surph/>). In addition, we conducted manual tests at each receiver line to determine their reception efficiency. For the estuarine lines this was done by releasing 8–10 tags upriver of a line and recording subsequent detections at the line. Each tag was attached to monofilament line that was hung below a float. We conducted three releases of these drones for each line across the width of the river. Using this method we tested receivers at the Co, CBR, and JF lines.

It is not possible to determine the probability of detection for the last line of receivers (in the ocean) using SURPH because of the lack of a downstream line. Thus, we relied on manual tests to estimate the likely efficiency of this line. Because of the unpredictable nature of currents in the area around the mouth of the estuary we could not release passive drones. Therefore, we used a boat to tow a single tag between 2 receivers. This was repeated 12 times over the entire inner line. We calculated the efficiency of the line by dividing the number of times the tag was towed through the line by the number of times it was detected at least twice during each tow. We did not measure the efficiency of the outer line.

To determine whether wave noise was a factor in the ability of the ocean receivers to detect fish we plotted wave height data from the closest weather buoy, located at the Columbia River mouth (buoy number 46029, www.ndbc.noaa.gov), 40 km north of the Nehalem estuary, against the times fish passed the line or were expected to pass the line (based on the time of last detection at the Jetty Fishery and the mean speed through the estuary on an outgoing tide)

2.6.2. Survival in the estuary and near-shore ocean

We used the detections of acoustically tagged fish at the 4 lines in the estuary to compile a complete capture history for each fish following the method described by Burnham et al. (1987). We then estimated survival using a single Cormack–Jolly–Seber (CJS) release–recapture design (Cormack, 1964; Jolly, 1965; Seber, 1965) where tag detections constituted recaptures. Survival estimates were generated by SURPH V3.0.9. When CJS survival estimates were

not available (at the ocean line), we used simple arithmetic to estimate the survival to the ocean as follows:

$$N/d * e$$

where N is the number of fish released, d is the number of fish detected on the ocean line, and e is the probability of detection (obtained from manual testing outlined in Section 2.5.3).

2.7. Statistical analysis

We used a maximum likelihood ratio test for logistic regression to test the null hypotheses that 1) there was no difference in survival between fish types within a release period (2002); 2) there was no difference in survival within a fish type throughout the year (2001, 2002); 3) there was no difference in survival between wild steelhead in 2001 and 2002; and 4) there was no difference in survival between hatchery and wild steelhead in 2002. The regressions were performed using Systat 11 (Systat Software Corp. Chicago, IL, USA).

3. Results

3.1. Migration rate

3.1.1. In-river

During both years we monitored for fish presence in the area ~1 km below the release site to determine whether fish migrated downstream after release. The majority of fish migrated out of this area within 1–2 d. However, in the last two releases in 2001 (June), 4 of the 8 fish were detected moving between/within pools in this area for up to a month suggesting that these fish were not migrating. Given this, we excluded the fish from these two releases in subsequent analyses. The only direct comparison between the three fish types occurred during the 2002 outmigration. In general, the wild steelhead took 139 ± 16 h (mean \pm SEM) (c.f. 126 ± 10 h in 2001) to migrate the 20.2 km down the North Fork Nehalem River from the lower screw trap to the confluence with the mainstem (Fig. 3). In contrast, the hatchery steelhead took an average of 65 ± 11 h to migrate 17 km from the hatchery to the estuary. The hatchery coho salmon were intermediate, taking an average of 86 ± 12 h to migrate from the hatchery to the estuary. However, there was considerable variability both within and between releases in all years.

Flow explained a large proportion of the variation in travel time to the estuary in 2001. The mean travel time increased as the mean flow (7 d average) decreased during the season ($P = 0.036$; $r^2 = 0.81$). The change in migration rate is given by the simple linear regression model: migration time (h) = $92.58 \text{ h} - (0.398 * 7 \text{ d mean flow})$. In 2002, flow was not correlated with travel time in the lower river. For both types of steelhead the regression was positive but not significant. For wild steelhead and hatchery coho the regressions had low r^2 values, indicating that any relationship between flow and travel time is tenuous (W. Steelhead: $r^2 = 0.02$, $P = 0.793$; H. Steelhead: $r^2 = 0.70$, $P = 0.370$; and H. coho: $r^2 = 0.04$, $P = 0.874$).

