

Mortality Estimates of Juvenile Spring–Summer Chinook Salmon in the Lower Columbia River and Estuary, 1992–1998: Evidence for Delayed Mortality?

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Abstract.—Recovery of Endangered Species Act–listed salmonids in the Columbia River basin has relied upon the efficacy of the U.S. Army Corps of Engineer’s juvenile salmon transportation program to move fish past Snake and Columbia River hydropower dams. The effectiveness of this program has been assessed by the indirect method of comparing smolt-to-adult returns. We present some of the first data and mortality estimates of barged and run-of-river (ROR) radio-tagged juvenile spring–summer Chinook salmon *Oncorhynchus tshawytscha* after release in the lower Columbia River, representing years of study. Our data suggest that smolt mortality (1) is very low for ROR and barged fish between Bonneville Dam and the estuary proper, a migratory distance of 180 river kilometers (rkm); (2) occurs in the lower estuary (rkm 0–46); (3) varies more across dates within a year than between years or between passage types (barged or ROR); (4) increases with time within a season and increasing numbers of avian predators, including Caspian terns *Sterna caspia* and double-crested cormorants *Phalacrocorax auritus*; and (5) is estimated to be 11–17% of all smolts annually. Preliminary evidence suggests that at least some smolt mortality is influenced by differential predation by avian predators on Chinook salmon infected with *Renibacterium salmoninarum* and possessing low smoltification levels (relatively low gill Na⁺,K⁺-ATPase activity). Fish type (barged or ROR) did not appear to influence mortality because of avian predation. This project was also the first to identify avian predators as a major source of mortality for out-migrant Columbia River basin salmonids.

Pacific salmon stocks have declined severely after impoundment of the Snake and Columbia rivers by hydropower dams (Kareiva and Marvier 2000). Hydropower dams have subjected smolts to delays in migration, gas supersaturation in the tailraces of dams, injuries and stress associated with dam passage, and depredation in dam reservoirs (Raymond 1979; ISG 1996; Kareiva and Marvier 2000; Budy et al. 2002; NOAA Fisheries 2004). Smolts migrating from the Snake River pass through as many as eight dams before reaching the unobstructed waterway of the lower Columbia River and estuary (Figure 1). Muir et al. (2001) estimated an average mortality of 6–14% per project per year for hatchery spring–summer Chinook salmon *Oncorhynchus tshawytscha* during 1993–1998, as well as an estimated 66% surviving between the lower four Snake River dams and McNary Dam on the Columbia River and 31–59% surviving between Lower

Granite Dam (the uppermost dam the fish must pass on the Snake River) and Bonneville Dam (BON; lowermost dam) on the Columbia River.

In an effort to reduce in-river mortality, the U.S. Army Corps of Engineers transports a large portion of smolts around the dams by barge, releasing them downstream of BON. Ward et al. (1997) reviewed several studies by NOAA Fisheries between 1968 and 1989 and, based upon smolt-to-adult returns (SARs), concluded that barged juvenile salmonids survived in higher proportions than their in-river counterparts. More recent data (1995–1996, 1998) support this conclusion (NOAA Fisheries 2000). However satisfactory the initial estimates of low direct mortality may be for the transportation program, the more important problem appears to be the extent of delayed mortality that is realized from transportation stressors (Budy et al. 2002). Comparing SARs of transported fish with that of in-river migrants alone may not reveal the extent of delayed mortality.

Whereas transportation reduces the direct mortality of spring–summer Chinook salmon to approximately 2% versus 6–14% per project per year in comparison with run-of-river (ROR) fish (Muir et al. 2001; Budy et al. 2002), indirect or delayed mortality of barged fish may offset the balance in favor of ROR fish in some years (Budy et al. 2002). Congleton et al. (2000)

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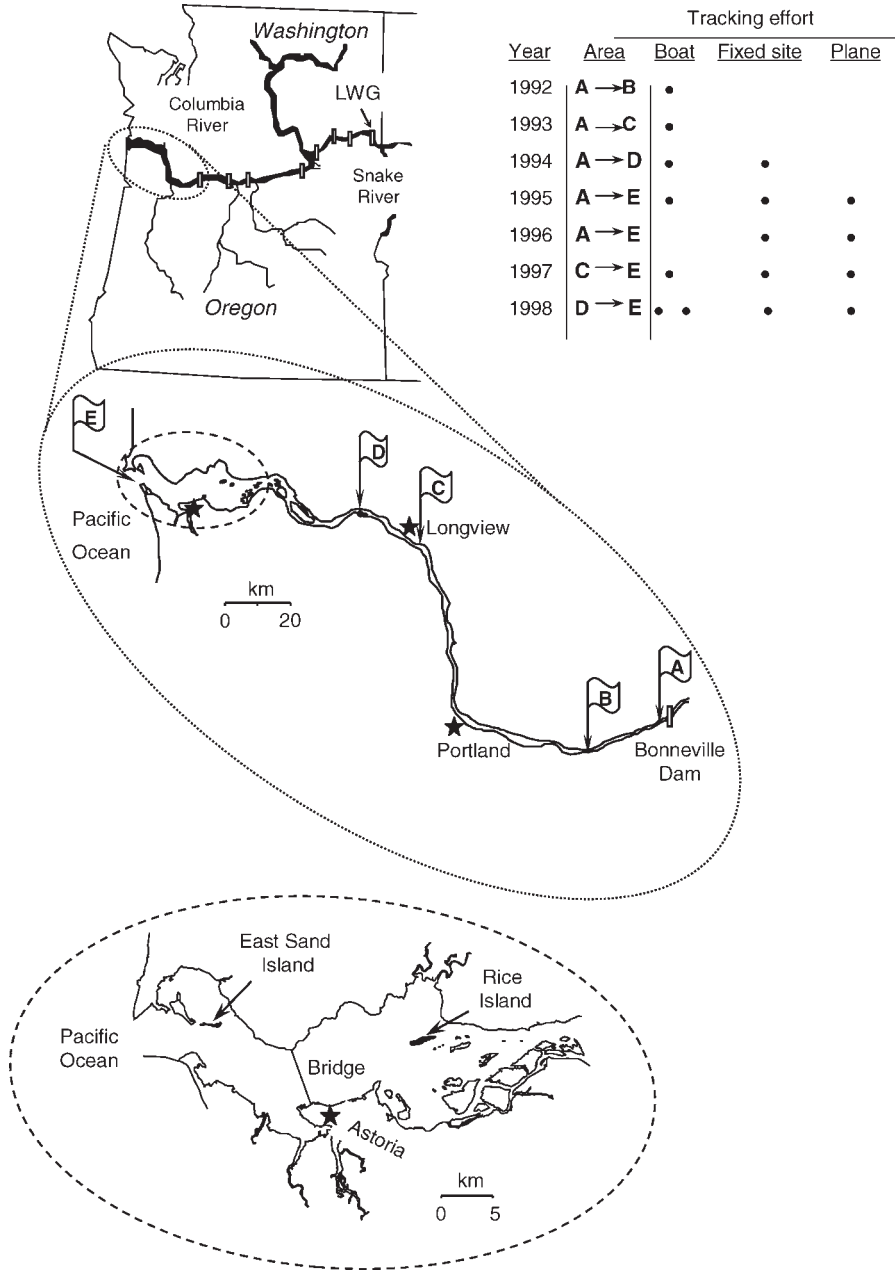


FIGURE 1.—Map of the Snake–Columbia River hydropower system. Vertical rectangles on the rivers indicate the eight hydropower dams passed by fish transport barges or run-of-river migrants from the Snake River basin. Lower Granite Dam (LWG) and Bonneville Dam are the first and last dams, respectively, where fish were radio-tagged. The first magnified image of the lower Columbia River and estuary shows the annual radio-tracking effort from Bonneville Dam (rkm 223) to the mouth of the Columbia River (rkm 0). Run-of-river fish were released at Bonneville Dam; barged fish were released at flag “A.” Flags indicate points where radio-tracking efforts began or ended and are referenced next to the corresponding year in the legend to indicate the area tracked for that year. The legend also indicates the level of effort within that study area. In 1998, two boats were used (indicated by two symbols). The lower magnified image shows the last 48 km of the Columbia River (lower estuary). The islands (Rice and East Sand) where radio tags were observed in avian predator colonies are indicated. These islands were surveyed during 1995–1998.

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reported high stress levels in spring–summer Chinook salmon that were correlated with barge loading densities and presence of steelhead *O. mykiss* in the barge holds, and Kelsey et al. (2002) further assessed the stressful impacts of cohabitation of spring–summer Chinook salmon with steelhead. Congleton et al. (2000) concluded that survival rates for Chinook salmon could be most impacted during midseason transportation, when steelhead densities were high.

Schreck et al. (1989) reported that transportation increases stress levels and can reduce SARs of coho salmon *O. kisutch*. Budy et al. (2002) summarized similar trends in SARs for spring–summer and fall Chinook salmon and steelhead from the Snake River during 1994–1998. In these cases, survival of transported fish was lower than for ROR fish (Budy et al. 2002).

The physiological impacts of dam passage by ROR fish are more intuitive than for transported fish. Stress levels are known to increase as fish travel through the collection system at a dam (Matthews et al. 1986; Maule et al. 1988). Barton et al. (1986) subjected juvenile Chinook salmon to sequential handling stresses and found that stress levels were cumulative. Maule et al. (1988) used a variety of physiological and performance tests to measure the effects associated with dam passage by ROR fish. They reported that stress levels increased sequentially as juvenile spring–summer Chinook salmon pass through the collection system of a dam but returned to pre-collection system levels within 24–48 h.

Evidence suggests that physiological stressors encountered during dam passage are realized as delayed mortality in the estuary or nearshore ocean (Budy et al. 2002; Wilson 2003). Stress resulting from dam passage can compromise a fish's energy reserves (Davis and Schreck 1997; Congleton et al. 2004), immune system (Maule et al. 1989; Schreck 1996; Maule and VanderKooi 1999), ability to smolt (Schreck 1982, 1992), and propensity to migrate (Clugston and Schreck 1992). Stress resulting from dam passage can be acute or chronic and accumulative and may lead to impaired physical abilities or even delayed mortality (Barton et al. 1986; Budy et al. 2002).

For the purposes of this paper, we refer to delayed mortality as physiological stress and concomitant aberrant behavior leading to death by predation (Mesa et al. 1994). Smolt predators are known to frequent areas where smolts experience stress and become concentrated for prolonged periods of time. These areas include the forebays and tailraces of dams, where rheotactic aberrations can cause smolts to aggregate or stress from dam passage can be manifested (Collis et al.

1995; Popper and Carlson 1998; Coutant and Whitney 2000; Budy et al. 2002). Estuarine influences including tides and the need to physiologically adjust to seawater can similarly slow smolt emigration, potentially causing them to reside for longer times than when migrating in-river (Moser et al. 1991).

Evidence exists for piscine (Ward et al. 1995; Beamesderfer et al. 1996; Zimmerman 1999), pinniped (Laake et al. 2002), and avian (Collis et al. 2001, 2002; Ryan et al. 2003) predation on smolts between BON (river kilometer [rkm] 232) and the Columbia River estuary (measuring from the mouth of the Columbia River). It is generally accepted that northern pike-minnow *Ptychocheilus oregonensis* are most abundant in the BON tailrace and lower Columbia River above the estuary (Kirm et al. 1986; Ward et al. 1995; Beamesderfer et al. 1996) and avian predators are most abundant in the Columbia River estuary (Collis et al. 2001); however, specific locations of smolt mortality by predators, if present, were unknown at the outset of our study.