3.1.2. In-estuary

The time to migrate through the estuary was calculated by subtracting the time fish were last heard at Co from the time the fish was last heard at JF, a total distance of 11.2 km. Thus, the estimate only takes into account those fish that survived to the lower estuary (JF). In 2002, migration times were 161 ± 20 , 57.5 ± 35.9 , and 24.5 ± 8.8 h (c.f. 15 ± 2 h in 2001) for hatchery coho and hatchery and wild steelhead, respectively (Fig. 4). The value for coho is likely an underestimate as many of these fish were regularly recorded moving both up- and down-stream between the upper and lower estuary. Thus, the last detection at the Jetty Fishery is not necessarily indicative of entry to the ocean.

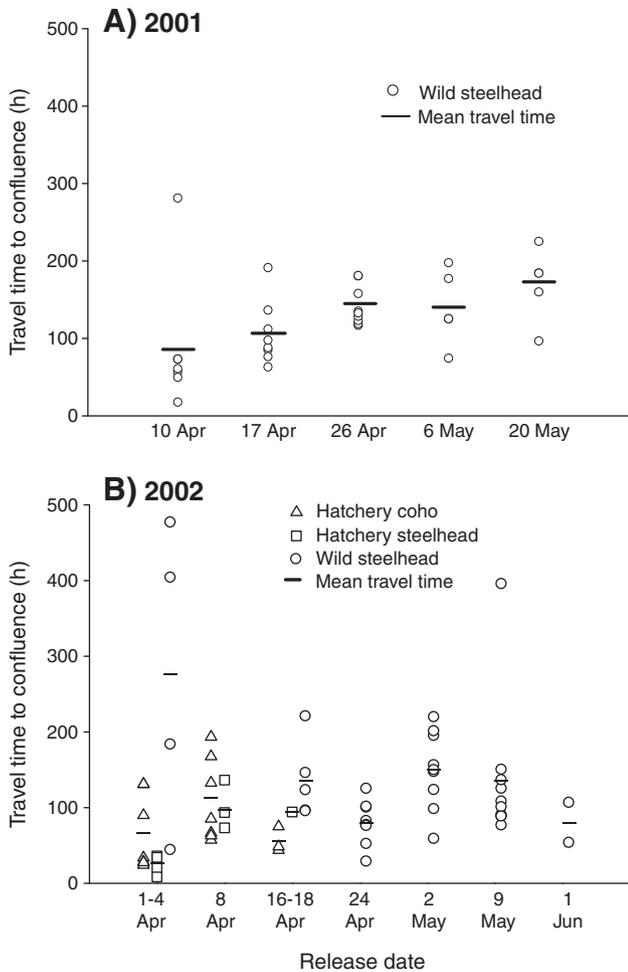


Fig. 3. Time taken for individual fish to migrate from the lower ODFW screw trap on the north fork of the Nehalem River (wild steelhead) or the North Fork Nehalem Fish hatchery (hatchery coho and steelhead) to the confluence with the mainstem Nehalem River in 2001 and 2002. In 2001 we released wild steelhead. In 2002 we released wild steelhead and hatchery steelhead and coho. Each point represents a single fish. Each bar represents the mean time for that fish type. Not all points are visible as some overlap with others.

3.2. Predation

In 2002, between 55 and 60% (Table 1) of all radio-tagged hatchery coho salmon that migrated to the estuary were consumed by cormorants. This estimate is likely a minimum as we were only able to detect predation by birds that roost on the cliffs at Neah-Ka-Nie. Although, in one instance, we did confirm that a radio tagged coho salmon smolt was consumed by a great blue heron.

Few wild steelhead were taken by cormorants from the Neah-Ka-Nie colony (2 of 32) in 2002. Similarly, we had only one documented incidence of depredation by a harbor seal during this year. We did not record any known incidences of avian or mammalian predation on hatchery steelhead in 2002.

3.3. Predator survey

Double-crested cormorants were the most abundant predator during both years. In 2002, we observed large numbers of double-crested cormorants in the estuary at the beginning of the study (Fig. 5). Numbers ranged from 13 to 147 (mean: 61 ± 4 birds/d). Caspian terns were also present in the system at the beginning of the outmigration season during all three years. However, the number of terns declined significantly by the end of April.