Estimates of the number of smolts successfully migrating to the Columbia River estuary are often based upon hatchery release numbers, predicted river flows, estimated numbers of barged fish, and direct mortality of ROR fish from passive integrated transponder (PIT) tag detectors at dams (i.e., failure to detect a given fish past a certain point) and back-calculation from SARs (USACE 2000; Budy et al. 2002; Roby et al. 2003). Because no population counts occur between the time a smolt passes a dam and when it returns as an adult (NOAA Fisheries 2000), it is not known when or where the majority of this mortality occurs or its source.

The goal of our research was to estimate mortality rates for salmonid smolts out-migrating from the Snake River basin within the lower Columbia River and estuary before entry into seawater (but after passage of the Columbia River hydropower system) to understand where significant mortality between the last dam (BON) and the nearshore ocean occurs. We first evaluated immediate posttransport effects of barging within the release area downstream of BON. Immediate deleterious effects of barging were expected to be either the direct loss of fish caused by the stress of transportation or predation by high densities of piscivores known to inhabit the release area (Ward et al. 1995; Beamesderfer et al. 1996). After we found no mortality in the vicinity of the release area, we concentrated our efforts downstream and in the estuary to determine sources of delayed mortality. We also compared mortality rates for barged fish (potentially affected by transportation) and ROR fish (potentially

affected by passage through numerous dams). In 1998, we tested the hypothesis of delayed mortality by assessing the physiological condition of smolts collected from the hydropower system (barge holds and in-river migrants) and from Caspian terns *Sterna caspia* near a breeding colony in the Columbia River estuary.

Our general methodological approach was to use radiotelemetry to systematically track smolts downstream in a spatially explicit manner after their release below BON. This study is the first direct estimate of mortality of migrating juvenile salmonids in the lower Columbia River. By understanding the degree of mortality and where it occurs in the system, we are able to suggest management options to decrease direct and indirect sources of mortality of juvenile salmonids passing through the Columbia River hydropower system.

Methods

We first evaluated the immediate posttransport effects of barging within the release area downstream of BON. Immediate deleterious effects of barging were hypothesized to be (1) loss of smolts from stress associated with transportation or (2) predation by

piscivorous northern pikeminnow that are known to inhabit the release areas downstream of BON (Ward et al. 1995; Beamesderfer et al. 1996). In ensuing years, as tracking efforts progressed downstream (Table 1; Figure 1), our focus could best be described as exploratory science or assessing potential problem areas to successful smolt emigration and survival. During 1995–1998, attention was focused on mortality estimates from piscivorous bird colonies in the lower estuary (Figure 1).

For both mortality rate and detection efficiency, telemetry data were analyzed in four different categories: (1) barged versus ROR (paired releases; exploratory hypotheses); (2) barged releases only; (3) ROR releases only; and (4) all releases combined. These four options involved hypotheses of intra- and interseasonal variability in survival. We define mortality rate as the percentage of released fish detected two or more times at a given location over an extended period of time. Detection efficiency is defined as the percentage of released fish that were detected migrating downstream, that is,

$$H/N;$$

where

H = total number of fish detected after release

TABLE 1.—Radio-tracking protocol detailing the degree of effort and explicit tracking areas depicted in Figure 1. Tracking was done with 4- or 6-element Yagi antennas. All tracking efforts were done manually unless noted as “fixed sites.” Day 0 signifies the release day of juvenile Chinook salmon.

Year	Tracking duration	Tracking effort	Specific tracking area
1992	Days 0–2	Boat	A–B
1993 ^a	Days 0–4	Boat	A–C
1994	Day 0	Boat	A–B
	Days 1–4	Boat	A–D
	Days 1–4	Fixed site ^b	D
1995	Day 0	Boat	A–B
	Day 1	Boat	A–D
	Days 2–3c	Plane or boat	D–E
	Day 4	Plane or boat	A–D
1996 ^d	Days 1–4	Fixed site	D
	Day 0	Plane	A–B
	Days 1–5	Plane	A–E
1997 ^{d,f}	Days 1–4	Fixed site ^e	D
	Days 2–6	Plane	A–E
	Days 3–6	Boat	D–E
1998 ^{e,f,g}	Days 1–4	Fixed site ^e	D
	Days 1, 5	Plane	D–E
	Days 2–4	Plane or boat	D–E
	Days 1–4	Fixed site ^h	D

^aReleases 1–2 involved tracking from a release site downstream (A–C); releases 3–7 involved tracking from downstream to upstream (C–A).

^bOne anchored boat was used as the fixed site between rkm 86 and 88.

^cBoat tracking occurred during the first two releases and plane tracking occurred during releases 3–6.

^dAs fish moved downstream, the portion of the river tracked also moved downstream.

^eOnly year in which Federal Communications Commission regulations required the use of 1-element instead of 4-element Yagi antennas.

^fWhen fish were passing rkm 48, 2 flights/d were conducted.

^gEntire estuary was searched up to 2 times/d.

^hA terrestrial monitoring station near Stella, Washington (rkm 89), was utilized.

TABLE 2.—Summary of releases of radio-tagged spring–summer Chinook salmon into the lower Columbia River, 1992–1998. Origin of the fish includes hatchery (H) and fish of unknown (U) hatchery or wild origin. Barged fish (BRG) were collected from the Lower Granite Dam (LWG) juvenile fish facility (JFF; rkm 172 on the Snake River) and run-of-river (ROR) fish were collected from the Bonneville Dam (BON) JFF (rkm 234 on the Columbia River). Also shown are the number of releases within each year, the total number of tagged fish released for a given year, and mean fork length (FL) and weight (SEs for the latter two variables are given in parentheses). All radio tags were gastrically implanted following the protocol of Ward and Miller (1988).

Year	Species	Origin	Collection site	Treatment	Number of releases	Fish per release (range)	Mean FL (mm)	Mean weight (g)
1992 ^a	Chinook salmon	U	LWG JFF	BRG	5	27 (4–8)	191 (2.5)	65.2 (2.3)
	Steelhead ^b							
1993 ^c	Chinook salmon	U	BON JFF	ROR	0	7	51 (4–8)	149 (1.7)
	Steelhead ^b	U	LWG JFF	BRG				
1994 ^c	Chinook salmon	U	BON JFF	ROR	0	80 (40)	139 (0.7)	27.5 (0.5)
	Chinook salmon	U	LWG JFF	BRG				
1995 ^c	Chinook salmon	U	BON JFF	ROR	5	186 (34–40)	141 (0.7)	28.2 (0.4)
	Chinook salmon	U	LWG JFF	BRG				
	Chinook salmon	U	BON JFF	ROR				
1996 ^c	Chinook salmon	H	LWG JFF	BRG	6	224 (35–39)	142 (0.7)	30.0 (0.5)
	Chinook salmon	U	BON JFF	ROR				
1997 ^c	Chinook salmon	U	BON JFF	ROR	7 ^b	112 (12–25)	153 (1.4)	36.3 (1.1)
	Chinook salmon	H	LWG JFF	BRG	6	210 (30–39)	152 (1.1)	37.6 (0.9)
	Chinook salmon	U	BON JFF	ROR	3	97 (30–34)	157 (1.6)	38.9 (1.3)
1998 ^{c,d}	Chinook salmon	H	LWG JFF	BRG	10	207 (14–26)	145 (0.7)	32.5 (0.5)
	Chinook salmon	U	BON JFF	ROR				

^aUsed beeper tags (Lotek Wireless, Inc., Newmarket, Ontario; 3.3 g in air, 18-d minimum battery life).

^bSimilar-sized steelhead were used in lieu of Chinook salmon in some releases because of limited availability.

^cUsed beeper tags (ATS; 1.2 g in air, 7-d minimum battery life).

^dIn 1998, 34 of the 207 radio tags used were pressure-sensitive depth tags (ATS; 1.9 g in air, 7-d minimum battery life). Depth data were illogical; therefore, tag detections were used only for mortality and efficiency estimates.

($D + e$), D = number of initial, novel detections upstream, e = number of secondary, novel detections downstream, and N = number of fish released.

Fish Collection and Tag Implantation

Barged spring–summer Chinook salmon were collected from Lower Granite Dam and ROR fish were collected from BON (Table 2). Fish were anesthetized with tricaine methanesulfonate (MS-222) buffered with NaHCO_3 and gastrically implanted with radio tags following the protocol of Ward and Miller (1988). Of all fish tagged during 1992–1998, weight of the radio tag ranged from 1.1% to 7.6% of fish body weight, averaging 3.1–4.9%. For fish implanted with the pressure-sensitive (depth) tags in 1998, minimum fish size was more than 27 g, meaning that these tags were less than 7.0% of the weight of the fish. All fish were within recommended limitations of tag size-to-body

weight ratios (Brown et al. 1999; Jepsen et al. 2005) for the objectives of this study.

Recovery

Barged fish.—After tag implantation, up to 8 fish were placed into covered rubber containers (125 L) with flow-through holes, and the containers were secured into barge holds. Fish were allowed to recover for 12–24 h. During this time, fish were checked for tag regurgitation or fish recovery problems 1 and 4 h posttagging and just before release into barge holds. Fish that regurgitated tags or died (such individuals were extremely rare) were replaced with other tagged fish. Before release into barge holds, implanted radio tags were again checked for transmission and detection ability. Tagged fish were released below BON in the Columbia River as part of the normal barge release (Figure 1).

Run-of-river fish.—After tagging, fish were held in

covered rubber containers (125 L) supplied with a constant supply of water. Fish were allowed to recover for 24–48 h before release and were checked periodically for tag regurgitation or recovery problems. After recovery, ROR fish were released into the juvenile bypass system at approximately the same time as the paired release group of barged fish was being released downstream of BON. Again, all tags were checked for functionality before release.

Releases

In general, the number of release groups and the number of tagged fish within those groups increased with each successive year (Table 2). Releases occurred during late April to early June, covering the period of peak out-migration. During 1995–1998, ROR fish releases were paired with barged fish releases late in the migration season. Releases of ROR fish started later in the season than those with barged fish because of the considerably longer time it takes migrants from the Snake River system to reach BON compared with those artificially transported.

Aircraft Tracking Protocol: 1995–1998

The tracking range from aircraft (0.4–1.6 km) was greater than that on boats (about 150 m; verified by preliminary experiments with known distances). The broad signal reception range from the aircraft was conducive to covering large areas of river over a short period of time. Planes flew transects so that the entire estuary and river were covered.

Establishing Mortalities on Piscivorous Bird Colonies: 1995–1998

During 1995, detections of radio-tagged Chinook salmon below rkm 89 were considered mortalities if they were heard two or more times in the exact same location (typically associated with land) on a given day or on subsequent days. During 1996–1998, tracking efforts included close observations of piscivorous bird colonies on Rice (rkm 35) and East Sand (rkm 5) islands or the wooden pilings nearby.