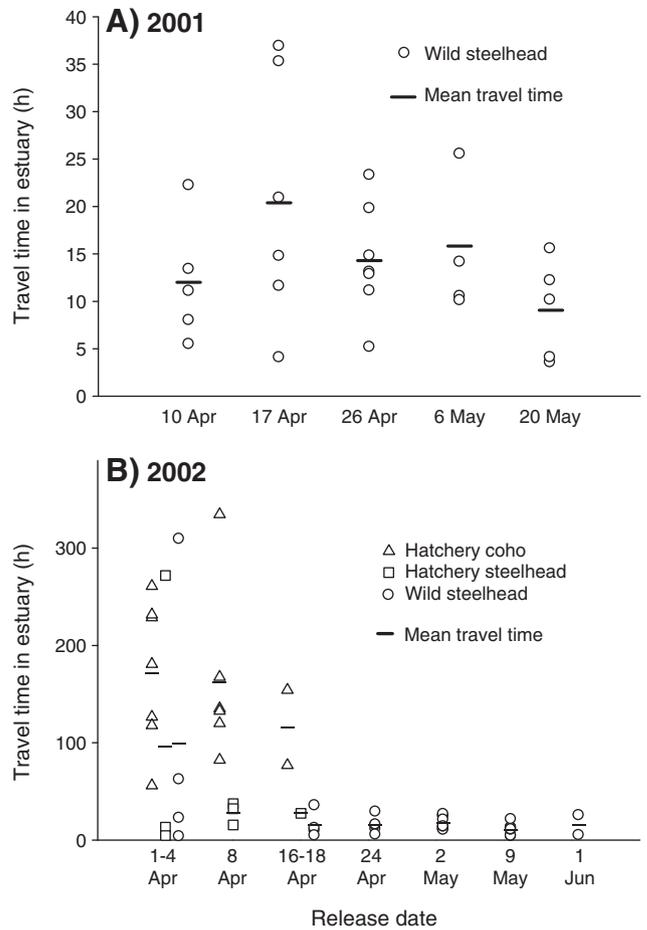


Fig. 4. Time taken for individual fish to migrate from the confluence of the north fork of Nehalem River and the mainstem Nehalem River to the Jetty Fishery (lower Estuary) in 2001 and 2002. In 2001 we released wild steelhead. In 2002 we released wild steelhead and hatchery steelhead and coho. Each point represents a single fish. Each bar represents the mean time for that fish type. Not all points are visible as some overlap with others.

Double-crested cormorants were most often observed near the middle of the estuary. We often observed cormorants roosting on the mudflats in Nehalem Bay at low tide and on the pilings between PC and JF. Furthermore, this area appeared to be the most common foraging site later in the season. Early in the outmigration season (~10 Apr–25 Apr), during periods when we were tracking migrants in the estuary, large numbers of cormorants (~40–100) were often observed swimming upriver between Nehalem and up to 1 km up the North Fork. This region was outside the area checked daily during the predator surveys.

The number of harbor seals in the Nehalem estuary approached or exceeded 100 on several occasions (Fig. 6). Most seals were observed at pullout sites on the beach near the mouth of the estuary. However, seals were also observed foraging upstream as far as Co, approximately 13 km upstream from pullout site. Interestingly, on April 3, 2002, we counted 143 seals (the maximum during the season), two days later a pod of orcas (*Orcinus orca*) was observed preying upon the seals in the lower estuary. Following this event seals were not observed again until April 14, and continued to decline in numbers throughout the season.

3.4. Survival

3.4.1. Acoustic receiver efficiency

The probability of detection was 100% at all upper estuary line locations (Co and CBR) in both 2001 and 2002. In most instances (15 of 17 releases in which fish migrated to the estuary), detection

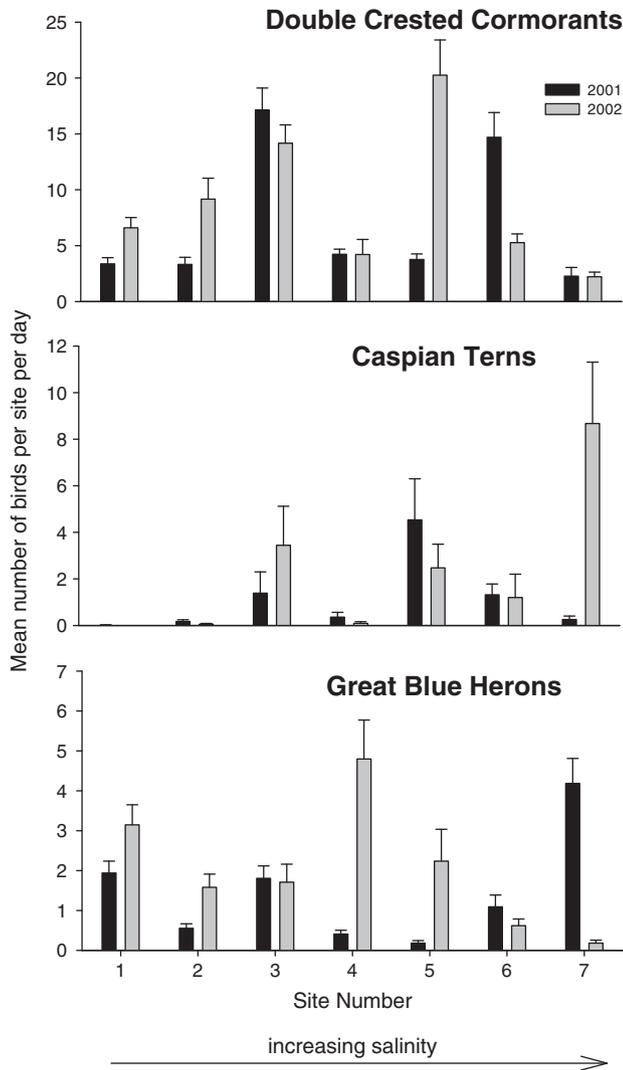


Fig. 5. Average number of avian predators (per day) present at each location in the Nehalem estuary during 2001, and 2002. Site numbers are identified in Fig. 1.

probabilities were also high (100%) at the mid estuary line (PC). However, this line did miss fish in the 2nd (1 of 5 fish from this release that passed this line) and 4th (1 of 9 fish from this release that passed this line) releases of wild steelhead in 2002 (Table 2B).

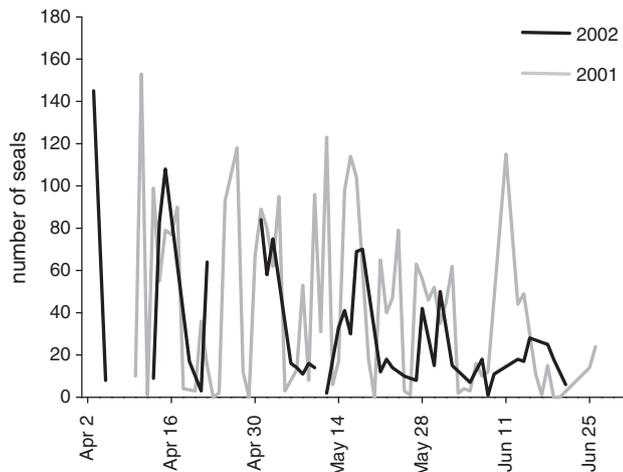


Fig. 6. Total number of harbor seals (per day) present in the Nehalem estuary during 2001 and 2002.

Table 3

Abundance of predators in the Nehalem estuary in 2001 and 2002. The values represent the average percent of total number of predators over the study. The most abundant predators are in bold.

Year	Predators				
	Double crested cormorant	Other corm.	Caspian tern	Great blue heron	Harbor seal
2001	43.1	6.1	7.3	9.1	34.5
2002	50.2	2.9	13.3	11.9	21.8

The probability of detection was 100% in all but one instance at the lower estuary line (JF). In addition, we observed 100% recovery of the passing tags during the manual tests. Thus, the SURPH model yielded very similar results to those obtained using drone tags. The probability of detection was ~83% for the ocean line. We used this figure to adjust all estimates of survival to the ocean. There was no apparent correlation between the ability of the receivers to hear fish and the significant wave height (calculated as the average of highest third of readings within 20 min) in both years (data not shown).