Data Reduction

All detections were individually screened for illogical data. Illogical data included simultaneous detections of a tag in two widely separated locations. During 1996, 1.5% of all tags (5 of 340 tags) were removed from the data set, and in 1997, 1.0% of all tags (3 of 304) were removed as a result of this protocol. Two additional radio-tagged fish, representing 0.7% of the 1997 sample, were removed because of tag failure.

Smoltification and Disease Status

Spring–summer Chinook salmon were collected at three locations in 1998: (1) on the barge downstream of BON (barged fish); (2) at BON (ROR fish); and (3) from avian predators (Caspian terns) near the breeding colony on Rice Island (transportation history unknown; hereafter termed “avian prey” fish). All fish were analyzed for smoltification (gill Na^+, K^+ -ATPase [enzyme number 3.6.1.36; IUBMB 1992] activities; hereafter termed “ATPase”) and disease (bacterial kidney disease [BKD; *Renibacterium salmoninarum*]) status. A total of 138 fish were collected from the bills of Caspian terns returning to Rice Island in the lower Columbia River estuary; only 9 of these were spring–summer Chinook salmon. Of the 9 fish, 3 had insufficient gill tissue to analyze for ATPase and 1 was below detection limits for *R. salmoninarum* infection. Collected fish were still alive or moribund. Birds were taken that visually were transporting a fish back to the colony. Barged and ROR fish were compared with avian prey fish collected from Rice Island to test the hypothesis that unsmolted and diseased Chinook salmon are more vulnerable to avian depredation.

Fish were immediately euthanatized with an overdose of MS-222 anesthetic buffered with NaHCO_3 . Fork length (FL) and weight were measured and gill filaments and kidneys were harvested. Gill filaments were placed into a buffered solution of sucrose, EDTA, and imidazole (Zaugg 1982) and then frozen on dry ice; kidneys were also frozen on dry ice. Gill filaments were sent to the U.S. Geological Survey [USGS] Northwest Science Center, Columbia River Field Station, for analysis of ATPase following a modified technique from Johnson et al. (1977). Kidneys were sent to the Northwest Science Center (Seattle) for analysis of the presence and severity of *R. salmoninarum* following the enzyme-linked immunosorbent assay (ELISA) technique of Pascho et al. (1993).

Data Analyses

For radio-tagged fish, we analyzed differences in mortality estimates and detection efficiencies. To calculate the proportion of mortality, we divided the number of radio tags detected on piscivorous bird colonies or pilings in the Columbia River estuary by the total number of fish released during 1995–1998, the years when work was done in the lower estuary and mortality was detected. Detection efficiencies were calculated by dividing the number of fish detected after release by the total number released. These efficiencies were used to determine the proportion of fish that successfully migrated downstream to a given point.

The distance downstream of the release site varied among years, but was consistently assessed during 1995–1998 near rkm 88 (Figure 1). Analyses were the same as those for mortality estimates, except all data (1992–1998) were used. Detection efficiencies were analyzed to determine whether tracking effort was consistent between years. We realized that our estimates of mortality would probably underestimate the true mortality rates because some dead individuals would go undetected; thus, our values represent a conservative index of mortality.

Because mortality and detection efficiencies are proportions, a logistic regression was used (Lewis 2004). Data were analyzed with the PROC GENMOD procedure in the SAS statistical package (SAS Institute 1996) and the natural log of the odds (logit link; Christensen 1990). Mortality and detection efficiency were included as response variables in the model. For a given release of barged or ROR fish, the variables were as follows:

$$\text{Logit}_{ij} = \log_e \left(\frac{P_{ij}}{1 - P_{ij}} \right),$$

where

i = specific release;

j = type of fish (barged, ROR, or both pooled);

$P_{ij} = R_{ij} / N_{ij}$;

R_{ij} = response variable (M_{ij} or H_{ij});

N_{ij} = number of fish released;

M_{ij} = number of fish taken by avian predators; and

H_{ij} = total number of fish detected after release.

The “ P ” was used for graphical representation of the data, the standard error (SE) of which under the logistic regression is

$$\text{SE}(P) = \sqrt{\frac{P(1-P)}{N}}.$$

The test used for the logistic regression was the χ^2 statistic, unless data were over- or underdispersed (determined if $P_D < \alpha_{\text{one-tailed}} = 0.025$, where P_D is the P -value for over- or underdispersion), in which case the SEs were adjusted and the more conservative F -statistic was used.

For mortality estimates and detection efficiency, radio-tag data were analyzed in four different sets: (1) barged versus ROR (paired releases), (2) barged releases only, (3) ROR releases only, and (4) all releases combined.

The first data set was used to compare mortality and detection efficiency by barged and ROR fish type. This set included data from releases when barged and ROR fish were paired (1995–1998). With this data set, the independent factors in the model were fish type (barged or ROR) and release date as categorical variables

within years. Across years, we analyzed the effects of fish type, release date within years, and year.

We analyzed the effects of release date on mortality and detection efficiency; release date was a continuous variable based on day of year to achieve adequate degrees of freedom within and across years. Interactions or linear and quadratic effects were analyzed for all data sets.

Contingency tables (row \times column) were constructed with the tag–body weight ratios being placed in rows and the proportion (for each ratio) detected on the piscivorous avian colonies in the Columbia River estuary being placed in columns. The χ^2 test was used to test whether greater tag weight-to-body weight ratios rendered smolts more vulnerable to avian predation during 1995–1998, as judged by the occurrence of the tags at pilings or in bird colonies.

For data representing physiology of fish in 1998, three tests were used: (1) multifactor analysis of variance (MANOVA), (2) Fisher’s least significant difference (LSD), and (3) Kruskal–Wallis (K–W). The MANOVAs were used to test for differences with respect to the severity of BKD infection or the level of ATPase activity with fish type (barged, ROR, and avian prey). Fisher’s LSD was used to test for pairwise differences. If the assumptions of equal variances for MANOVA were not met, the nonparametric K–W test was conducted. To reflect the nature of the prey base that was available, data from barged and ROR fish were pooled and compared with avian prey fish that were captured by Caspian terns below BON. Knowing the exact nature of the physiology of the fish when they entered the zone of predation is imprecise because the data reflect fish sampled over 100 km upstream.

Results

No mortality was observed within the barge holds or in the river at the time tagged fish were released during any year. These observations included extensive use of an underwater video camera to visualize fish in barge holds when only a few dead individuals were detected relative to the tens of thousands of fish observed. When the release area was intensively radio-tracked during 1992–1995, radio-tagged fish rapidly emigrated from the area after release, generally moving more than 0.8 km within 15 min. During 1992–1994, no mortality was evident within the study area (Figure 1; area between A and B).

Mortality Estimates

A total of 11–17% of all radio-tagged smolts released each year during 1995–1998 were detected on the piscivorous bird colonies on Rice and East Sand

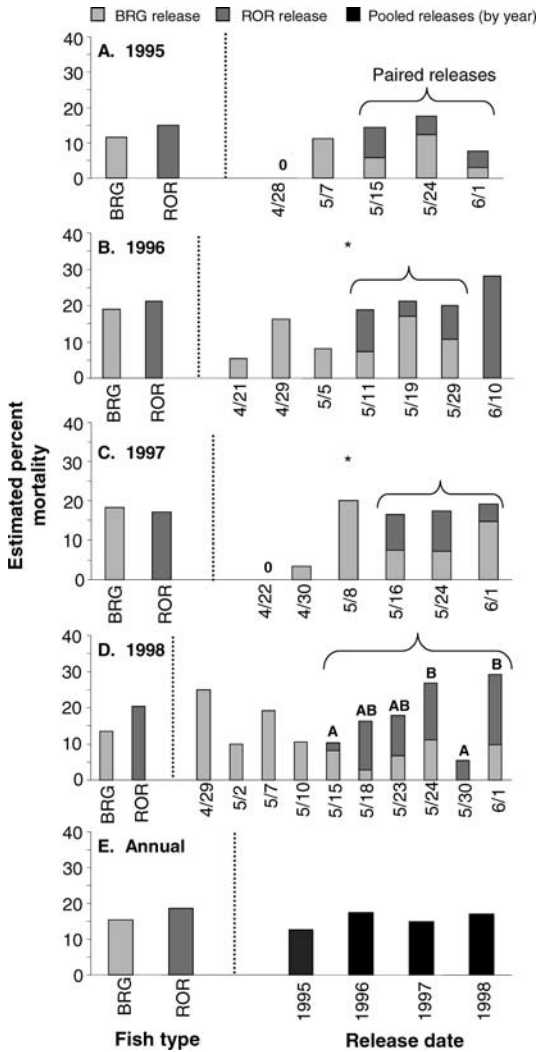


FIGURE 2.—Estimated mortality (percentage of released fish detected two or more times within a given location) of radio-tagged spring-summer Chinook salmon between Bonneville Dam (rkm 234) and the Columbia River estuary (rkm 0), 1995–1998. Data for 1992–1994 are not shown because there was no mortality observed within the study sites. To the left of the dotted vertical line in all figures are the pooled values of barged (BRG) and run-of-river (ROR) fish for the (A–D) given year or (E) all years. To the right of the dotted line in (A–D) are the barged and ROR data sets by release dates. No estimated mortality is indicated with a “0” above the date for a given release. To the right of the dotted bar for all years (E) are the pooled values for the respective year. For paired barged and ROR releases (indicated by brace), each graph corresponds to a logistic regression model, the two sections of each graph being the two factors tested (i.e., BRG or ROR or release date or year). Releases were used as a continuous factor and years were used as a categorical factor in the logistic regressions to see whether mortality changed across release dates or years. Asterisks indicate a significant

difference ($P \leq 0.05$) in mortality across dates. Different letters indicate significant differences in mortality with respect to individual release dates.

islands. Mortality by fish type, release, and year are shown in Figure 2. All mortalities were attributed to avian predators, and in 1995, approximately 21% of all estimated mortalities were observed between Jones Beach (rkm 75) and Jim Crow Point (rkm 46); the remaining mortalities were observed below rkm 46 throughout the estuary. These mortalities were often associated with pile dikes frequented by birds and were also associated with the periphery of Rice (rkm 35) and East Sand (rkm 8) islands.

During 1996–1998, all mortalities were found on Rice and East Sand islands. The majority of mortalities occurred on Rice Island, where 74–77% of all mortalities consistently occurred here and 26–23% occurred on East Sand Island in individual years (1996–1998).

Paired Releases (Barged versus ROR)

During 1995–1998, there were few differences in mortality or detection efficiency among paired releases (Table 3; Figures 2e and 3h). Estimated mortality in the estuary below rkm 89 ranged between 5% and 29% for individual paired releases (Figure 2A–D) and were 15–19% by fish type across years (Figure 2E). Annual estimated mortality for barged fish ranged from 12% to 19%, whereas ROR fish ranged from 15% to 21% (pooled releases by fish type and year; Figure 2A–D). Annual detection efficiencies ranged between 74% and 98% for individual paired releases (Figure 3A–G) and across years were 91–84% by fish type (Figure 3H). There were no differences between releases or barged versus ROR fish types (χ^2 : $P = 0.0716$; Table 3; Figure 2D). Mortality increased with each release in 1998; the exception was the second to last release, when mortality was very low (Table 3; Figure 2D). Also, detection efficiency differed between releases (χ^2 : $P = 0.0186$) and fish types, decreasing with each release; the exception was the last release in which most fish were detected (χ^2 : $P = 0.0030$; Table 3; Figure 3G). Detection efficiency for barged fish was higher than for ROR fish (Table 3; Figure 3G).