3.4.2. Survival in the estuary and near-shore ocean

The proportion of wild steelhead that migrated from the release site to the lower estuary ranged between 0.00 and 0.60 ± 0.17 in 2001. Survival was significantly higher in 2002 (Chi square = 5.25; $df = 1$; $P = 0.02$), ranging between 0.63 ± 0.17 and 1.00 (Table 3). We estimated that survival to the ocean was between 0–0.54 and 0.30–1.00 in 2001 and 2002, respectively (Table 3). There was no difference in wild steelhead survival between releases within a year (excluding the last three releases in 2001 when fish did not migrate).

The proportion of hatchery steelhead that migrated from the release site to the lower estuary ranged from 0.00 to 0.30 ± 0.14 in 2002. Survival to the ocean ranged from 0.00 to 0.24. The survival of hatchery steelhead was significantly lower in the estuary than for wild steelhead in 2002 (Chi square = 5.40; $df = 1$; $P = 0.02$).

The proportion of hatchery coho that migrated from the release site to the lower estuary ranged from 0.20 ± 0.13 to 0.70 ± 0.14 in 2002 (Table 3). Survival to the ocean ranged from 0.12 to 0.36.

4. Discussion

It is thought that salmonid year class strength is determined during the period shortly after smolts enter saltwater (Fisher and Percy, 1988; Ricker, 1976). Beamish et al. (1992) suggest that this may be due primarily to predation in this region. Our data support this contention as, during two consecutive years, we have shown that a large proportion of juvenile steelhead trout and coho salmon migrants do not reach the ocean following release at the last enumeration site in the lower river. Furthermore, it appears that there are differences in behavior between salmon species that may contribute to differential vulnerability to predators such as cormorants or seals in the estuary.

4.1. Survival

We estimated that 40–78% of the annual outmigration of wild juvenile steelhead either died or did not migrate between the life cycle monitoring site and the ocean. The majority of this loss occurred during the early period of the outmigration in both 2001 and 2002. It is not clear why migration success differed so markedly among years. We hypothesize that the higher survival in 2002 may be explained by changes in predator abundance/motivation. In 2002, there was very little temporal overlap between Caspian terns and the outmigrating wild steelhead. Furthermore, we observed a decline in harbor seal numbers during the peak period of wild steelhead outmigration, due to depredation by orca. Our estimates of wild and hatchery steelhead mortality in the Columbia River estuary were also significantly

lower during 2002 than in 2001 (Schreck et al., 2002a, 2002b). Thus, we speculate that large-scale variables, such as the availability of alternate prey (e.g., herring *Clupea pallasii*), may also have contributed to higher survival during the freshwater/estuarine phase of the outmigration in 2002. Interestingly, some fish that were termed “migrants” were not actually migrating. In 2001, none of the fish in the last 3 release groups entered the estuary. Several of these fish were heard near the release site during the month after release, and were apparently alive based on their movement among and within pools in that section of the river. Classification of these fish as migrants will negatively bias the estimates for ocean survival.

In the only year for which we have a direct comparison (2002), the outmigration success of both species of hatchery migrants was lower than for wild steelhead. We estimated that only ~14% of hatchery steelhead and ~20% of hatchery coho salmon entered the ocean (c.f. 60% for wild steelhead). In other rivers, there is a relatively large body of evidence to suggest that hatchery-reared salmonids experience higher mortality following release than do their naturally reared counterparts (e.g., Einum and Fleming, 2001; Miller, 1954; Osterdahl, 1969; Raymond, 1988; Reisenbichler and McIntyre, 1977), likely due to differences in both behavioral and physical traits. For example, hatchery reared fish lack many predator avoidance strategies (Jaervi and Uglem, 1993; Olla and Davis, 1989; Suboski and Templeton, 1989). In the Columbia River estuary, Collis et al. (2001) found that hatchery reared steelhead were more vulnerable to predation by surface feeding Caspian terns during some years, yet predation by double-crested cormorants was similar for both hatchery and wild steelhead. These findings are consistent with other studies (Mason et al., 1967; Sosiak et al., 1979; Vincent, 1960) and suggest that hatchery reared fish spend a greater amount of time near the surface where they are more vulnerable to surface feeding birds, such as Caspian terns. Given this it would be interesting to compare the depth at which hatchery and wild steelhead migrate in the Nehalem. It would also be interesting to evaluate the behavior and survival of wild coho outmigrants, which could not be tagged at the time of the study due to their small size.