Differences in mortality estimates and differences in detection efficiencies through time occurred only in 1998. Differences in mortality estimates among releases were evident (χ^2 : $P = 0.0340$), but probably not between barged and ROR fish types (χ^2 : $P = 0.0716$; Table 3; Figure 2D). Mortality increased with each release in 1998; the exception was the second to last release, when mortality was very low (Table 3; Figure 2D). Also, detection efficiency differed between releases (χ^2 : $P = 0.0186$) and fish types, decreasing with each release; the exception was the last release in which most fish were detected (χ^2 : $P = 0.0030$; Table 3; Figure 3G). Detection efficiency for barged fish was higher than for ROR fish (Table 3; Figure 3G).

difference ($P \leq 0.05$) in mortality across dates. Different letters indicate significant differences in mortality with respect to individual release dates.

TABLE 3.—Summary of statistical analyses of mortality estimates and detection efficiencies for radio-tagged spring–summer Chinook salmon emigration between Bonneville Dam (BON; rkm 234) and the Columbia River estuary (rkm 0), 1992–1998. The “Data” column indicates the data set used in the respective analyses and “BRG/ROR” indicates only paired releases of barged (BRG) and run-of-river (ROR) fish that were used in analyses. For all other analyses, all releases of BRG, ROR, or pooled BRG and ROR smolts were used. For model factors, “Release” indicates different releases as a categorical variable (e.g., release 1, 2, 3, etc.) and “Date” indicates different releases as a continuous variable. “Type” is the effect of fish type (BRG and ROR; only present in analyses of “BRG/ROR” data). Tests used in the logistic regression (χ^2 if the data were not dispersed or F -test if they were dispersed) are given. “Figure” denotes the panel on Figure 2 or 3 where the data involved in the statistics can be visualized.

Response variable	Data	Year(s)	Model factors	df	P	Test	Figure
Mortality	BRG/ROR	1998	Release	5	0.0340	χ^2	2D
			Type	1	0.0716		
	BRG/ROR	1995–1998	Year	3	0.3144	χ^2	2A–D
			Release (year)	11	0.1662		
			Type	1	0.1306		
	BRG	1996	Date	1	0.0255	χ^2	
			Date	1	0.0018		
	BRG	1995–1998	Year	3	0.8714	F	
			Date	1	0.0457		
	Pooled data	1996	Date	1	0.0078	χ^2	2B
			Date	1	0.0064		
	Pooled data	1997	Date	1	0.0064	χ^2	2C
			Date	1	0.0017		
	Pooled data	1995–1998	Year	3	0.3932	χ^2	2E
Date			1	0.0017			
Efficiency	BRG/ROR	1998	Release	5	0.0186	χ^2	3G
			Type	1	0.0030		
	BRG/ROR	1995–1998	Year	3	0.9695	F	3D–G
			Release (year)	11	0.4934		
			Type	1	0.1546		
	BRG	1992–1998	Year	6	0.0238	F	3H
			Date	1	0.0256		
	ROR	1995	Date	1	0.0001	χ^2	
			Date	1	0.0062		
	Pooled data	1995	Date	1	0.0458	χ^2	3D
			Date	1	0.0001		
	Pooled data	1992–1998	Year	6	0.0824	F	3H
			Date	1	0.2036		

Separate Barged and ROR and Pooled Releases

Because all releases are included when individual fish types and both types combined were analyzed for trends, the variability in mortality estimates and detection efficiencies increased between years and for releases within years (Figures 2 and 3). For releases of either barged or ROR fish, mortality rates within years ranged from 0% to 28% (Figure 2A–D), but were 15–19% across years (Figure 2E). Overall mortality rate for all years combined was 15% for barged smolts, 18% for ROR smolts, and ranged from 11% to 17% when smolts were pooled within years (Figure 2E). Detection efficiency (the probability of detecting a fish once it has been released) among individual releases ranged from 48% to 100% (Figure 3A–G) and from 78% to 98% across years (Figure 3H).

Although overall total mortality did not change between years, within certain years there was a consistent increase in mortality through time. In 1996 and 1997, mortality of barged (χ^2 : $P = 0.0255$ and $P = 0.0018$, respectively) and barged and ROR pooled (χ^2 : $P = 0.0078$ and $P = 0.0064$, respectively; Figure 2B–C) increased significantly through time (Table 3).

No differences existed between years for either barged or ROR fish type (Table 3). There was a significant effect of date on mortality for both barged (F -test: $P = 0.0457$) and pooled (χ^2 : $P = 0.0017$) fish types, where fish at the end of the run experienced more mortality.

There were no differences in detection efficiency among releases within years for barged fish. However, differences did exist between years (F -test: $P = 0.0238$; Table 3) and efficiency changed with date (F -test: $P = 0.0256$; Table 3). In 1995 ROR efficiency decreased through time (χ^2 : $P = 0.0001$; Table 3) and in 1996 ROR efficiency increased through time (χ^2 : $P = 0.0062$; Table 3). For pooled analyses, in 1995 efficiency decreased through time (χ^2 : $P = 0.0458$; Table 3; Figure 3D) and in 1997 efficiency increased through time (χ^2 : $P = 0.0001$; Table 3; Figure 3F). There were no differences in efficiency across years for ROR or pooled fish combined (Figure 3H).

The effect of tag weight-to-body weight ratios on vulnerability to avian predation appeared somewhat variable (Figure 4). There was no significant difference in the proportion of fish with larger tag-to-body weight ratios detected on the piscivorous bird colonies in each

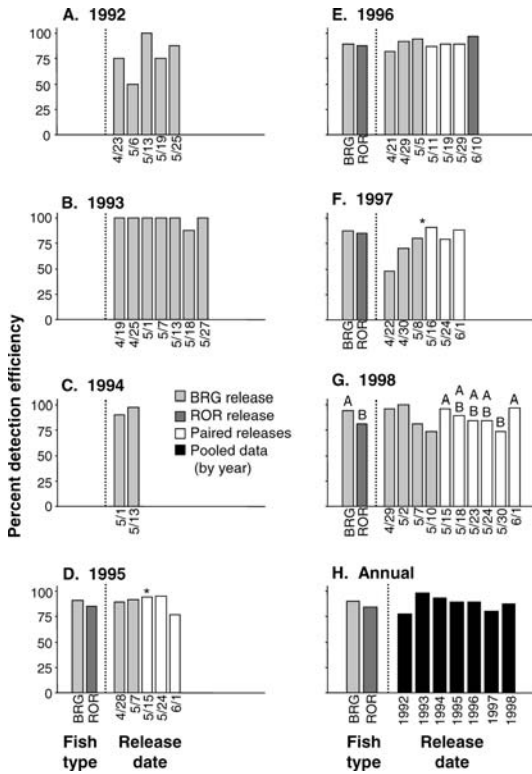


FIGURE 3.—Detection efficiencies (percentage of released fish that were detected migrating downstream) for radio-tagged Chinook salmon between Bonneville Dam (rkm 234) and the Columbia River estuary (rkm 0) for (A–G) particular dates in 1992–1998 and (H) on an annual basis. Detection efficiencies for paired releases (1995–1998) of barged (BRG) and run-of-river (ROR) fish are shown with all data pooled together. Paired releases are indicated with white bars. Graph and statistical descriptions are the same as for Figure 2. Panels (D–G) correspond to Figure 2A–D, panel (H) to Figure 2E.

of the years examined (χ^2 : 1995– $P = 1.0000$, $df = 14$; 1996– $P = 0.0822$, $df = 9$; 1997– $P = 0.6871$, $df = 10$; 1998– $P = 1.0000$, $df = 14$).

Smoltification and Disease Status

Three of the 9 spring–summer Chinook salmon obtained from Caspian terns returning to Rice Island were positively identified as hatchery fish. Five others were unclipped and, thus, could represent wild or hatchery fish. The marking status of 1 individual was indistinguishable. Of these 9 fish, BKD status could be measured in 8 individuals and gill ATPase activity could be measured in 6. Eighty-eight percent (7 of 8) of the Chinook salmon taken by Caspian terns were infected with *R. salmoninarum*, the causative agent of BKD. Hatchery barged fish (57%; 41 of 72) were

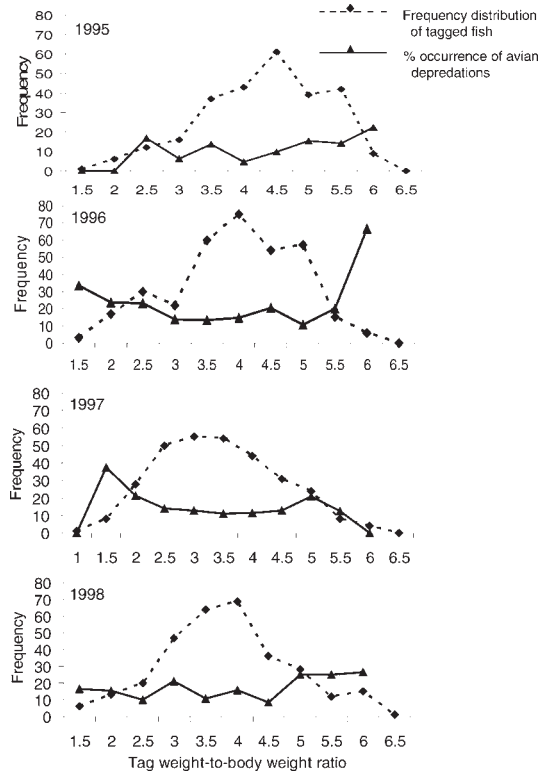


FIGURE 4.—Frequency (by number) of tag weight-to-body weight ratios at release for all radio-tagged spring–summer Chinook salmon (dotted lines) and the percentage of mortality via piscivorous birds during 1995, 1996, 1997, and 1998. Four tagged fish (for which no avian depredations were observed) were tagged at ratios of 6.5–8.5% during 1998 (data not shown). During 1995, the percentage of mortality was determined by recurring detections of radio tags below rkm 89 (Columbia River estuary); during 1996–1998, the percentage of mortality was determined by recurring detections of radio tags on avian colonies (either Rice [rkm 35] or East Sand [rkm 8] islands). The effect of tag weight-to-body weight ratios greater than 5% on vulnerability to avian predation was not significant (χ^2 test; 1995: $P = 1.0000$; 1996: $P = 0.0822$; 1997: $P = 0.6871$; 1998: $P = 1.0000$).

comparable with ROR fish (64%; 28 of 44) in infection rates (Figure 5). Twenty-five percent (2 of 8) of the fish captured by Caspian terns had medium or high levels of BKD compared with 11% (5 of 44) for ROR fish and 8% (6 of 72) for barged fish (Figure 5) in the population available as prey. There was no difference in fork length of fish captured by birds or sampled by us at BON (barged and ROR) for either *R. salmoninarum* infection (K–W: $P = 0.1635$) or gill ATPase activity (K–W: $P = 0.1358$; Table 4; Figure 6), suggesting that differences in smoltification or disease were not attributable to a body-size effect on the fish

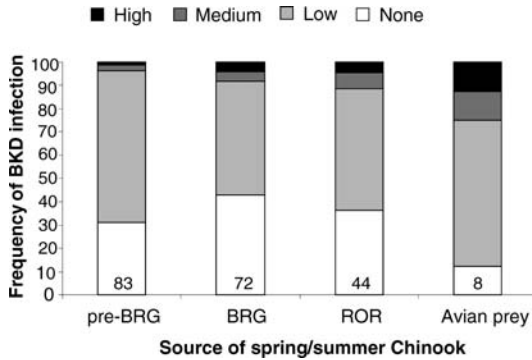


FIGURE 5.—Proportion and severity of infection levels of *Renibacterium salmoninarum*, the causative agent of bacterial kidney disease (BKD) of spring–summer Chinook salmon collected from the Lower Granite Dam fish collection facility (Snake River) 456 km above Bonneville Dam (pre-BRG; data shown for comparison only), from barge holds (BRG; rkm 234), from the Bonneville Dam fish collection facility (run-of-river [ROR]; rkm 234), and from the bills of Caspian terns on Rice Island (rkm 35) in the Columbia River estuary (avian prey). Sample size is indicated at the bottom of each bar. Fish were categorized into one of three disease levels (low, medium, and high) based upon Pascho et al. (1993). The BKD levels were significantly higher in avian prey fish than in barged or ROR fish (Fisher's LSD: $P < 0.050$; see also Table 4).

BKD levels, which were significantly higher in fish captured by Caspian terns in comparison with barged and ROR fish (Table 4; Fisher's LSD: $P < 0.050$). Gill ATPase activity levels were significantly lower in avian prey compared with barged and ROR fish (Table 4; Figure 7; Fisher's LSD: $P < 0.050$). Three of the spring–summer Chinook salmon collected from the bills of Caspian terns late in the out-migration season (June–July) had the lowest ATPase activity levels.

Discussion

The goal of our study was to estimate mortality of barged and ROR spring–summer Chinook salmon smolts in the lower Columbia River and estuary to

understand if and where mortality occurs. We found that 11–17% of all smolts, by year, were taken by avian predators in the Columbia River estuary downstream of rkm 75 during 1995–1998. These are minimum mortality estimates because they do not account for predation and subsequent deposition of radio tags beyond our detection range (i.e., in deep water, seawater, or outside of our search area) or other potential sources of mortality. During 1996–1998, all mortalities were associated with Rice (rkm 35) and East Sand (rkm 8) islands in the Columbia River estuary, where there were large Caspian tern and double-crested cormorant *Phalacrocorax auritus* colonies, respectively. The initial years of our study (data starting in 1995) were the first to document mortality attributable to the birds associated with specific estuarine islands as major sources of salmonid mortality. This is also the only study demonstrating that these birds are the primary proximate sources of mortality for peripartetic juvenile salmonids between BON and the Pacific Ocean.

Because of our ability to detect migrating fish in the lower Columbia River and estuary (i.e., $\geq 78\%$ detection efficiency per year) and pinpoint mortalities (recurring tag detections in one location over extended periods of time), it seems likely that any fish not observed as a mortality in the estuary could have migrated successfully through the estuary. By this premise, a maximum of 83–89% of all tagged fish during 1995–1998 migrated successfully through the Columbia River estuary. However, further research is necessary to verify these survival estimates.

All tags were known to be functioning immediately before release, so undetected fish are probably the result of (1) fish that died after release and sank out of radio range, (2) fish that were taken by predators and whose remains were deposited out of radio range, (3) regurgitated tags that sank out of detection range, or (4) individuals that migrated successfully but were not detected. Tag signal transmission in the Columbia River is impeded at depths greater than 5 m, and we have generally found that radio tags cannot be heard

TABLE 4.—Mean values of variables related to smoltification and bacterial kidney disease in spring–summer Chinook salmon collected from the bills of Caspian terns on Rice Island at rkm 35 in the Columbia River estuary (avian prey); from barge holds (BRG); and from the fish facility at Bonneville Dam (ROR) at rkm 234. Variables are as follows: gill Na^+, K^+ -adenosine triphosphatase (ATPase; $\mu\text{mol P}_i \cdot \text{mg protein}^{-1} \cdot \text{h}^{-1}$), weight (g), FL (mm), and infection with *Renibacterium salmoninarum* (BKD; ELISA absorbance).

Fish source	Origin ^a	Smoltification		Disease	
		ATPase	N	BKD	N
Avian prey	H, W	23.13 (3.13)	6	0.476 (0.319)	8
BRG	H	31.50 (1.58)	67	0.186 (0.040)	72
ROR	H	29.06 (1.79)	40	0.195 (0.052)	44

^aH = hatchery, W = wild; the exact origin of the latter is unknown.

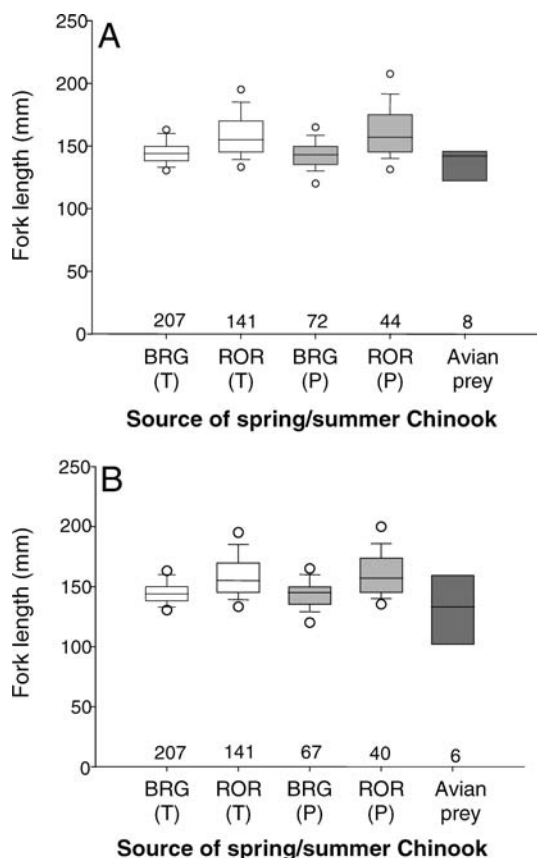


FIGURE 6.—Fork lengths of spring–summer Chinook salmon collected between Bonneville Dam (rkm 234) and the lower Columbia River estuary (rkm 0) that included barged fish (BRG), run-of-river fish (ROR), fish taken from the bills of Caspian terns on Rice Island (avian prey), telemetry (radio-tagged; T), and Chinook salmon from which physiological samples were taken (P) to assess the presence of (A) bacterial kidney disease (*Renibacterium salmoninarum*) and (B) smoltification status (Na^+ , K^+ -ATPase activity). Boxes represent 25th–75th percentile ranges, horizontal lines within boxes are the median fork lengths, vertical lines above and below the boxes are the 10th–90th percentile ranges, and the dots depict the 5th–95th percentile ranges. Sample size is shown at the bottom of each graph.

within the brackish environment of the lower estuary (rkm ≤ 22). The tags we used had minimum battery lives of 7 d (our experience is that battery life is typically considerably longer), and recent data collected by our laboratory indicate that a small number of spring–summer Chinook salmon may take as long as 30 d to exit the lower Columbia River (Schreck et al. 2005).

Immediate postrelease survival for barged or ROR smolts was near 100% for all years (1992–1998), suggesting that any negative effects of transportation or

dam passage were not immediately realized within the 2- to 4-d travel time between the release site and the river–estuary transition area at rkm 89. This was surprising, given that northern pikeminnow are known to aggregate in areas of high smolt density, such as at the barged and BON release sites, and are estimated to consume 5% (9.7 million) of all smolts between BON and the Columbia River estuary (Poe et al. 1991; Collis et al. 1995; Beamesderfer et al. 1996).

Northern pikeminnow prefer slow-water habitat, suggesting that they do not frequent the open stretch of faster water away from shore (Scott and Crossman 1973; Mesa and Olson 1994; Ward et al. 1997) where our radio-tagged fish were released. Most Chinook salmon moved rapidly away from the barge release sites, moving more than 0.8 rkm within 15 min. This rapid exodus took these fish past areas known to be high in northern pikeminnow abundance (Ward et al. 1995; Beamesderfer et al. 1996).

During the years in which the lower estuary was scanned for radio tags (1995–1998), we estimated significant mortality (11–17%) of out-migrating Chinook salmon in the Columbia River estuary as evidenced by recurring tag detections on pilings and on the piscivorous Caspian tern and doubled-crested cormorant colonies of Rice and East Sand islands. Tag detections on these islands were corroborated by visual observation of numerous tags lying on the surface of the bird colonies. Mortalities were linked to known colonies and, thus, could be linked to avian predation, except in 1995, when 21% of all estimated mortalities were observed between Jones Beach (rkm 75) and Jim Crow Point (rkm 46). Although northern pikeminnow are abundant in this area, smolts have not been found in diets of these fish at this river reach (Kirm et al. 1986). Therefore, we attributed these mortalities to avian predation and subsequent tag expulsion in this area.

Approximately 74–77% of smolt mortalities were consistently found on or near Rice Island (large Caspian tern colony and smaller gull *Larus* spp. and double-crested cormorant colonies) and the remainder were found in association with East Sand Island (double-crested cormorant and gull colony) during 1996–1998. We were unable to distinguish which avian species was responsible for taking any given fish. The larger proportion of mortalities attributed to Rice Island is probably the result of the lower marine forage fish availability in this midestuarine location (Collis et al. 2002; Roby et al. 2002). It should be pointed out that the Caspian tern colony has now shifted from Rice Island to East Sand Island, where salmonid smolts are less prevalent in Caspian tern diets (Roby et al. 2002). For this reason and the fact that the birds are federally protected, we were unable to repeat our work

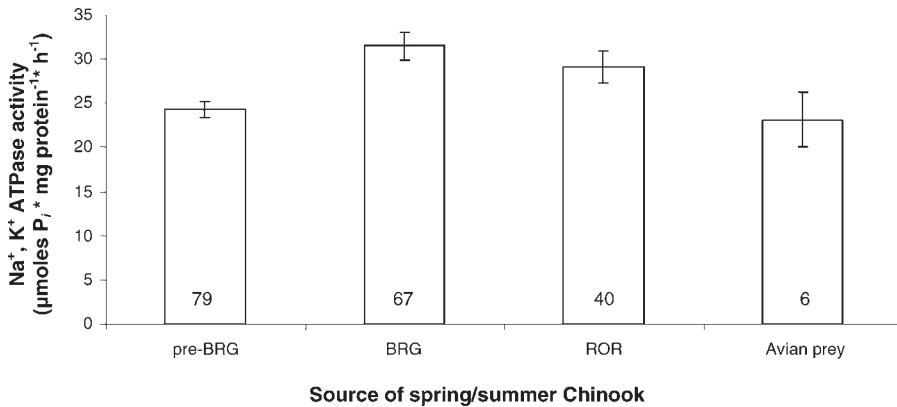


FIGURE 7.—Mean (\pm SE) Na^+ , K^+ -ATPase activity of spring–summer Chinook salmon collected from the Lower Granite Dam fish collection facility (Snake River) 456 km above Bonneville Dam (pre-BRG; data shown for comparison only), from barge holds (BRG; rkm 234), from the Bonneville Dam fish collection facility (run-of-river [ROR]; rkm 234), and from the bills of Caspian terns on Rice Island (rkm 35) in the Columbia River estuary (avian prey). Sample size is indicated at the bottom of each bar. Gill ATPase activity levels were significantly lower in avian prey fish than in barged and ROR fish (Fisher's LSD: $P < 0.050$; see also Table 4).

concerning analysis for *R. salmoninarum* infection or gill ATPase activity of fish captured by Caspian terns.