4.2. Relationship between migratory behavior and survival

A relatively significant proportion of hatchery coho salmon (20%) and hatchery steelhead (16%) that entered the estuary were likely consumed in the upper estuary, whereas none of the wild steelhead were lost in this region. Moore et al. (1995) reported that the migration of wild Atlantic salmon (*Salmo salar*) smolts in the river was primarily nocturnal. They further suggest that this may be an adaptation to reduce predation pressure from birds that feed during the day. However, the higher survival of the wild steelhead relative to hatchery steelhead and coho salmon in the upper part of the estuary does not appear to be related to the mean time of arrival into the estuary: 13:00 h for hatchery steelhead, 11:00 h for hatchery coho salmon, and 08:00 h for wild steelhead. Furthermore, we have never observed a diel pattern of downstream movement in either the Nehalem or Columbia River Estuaries. Based on the recovery of radio tags at a nearby cormorant colony, it is likely the majority of the coho that perished in the upper estuary were consumed by cormorants. We observed large numbers of cormorants swimming upriver near the middle of the estuary early during the outmigration season (April 1–30) in all 3 years. Our observations suggest that the birds work cooperatively to “herd” the fish into shallow areas in this upper section of the estuary. Interestingly, we did not recover any tags from hatchery steelhead at the colony, suggesting the birds may be selective for coho. However, very few radio tagged hatchery steelhead migrated to the estuary so we have little power to determine the origin of the predators.

The majority of the loss of hatchery and wild steelhead occurred in a relatively small zone (~1 km) near the mouth of the estuary. In the Nehalem, this region contains a large population of harbor seals,

which are known to consume significant numbers of juvenile salmonids in some areas (Laake et al., 2002; Olesiuk et al., 1995). The number of harbor seals has increased significantly throughout the Pacific Northwest since the implementation of the Marine Mammal Protection Act and numbers may now be at record levels (Carretta et al., 2007). Thus, it is conceivable that pinniped predation of juvenile salmonids is currently at levels not historically observed. Despite the correlation between mortality and the presence of harbor seals in the Nehalem we are unable to confirm whether the seals are a significant cause of mortality for the salmonids as we cannot rule out the influence of other predators in the near-ocean region of the estuary, the region of highest loss for steelhead. We observed very few avian predators in this region but we have no data on the degree of piscivory, which can account for a significant number of smolts in some areas (Beamish et al., 1992; Hvidsten and Mokkelgjerd, 1987; Larsson, 1985).

Given that hatchery coho salmon juveniles were often observed swimming upriver, we expanded the likely area of loss to include all regions downriver of PC. A high proportion (at least 40%) of the tagged coho salmon were consumed by cormorants in 2002. This compares with an overall estimate of 80% mortality (coho salmon) using acoustic telemetry. Taken together, these data suggest that predation by cormorants accounts for the majority of hatchery coho salmon that do not enter the ocean. We investigated whether the distribution of cormorants within the estuary changed over time during each of the three years, and was associated with the presence of hatchery fish. Early in the season it appears that the majority of the cormorants were foraging further up in the estuary near the town of Nehalem (data not shown). This trend has been observed over the three years, and we speculate that the distribution of cormorants during this part of the smolt outmigration may be a response to the release of hatchery fish at this time of the year. The numbers of cormorants tended to increase between PC and JF later in the season (after 1 May in 1999; after 14 May 2001/02), coincident with a decrease in cormorant numbers further up in the estuary. Thus, we hypothesize that the cormorants move into the estuary to take advantage of the increase in prey, then move further down the estuary once the majority of hatchery fish have passed through the upper region.