We do not know where depredated fish with radio tags were captured, although it could be a considerable distance from the avian colonies. In the Columbia River estuary, double-crested cormorants and Caspian terns can forage up to 50 km from their roosts, although most foraging occurred within 30 km (Anderson et al. 2004; Lyons 2004).

Tag weight-to-body weight ratios were somewhat variable across our study and had no significant effect on vulnerability to predation. Adams et al. (1998) reported that gastrically implanted radio tags did not affect swimming performance 24 h after tagging but did affect swimming performance 21 d after tagging. Given the comparatively short battery life of our radio tags (7 d) and the near-perfect migration success (no observed mortalities) from the BON tailrace to the Columbia River estuary, we believe that any stress effects from tagging during the 7-d time frame were minimal. Jepsen et al. (2001) found no significant differences between cortisol, glucose, or lactate levels in similar-sized (140–260 mm FL) hatchery Chinook salmon after 7 and 14 d.

Roby et al. (2003) used a bioenergetics model to estimate a mortality range of 6.6–14.2% for Caspian tern-related predation on spring–summer Chinook salmon during 1998. Our mortality estimates are toward the upper end of this range and are inclusive of other piscivorous bird species, such as double-crested cormorants and gulls. During 1997–2000, mortality estimates of PIT-tagged spring–summer Chinook salmon by all species of avian predators

ranged from 2 to 4% (Collis et al. 2001; Ryan et al. 2003). The estimates of Collis et al. (2001) and Ryan et al. (2003) were 10–13 percentage points lower than our own estimates for radio-tagged spring–summer Chinook salmon during 1995–1998. This could be the result of differences in recovery or detection of tags or study design.

Detection of PIT tags is limited to land-based recovery (Ryan et al. 2001), whereas radio tags deposited by birds in the shallow water around the periphery of Rice and East Sand islands are detectable. Collis et al. (2001) and Ryan et al. (2003) employed a study design that used detections of PIT-tagged fish passing BON and entering transportation barges upstream. This type of design implicitly assumes that all fish detected upstream would migrate into the Columbia River estuary where piscivorous bird-related mortality is highest. The PIT-tagged fish encompass a broader range of juvenile salmon sizes (down to 65 mm; optimum = 80–150 mm; PTSC 1999) compared with our radio-tagged fish (Table 2). We were essentially limited to tagging fish large enough to hold radio tags. An unknown portion of the PIT-tagged spring–summer Chinook salmon, especially small individuals, may not be physiologically ready to migrate. In contrast, we have shown that nearly all of our radio-tagged fish migrated. If a substantial number of PIT-tagged fish do not migrate, then the PIT tag studies are underestimating mortality. It is equally conceivable that we are overestimating mortality because we are selecting for large fish. Our mortality estimates are comparable with those of PIT-tagged steelhead, which may be especially vulnerable to avian

predation because of their large body size and their unsubstantiated propensity to migrate in shallower water relative to other juvenile salmon (Collis et al. 2001; Ryan et al. 2003). This could suggest that either the larger body size of our radio-tagged fish or a propensity to migrate in shallow water made them susceptible to avian predation in a manner similar to that hypothesized for steelhead.

Our radio-tagged spring–summer Chinook salmon traveled at the same rate as PIT-tagged Chinook salmon between BON and rkm 89 (Ledgerwood et al. 1998), indicating that there were minimal tag effects on swimming performance. In contrast, Hockersmith et al. (2003) reported that juvenile spring–summer Chinook salmon with gastrically implanted radio tags traveled significantly faster than PIT-tagged individuals through the lower Snake and middle Columbia rivers; however, these animals had survival rates comparable with PIT-tagged fish for median travel times corresponding to 6 d and 106 km of travel distance.

There were no differences in mortality rates of radio-tagged spring–summer Chinook salmon between releases or barged versus ROR fish types during 1995–1997. Likewise, there were no differences in mortality rates among years during 1995–1997. Mortality rate increased through time in 1996, 1997, and across years (when day of year was selected as a continuous variable) for barged fish and barged and ROR fish combined, when all releases were included in analyses independent of fish type. These increases in smolt mortality over time may be attributed to the arrival of increasing numbers of nesting avian predators in the estuary as the spring–summer Chinook salmon out-migration progressed (Ryan et al. 2003). Indeed, the peak out-migration of spring–summer Chinook salmon smolts coincides with the first half of the breeding season of piscivorous birds in the Columbia River estuary (Collis et al. 2001; Roby et al. 2002; Ryan et al. 2003).

Our physiological data suggest that Caspian terns captured fish with high *R. salmoninarum* levels and low gill ATPase activity levels relative to barged and ROR fish 199 km upstream. If this is true, then diseased and less well-smolted fish may be more vulnerable to birds than healthy individuals, suggesting that not all smolt mortality caused by avian predation is additive. One caveat to this conclusion is that fish taken by piscivorous birds may be from a different cohort than the barged or ROR fish that we sampled for physiology and, thus, may not have experienced the same passage stressors, infection corridors, or smoltification development pattern as barged and ROR fish.

Mesa et al. (1998) hypothesized that Chinook salmon infected with BKD were more vulnerable to

predation because they had a reduced metabolic scope for activity that compromised predator avoidance capabilities. They suggested that this might explain why high infection levels are relatively rare in Columbia River salmonids (Maule et al. 1996; Mesa et al. 1998).

Bacterial kidney disease can be a chronic stressor, compromising osmoregulation and increasing the overall mortality and vulnerability of juvenile Chinook salmon to predation (Elliott et al. 1995; Mesa et al. 1998, 1999; Seals-Price and Schreck 2003a, 2003b). Mesa et al. (1999) found that the severity of BKD infection was unrelated to ATPase activity, which agrees with the findings of our study. If the supposition of Mesa et al. (1999) that smolting-induced stress causes an increase in severity of BKD infection, then the interaction between smolting and BKD is probably as complex as the exogenous and endogenous cues that lead to the phenomenon of smoltification itself (Hoar 1988). The severity of the infection may be regulated by genetic differences in stocks (Mesa et al. 1999) and environmental factors (Elliott et al. 1995, 1997).

We postulate that the quality (general health condition) of migrants reaching the lower Columbia River (by either barge or in-river migration) determines subsequent behavior and vulnerability to predation. Stressors incurred while passing through the Columbia River hydropower system could affect the degree of preparedness of smolts for seawater entry. Stress alters disease resistance in salmonids through effects on both immune system function and nonspecific resistance factors (Maule et al. 1989; Schreck et al. 1993; Schreck 1996). Because in-river migration stimulates and advances the process of smoltification (Zaugg et al. 1985), immune function in migrating smolts may be more sensitive to stress than immune function in parr or nonmigrating (confined) smolts. Stress can reduce the ability of smolts to resist novel pathogens (Maule et al. 1989; Schreck et al. 1993; Schreck 1996; Maule and VanderKooi 1999) encountered in the marine environment as well as *R. salmoninarum*. Almost all out-migrating hatchery-reared and wild Chinook salmon are carriers of this pathogen, which is suspected to be a significant cause of mortality after the fish enter seawater. Stress, albeit briefly (Olla and Davis 1989; Olla et al. 1992, 1995; Mesa 1994; Schreck et al. 1997), and disease (Mesa et al. 1998) hinder predator avoidance. Stress (McInerney 1964; Schreck 1982, 1992) and disease (Schreck 1996) also may retard developmental processes such as smoltification and seawater entry behavior. Salmonids with BKD appear particularly ill-suited for entry into seawater (Banner et al. 1983; Moles 1997). This, in conjunction with the fact that transportation moves fish downstream at

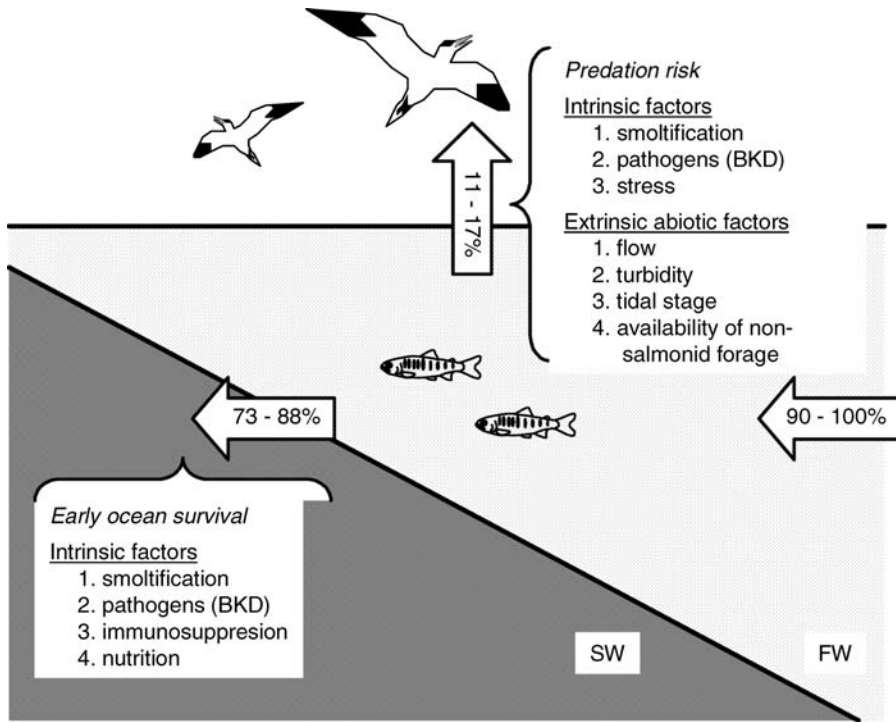


FIGURE 8.—Conceptual model of the Columbia River seawater wedge with actual survival estimates of radio-tagged spring–summer Chinook salmon based on detection efficiencies and mortality estimates. Included in the model are potential intrinsic (leading to delayed mortality by predation) and extrinsic factors affecting the probability that juvenile Chinook salmon will prolong their residence time in the upper freshwater lens. We hypothesize that, in the face of predation from avian predators, this would make the fish more vulnerable to predation, particularly by surface-oriented birds like Caspian terns or gulls. The percentages reflect our estimates regarding the fate of spring–summer Chinook salmon reaching the lower Columbia River estuary.

a greatly increased rate from those remaining in-river, effectively reducing the development time of smolts preparing to enter seawater, could possibly contribute to inadequately evasive or smolted fish at the time they reach the estuary. This may cause behaviors (e.g., holding, change in direction consequent to tidal changes, and seawater avoidance) that could result in higher predation rates by increasing the amount of time the migrants spend in the surface freshwater lens. At the surface, fish are exposed to large concentrations of birds that forage at or near the surface, such as Caspian terns and gulls. Laboratory experiments show that fish not fully smolted will avoid seawater (McInerney 1964) and remain in freshwater at the surface in situations where the halocline is horizontally stratified (Iwata et al. 1990; Iwata 1995; Seals-Price and Schreck 2003a, 2003b) or they are not as proficient in adapting to seawater (Schreck et al. 1985; Patino et al. 1986). Behaviors relating to seawater avoidance are perhaps more of an issue for fish emigrating through estuaries smaller than that of the Columbia. By affecting

behavior, smoltification, disease, and stress status may, thus, influence smolt vulnerability to predators. Figure 8 presents a visual conceptual model of how we view factors affecting success of fish entering the ocean, integrating demographic, physiological, and environmental factors.

Conclusions

Reduction of smolt losses in the Columbia River estuary could reverse current population declines (Kareiva and Marvier 2000), although management for piscivorous bird populations alone will not reverse this trend (NOAA Fisheries 2002). Delayed mortality of juvenile salmon is the result of dam passage or transportation history (Budy et al. 2002; Wilson 2003) and our results suggest that it is partly realized before ocean entry in the Columbia River estuary where avian predators consume fish, many of which are infected with *R. salmoninarum*. Mitigation for delayed mortality losses would be best realized by improving fish passage and transportation facilities upstream so that

juvenile salmon can enter the Columbia River estuary with minimal “stress deficits” (i.e., allostatic load: McEwen and Stellar 1993) to repay and in sufficient time to smoltify. Evidence suggests that juvenile salmon in advanced states of smoltification prefer seawater (McInerney 1964) and will, therefore, enter it more quickly (Seals-Price and Schreck 2003a), potentially leaving less exposure time to avian predators in the Columbia River estuary. There is a need to better understand the complex relationship between passage and transportation history, stress, smoltification, and disease as they relate to migration, estuarine residence behavior, and vulnerability to avian predation. Further research is needed to measure the extent to which depredation by piscivorous birds in the Columbia River estuary is compensatory.

Given the estimates of predation rates by avian predators from the present study and others (Collis et al. 2001; Roby et al. 2003; Ryan et al. 2003), management of bird colonies was implemented by moving the Caspian tern colony from Rice Island to East Sand Island (Roby et al. 2002). Other actions are planned to move some of the Caspian terns out of the basin entirely (USFWS 2005). This management action has occurred and is ongoing, even though we cannot be certain that it will result in an appreciable increase in adult salmon returns. Increased SARs would be unlikely if most of the depredated fish would have died from other causes (i.e., BKD or improper smoltification) anyway. However, it seems more likely that managing the piscivorous bird colonies will result in higher adult returns for the most depredated stocks such as steelhead, which have experienced relatively high mortality rates from Caspian tern predation (Collis et al. 2001; NOAA Fisheries 2002; Roby et al. 2003; Ryan et al. 2003). The benefits to salmonids of reduced avian predation would be expected even if much (~50%) of the mortality is compensatory rather than additive. Also, historical predation rates are not known. Perhaps salmon populations always sustained themselves under this predation pressure. For example, the eminent ornithologist J. K. Townsend (1839) reported large numbers of piscivorous birds as he sailed out of the mouth of the Columbia shortly after Lewis and Clark visited the area. The role of hatchery-reared fish in the estuarine community should be considered as well. Perhaps hatchery fish mitigate not only for fish-deprived people, but also for piscivorous birds.

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References

- Adams, N. S., D. W. Rondorf, S. D. Evans, J. E. Kelly, and R. W. Perry. 1998. Effects of surgically and gastrically implanted radio transmitters on swimming performance and predator avoidance of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 55:781-787.
- Anderson, C. D., D. D. Roby, and K. Collis. 2004. Foraging patterns of male and female double-crested cormorants nesting in the Columbia River estuary. *Canadian Journal of Zoology* 82:541-554.
- Banner, C. R., J. S. Rohovec, and J. L. Fryer. 1983. *Renibacterium salmoninarum* as a cause of mortality among spring chinook salmon in saltwater. *Journal of the World Mariculture Society* 14:236-239.
- Barton, B. A., C. B. Schreck, and L. A. Sigismondi. 1986. Multiple acute disturbances evoke cumulative physiological stress responses in juvenile Chinook salmon. *Transactions of the American Fisheries Society* 115:245-251.
- Beamesderfer, R. C. P., D. L. Ward, and A. A. Nigro. 1996. Evaluation of the biological basis for a predator control program on northern squawfish (*Ptychocheilus oregonensis*) in the Columbia and Snake rivers. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2898-2908.
- Brown, R. S., S. J. Cooke, W. G. Anderson, and R. S. McKinley. 1999. Evidence to challenge the “2% rule” for biotelemetry. *North American Journal of Fisheries Management* 19:867-871.
- Budy, P., G. P. Thiede, N. Bouwes, C. E. Petrosky, and H. Schaller. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. *North American Journal of Fisheries Management* 22:35-51.
- Christensen, R. 1990. *Log-linear models*. Springer-Verlag, New York.

- Clugston, D. A., and C. B. Schreck. 1992. Movement, distribution, and behavior of juvenile salmonids passing through Columbia and Snake River dams, 1992. Annual report of the Oregon Cooperative Fish and Wildlife Research Unit, Oregon State University, to the Bonneville Power Administration, Portland, Oregon.
- Collis, K., R. E. Beaty, and B. R. Crain. 1995. Changes in catch rate and diet of northern squawfish associated with the release of hatchery-reared juvenile salmonids in a Columbia River reservoir. *North American Journal of Fisheries Management* 15:346–357.
- Collis, K., D. D. Roby, D. P. Craig, S. Adamany, J. Y. Adkins, and D. E. Lyons. 2002. Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: implications for losses of juvenile salmonids to avian predation. *Transactions of the American Fisheries Society* 131:537–550.
- Collis, K., D. D. Roby, D. P. Craig, B. A. Ryan, and R. D. Ledgerwood. 2001. Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary: vulnerability of different salmonid species, stocks, and rearing types. *Transactions of the American Fisheries Society* 130:385–396.
- Congleton, J. L., W. J. LaVoie, C. B. Schreck, and L. E. Davis. 2000. Stress indices in migrating juvenile Chinook salmon and steelhead of wild and hatchery origin before and after barge transportation. *Transactions of the American Fisheries Society* 946–961.
- Congleton, J. L., T. Wagner, J. Evavold, J. Hafner, D. Fryer, and B. Sun. 2004. Evaluation of physiological differences in transported, in-river migrating, and multiple-bypassed juvenile salmon. 2002 Annual report of the Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho, to the U.S. Army Corps of Engineers, Walla Walla, Washington.
- Coutant, C. C., and R. R. Whitney. 2000. Fish behavior in relation to passage through hydropower turbines: a review. *Transactions of the American Fisheries Society* 129:351–380.
- Davis, L. E., and C. B. Schreck. 1997. The energetic response to handling stress in juvenile coho salmon. *Transactions of the American Fisheries Society* 126:248–258.
- Elliott, D. G., R. J. Pascho, L. M. Jackson, G. M. Matthews, and J. R. Harmon. 1997. *Renibacterium salmoninarum* in spring-summer Chinook salmon smolts at dams on the Columbia and Snake rivers. *Journal of Aquatic Animal Health* 9:114–126.
- Elliott, D. G., R. J. Pascho, and A. N. Palmisano. 1995. Brood stock segregation for the control of bacterial kidney disease can affect mortality of progeny Chinook salmon (*Oncorhynchus tshawytscha*) in seawater. *Aquaculture* 132:133–144.
- Hoar, W. S. 1988. The physiology of smolting salmonids. Pages 275–343 in W. S. Hoar and D. J. Randall editors. *Fish physiology*, volume 11, part B. Academic Press, New York.
- Hockersmith, E. E., W. D. Muir, G. S. Steven, and B. P. Sandford. 2003. Comparison of migration rate and survival between radio-tagged and PIT-tagged migrant yearling Chinook salmon in the Snake and Columbia rivers. *North American Journal of Fisheries Management* 23:404–413.
- ISG (Independent Scientific Group). 1996. Return to the river: restoration of salmonid fishes in the Columbia River ecosystem. U.S. Department of Energy, Northwest Power Planning Council, Publication 96-6, Portland, Oregon.
- IUBMB (International Union of Biochemistry and Molecular Biology). 1992. *Enzyme nomenclature 1992*. Academic Press, San Diego, California.
- Iwata, M. 1995. Downstream migratory behavior of salmonids and its relationship with cortisol and thyroid hormones: a review. *Aquaculture* 135:131–139.
- Iwata, M., K. Yamauchi, R. S. Nishioka, R. Lin, and H. Bern. 1990. Effects of thyroxine, growth hormone, and cortisol on salinity preference of juvenile coho salmon (*Oncorhynchus kisutch*). *Marine Behavioral Physiology* 17:191–201.
- Jepsen, N., L. E. Davis, C. B. Schreck, and B. Siddens. 2001. The physiological response of Chinook salmon smolts to two methods of radio-tagging. *Transactions of the American Fisheries Society* 130:495–500.
- Jepsen, N., C. Schreck, S. Clements, and E. B. Thorstad. 2005. A brief discussion on the 2% tag/body weight rule of thumb. Pages 255–259 in M. T. Spedicato, G. Lembo, and G. Marmulla, editors. *Aquatic telemetry: advances and applications*. Food and Agriculture Organization of the United Nations, Rome.
- Johnson, S. L., R. D. Ewing, and J. A. Lichatowich. 1977. Characterization of gill Na^+ , K^+ -activated adenosine triphosphatase from Chinook salmon, *Oncorhynchus tshawytscha*. *Journal of Experimental Zoology* 199:345–354.
- Kareiva, P., and M. Marvier. 2000. Recovery and management options for spring/summer Chinook salmon in the Columbia River. *Science* 290:977–979.
- Kelsey, D. A., C. B. Schreck, J. L. Congleton, and L. E. Davis. 2002. Effects of juvenile steelhead on juvenile Chinook behavior and physiology. *Transactions of the American Fisheries Society* 131:676–689.
- Kim, R. A., R. D. Ledgerwood, and R. A. Nelson. 1986. Increased abundance and the food consumption of northern squawfish (*Ptychocheilus oregonensis*) at river kilometer 75 in the Columbia River. *Northwest Science* 60:197–200.
- Laake, J. L., P. Browne, R. L. DeLong, and H. R. Huber. 2002. Pinniped diet composition: a comparison of estimation models. *Fishery Bulletin* 100:434–447.
- Ledgerwood, R. D., B. A. Ryan, E. P. Nunnallee, and J. W. Ferguson. 1998. Estuarine recovery of PIT-tagged juvenile salmonids from the Lower Granite Dam transportation study, 1998. Annual report of NOAA Fisheries, Northwest Fisheries Science Center, to the U.S. Army Corps of Engineers, Walla Walla, Washington.
- Lewis, K. P. 2004. How important is the statistical approach for analyzing categorical data?: a critique using artificial nests. *Oikos* 104:305–315.
- Lyons, D. E. 2004. Foraging ecology of Caspian terns and double-crested cormorants in the Columbia River estuary. Master's thesis. Oregon State University, Corvallis.
- Matthews, G. M., D. L. Park, S. Achord, and T. E. Ruehle.