The area between PC and JF coincides with the freshwater/saltwater interface. It is thought that inadequately smolted fish are most likely to delay downstream movement in this region (Seals and Schreck, 2003), thus making them more vulnerable to predation. In the Columbia River, there is evidence that salinity structure has a strong effect on spatial distribution of forage fishes (including salmonids) (Zamon et al., 2010). Thus, the authors hypothesized that the tidal dynamics of river plumes may be a general structural mechanism affecting predator–prey interactions. The hatchery coho salmon spent considerably more time at the salt/freshwater interface than either type of steelhead. The wild and hatchery steelhead tended to move very quickly through this area of the estuary (<1 d). In general, their movement appeared to be correlated to the influence of the tidal cycle. Steelhead tended to move through the estuary on an outgoing tide and were stationary on a slack or incoming tide. The only holding behavior we observed for steelhead was due to the influence of the tides rather than any apparent ‘decision’ by the fish to remain in a particular area. In contrast, several coho salmon were regularly observed moving both up- and down-stream between the mid and lower estuary. Furthermore, several coho tended to hold in the lower part of the estuary for several days. This behavior may prolong the period of time that these fish are vulnerable to avian predators.

4.3. Management implications

To mitigate for the loss of salmonid migrants, options include the management of habitat or predators in the river and estuary. For example, one could manage habitat (physical and biotic components) in the lower river and estuary to increase survival in these areas. It is

likely that the quantity of structure providing both forage and cover opportunities for salmonids in the estuary was much greater historically. Woody debris was certainly more plentiful historically and dredging and drainage have likely simplified the habitat (Independent Multidisciplinary Science Team, 2002). Interestingly, we might also be able to increase survival in the ocean through upstream management. The “health” of a watershed is generally determined by the quantity of migrants produced. However, enumeration may not be a sufficient index of adult survival because fish quality is not considered. To illustrate this point, hatcheries produce a large number of fish, but it is generally accepted (Einum and Fleming, 2001; Miller, 1954; Osterdahl, 1969; Raymond, 1988; Reisenbichler and McIntyre, 1977) that survival of these fish is lower than wild fish. The same may hold true for wild migrants; different habitats may produce fish of different quality. Is it possible that seemingly good practices that increase fish abundance upstream could cause inadvertent problems by decreasing the quality of outmigrant fish, thereby lowering their survival after emigration. Hence, another management option might be to manage upstream habitat to produce fish with greater fitness which survive better in the open ocean (consistent with Bond et al. 2008). Beamish et al. (1992), discussed how changes in hatchery output and release schedule may lead to increased survival of these fish. The authors also point out that any changes may not result in immediate benefits as predators have adapted to the current level of releases. In 2001, but not 2002, the migration of the wild steelhead was closely linked to periods of precipitation and river flow. It is unclear what conditions contributed to these behavioral differences. However, given the influence of the physical characteristics of the catchment on river flow, efforts should continue to understand how such practices as deforestation and the resultant increase in the ‘flashiness’ of the river impact the migratory behavior of these fish. We collected physiological data from subsamples of fish during all years in an attempt to correlate habitat quality, physiology and behavior/survival. No correlation was ever shown between the measured parameters (cortisol and ATPase) and behavior or survival (unpublished data). This is likely due to the inherent difficulties in trying to relate physiology to behavior when using different groups of fish.

4.4. Assumptions of using telemetry to estimate survival

Using hydroacoustic telemetry to estimate predation loss depends on two basic assumptions: 1) untagged fish will survive at the same rate as tagged fish and 2) that any fish that perished did so because of predation rather than of other factors such as disease. A number of studies have demonstrated that tags do not compromise a fish's ability to avoid predators (Adams et al., 1998; Jepsen et al., 1998; Martinelli et al., 1998; Moore et al., 1990) or migrate (Ledgerwood et al., 2000; Ledgerwood et al., 2001; Schreck et al., 2001a, 2001b; Schreck et al., 2002a, 2002b). Similarly, it is unlikely that factors such as disease resulted in direct mortality given the low levels of BKD we observed and the short period of time between tagging and ocean entry or disappearance. However, we cannot rule out the possibility that the mortality of tagged fish was, in general, higher than for untagged fish.

4.5. Summary

We have shown that a large proportion of salmonid outmigrants may be lost prior to, or immediately upon entry, to the ocean. For hatchery coho salmon the loss appears to be attributable to predation by cormorants and may be exacerbated by their relatively long residence time in the estuary. It will be important to understand and incorporate this loss into models of ocean survival to ensure that recovery planning options target the areas most likely to yield benefits. Research that focuses on how upper-watershed effects contribute to downstream or ocean mortality may contribute to the

development of prioritized management plans intended to increase the survival of salmonids during their outmigration.

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