1986. Static seawater challenge test to measure relative stress levels in spring Chinook salmon smolts. *Transactions of the American Fisheries Society* 115:236–244.
- Maule, A. G., D. W. Rondorf, J. Beeman, and P. Haner. 1996. Incidence of *Renibacterium salmoninarum* infections in juvenile hatchery spring Chinook salmon in the Columbia and Snake rivers. *Journal of Aquatic Animal Health* 8:37–46.
- Maule, A. G., C. B. Schreck, C. S. Bradford, and B. A. Barton. 1988. Physiological effects of collecting and transporting emigrating juvenile Chinook salmon past dams on the Columbia River. *Transactions of the American Fisheries Society* 117:245–261.
- Maule, A. G., R. A. Tripp, S. L. Kaattari, and C. B. Schreck. 1989. Stress alters immune function and disease resistance in Chinook salmon (*Oncorhynchus tshawytscha*). *Journal of Endocrinology* 120:135–142.
- Maule, A. G., and S. P. VanderKooi. 1999. Stress-induced immune–endocrine interaction. Pages 205–245 in P. H. M. Balm editor. *Stress physiology in animals*. CRC Press, Boca Raton, Florida.
- McEwen, B. S., and E. Stellar. 1993. Stress in the individual: mechanisms leading to disease. *Archives of Internal Medicine* 153:2093–2101.
- McInerney, J. E. 1964. Salinity preference: an orientation mechanism in salmon migration. *Journal of the Fisheries Research Board of Canada* 21:995–1018.
- Mesa, M. G. 1994. Effects of multiple acute stressors on the predator avoidance ability and physiology of juvenile Chinook salmon. *Transactions of the American Fisheries Society* 123:786–793.
- Mesa, M. G., A. G. Maule, T. P. Poe, and C. B. Schreck. 1999. Influence of bacterial kidney disease on smoltification in salmonids: is it a case of double jeopardy? *Aquaculture* 174:25–41.
- Mesa, M. G., and T. M. Olson. 1994. Prolonged swimming performance of northern squawfish: can water velocity be used to reduce predation on juvenile salmonids at Columbia River dams? Pages 35–36 in T. P. Poe and D. M. Gadomski editors. *Significance of selective predation and development of prey protection measures for juvenile salmonids in the Columbia and Snake River reservoirs: annual report, February 1992–February 1993*. Bonneville Power Administration, Portland, Oregon.
- Mesa, M. G., T. P. Poe, D. M. Gadomski, and J. H. Petersen. 1994. Are all prey created equal?: a review and synthesis of differential predation on prey in standard condition. *Journal of Fish Biology* 45(Supplement A):81–96.
- Mesa, M. G., T. P. Poe, A. G. Maule, and C. B. Schreck. 1998. Vulnerability to predation and physiological stress responses in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) experimentally infected with *Renibacterium salmoninarum*. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1599–1606.
- Moles, A. 1997. Effect of BKD on saltwater adaptation of coho salmon smolts. *Journal of Aquatic Animal Health* 9:230–233.
- Moser, M. L., A. F. Olson, and T. P. Quinn. 1991. Riverine and estuarine migratory behavior of coho salmon (*Oncorhynchus kisutch*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1670–1678.
- Muir, W. D., S. G. Smith, J. G. Williams, E. E. Hockersmith, and J. R. Skalski. 2001. Survival estimates for migrant yearling Chinook salmon and steelhead tagged with passive integrated transponders in the lower Snake and lower Columbia rivers, 1993–1998. *North American Journal of Fisheries Management* 21:269–282.
- NOAA Fisheries. 2000. Summary of research related to transportation of juvenile anadromous salmonids around Snake and Columbia River dams. NOAA Fisheries, Northwest Fisheries Science Center, Seattle.
- NOAA Fisheries. 2002. Caspian tern predation on salmon and steelhead smolts in the Columbia River estuary. NOAA Fisheries, Northwest Fisheries Science Center, Portland, Oregon.
- NOAA Fisheries. 2004. Biological opinion, Endangered Species Act section 7(a)(2) consultation: consultation on remand for operation of the Columbia River Power System and 19 Bureau of Reclamation projects in the Columbia basin. NOAA Fisheries, Seattle. Available: http://www.salmonrecovery.gov/R_biop_final.shtml.
- Olla, B. L., and M. W. Davis. 1989. The role of learning and stress in predator avoidance of hatchery-reared coho salmon (*Oncorhynchus kisutch*) juveniles. *Aquaculture* 76:209–214.
- Olla, B. L., M. W. Davis, and C. B. Schreck. 1992. Comparison of predator avoidance capabilities with corticosteroid levels induced by stress in juvenile coho salmon. *Transactions of the American Fisheries Society* 121:544–547.
- Olla, B. L., M. W. Davis, and C. B. Schreck. 1995. Stress-induced impairment of predator evasion and nonpredator mortality in Pacific salmon. *Aquaculture Research* 26:393–398.
- Pascho, R. J., D. G. Elliott, and S. Achord. 1993. Monitoring of the in-river migration of smolts from two groups of spring Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), with different profiles of *Renibacterium salmoninarum* infection. *Aquaculture and Fisheries Management* 24:163–169.
- Patino, R., C. B. Schreck, J. L. Banks, and W. S. Zaugg. 1986. Effects of rearing conditions on the developmental physiology of smolting of coho salmon. *Transactions of the American Fisheries Society* 115:828–837.
- Poe, T. P., H. C. Hansel, S. Vigg, D. E. Palmer, and L. A. Prendergast. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:405–420.
- Popper, A. N., and T. J. Carlson. 1998. Application of sound and other stimuli to control fish behavior. *Transactions of the American Fisheries Society* 127:673–707.
- PTSC (PIT Tag Steering Committee). 1999. PIT tag marking procedures manual, version 2.0. Columbia Basin Fish and Wildlife Authority. Available: http://www.psmfc.org/pittag/Software_and_Documentation/index.html. (June 2005).
- Raymond, H. L. 1979. Effects of dams and impoundments on migrations of juvenile Chinook salmon and steelhead from the Snake River, 1966 to 1975. *Transactions of the American Fisheries Society* 108:505–529.
- Roby, D. D., K. Collis, D. E. Lyons, D. P. Craig, J. Y. Adkins, and A. M. Myers. 2002. Effects of colony relocation on

- diet and productivity of Caspian terns. *Journal of Wildlife Management* 66:662–673.
- Roby, D. D., D. E. Lyons, D. P. Craig, K. Collis, and G. H. Visser. 2003. Quantifying the effect of predators on endangered species using a bioenergetics approach: Caspian terns and juvenile salmonids in the Columbia River estuary. *Canadian Journal of Zoology* 81:250–265.
- Ryan, B. A., J. W. Ferguson, R. D. Ledgerwood, and E. P. Nunnallee. 2001. Detection of passive integrated transponder tags from juvenile salmonids on piscivorous bird colonies in the Columbia River basin. *North American Journal of Fisheries Management* 21:149–153.
- Ryan, B. A., S. G. Smith, J. M. Butzerin, and J. W. Ferguson. 2003. Relative vulnerability to avian predation of juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary, 1998–2000. *Transactions of the American Fisheries Society* 132:275–288.
- SAS Institute. 1996. SAS/STAT user's guide version 6. SAS Institute, Cary, North Carolina.
- Schreck, C. B. 1992. Glucocorticoids: metabolism, growth, and development. Pages 367–392 in M. P. Schreiber, C. G. Scanes, and P. K. T. Pang, editors. *The endocrinology of growth, development, and metabolism in vertebrates*. Academic Press, New York.
- Schreck, C. B. 1982. Stress and rearing of salmonids. *Aquaculture* 28:241–249.
- Schreck, C. B. 1996. Immunomodulation: endogenous factors. Pages 311–337 in G. Iwama and T. Nakanishi editors. *Fish physiology*, volume 15. Academic Press, New York.
- Schreck, C. B., M. D. Karnowski, and B. J. Clemens. 2005. Evaluation of postrelease losses and barging strategies that minimize postrelease mortality. Final report of the Oregon Cooperative Fish and Wildlife Research Unit, Oregon State University, to the U.S. Army Corps of Engineers, Walla Walla, Washington.
- Schreck, C. B., A. G. Maule, and S. L. Kaattari. 1993. Stress and disease resistance. Pages 170–175 in J. F. Muir and R. J. Roberts editors. *Recent advances in aquaculture*. Blackwell Scientific Publications, London.
- Schreck, C. B., B. L. Olla, and M. W. Davis. 1997. Behavioral responses to stress. Pages 145–170 in G. K. Iwama, A. D. Pickering, J. P. Sumpter, and C. B. Schreck editors. *Fish stress and health in aquaculture*. Cambridge University Press, Cambridge, UK.
- Schreck, C. B., R. Patino, C. K. Pring, J. R. Winton, and J. E. Holway. 1985. Effects of rearing density on indices of smoltification and performance of coho salmon, *Oncorhynchus kisutch*. *Aquaculture* 45:345–358.
- Schreck, C. B., M. F. Solazzi, S. L. Johnson, and T. E. Nichelson. 1989. Transportation stress affects performance of coho salmon, *Oncorhynchus kisutch*. *Aquaculture* 82:15–20.
- Scott, W. B., and E. J. Crossman. 1973. *Freshwater fishes of Canada*. Fisheries Research Board of Canada Bulletin 183.
- Seals-Price, C., and C. B. Schreck. 2003a. Effects of bacterial kidney disease on saltwater preference of juvenile spring Chinook salmon, *Oncorhynchus tshawytscha*. *Aquaculture* 222:331–341.
- Seals-Price, C., and C. B. Schreck. 2003b. Stress and saltwater-entry behavior of juvenile Chinook salmon (*Oncorhynchus tshawytscha*): conflicts in physiological motivation. *Canadian Journal of Fisheries and Aquatic Sciences* 60:910–918.
- Townsend, J. K. 1839. *Narrative of a journey across the Rocky Mountains to the Columbia River*. Reprint 1999. Oregon State University Press, Corvallis.
- USACE (U.S. Army Corps of Engineers). 2000. Caspian tern relocation FY 2000 management plan and pile dike relocation, Clatsop County, Oregon, and Grays Harbor County, Washington: environmental assessment and finding of no significant impact. USACE, Portland, Oregon.
- USFWS (U.S. Fish and Wildlife Service). 2005. Caspian tern management to reduce predation of juvenile salmonids in the Columbia River estuary: final environmental impact statement, January 2005. USFWS, Portland Oregon.
- Ward, D. L., R. B. Boyce, F. R. Young, and F. E. Olney. 1997. A review and assessment of transportation studies for juvenile Chinook salmon in the Snake River. *North American Journal of Fisheries Management* 17:652–662.
- Ward, D. L., and L. M. Miller. 1988. Using radiotelemetry in fisheries investigations. Oregon Department of Fish and Wildlife, Information Report 88-7, Portland.
- Ward, D. L., J. H. Petersen, and J. J. Loch. 1995. Index of predation on juvenile salmonids by northern squawfish in the lower and middle Columbia River and in the lower Snake River. *Transactions of the American Fisheries Society* 124:321–334.
- Wilson, P. H. 2003. Using population projection matrices to evaluate recovery strategies for Snake River spring and summer Chinook salmon. *Conservation Biology* 17:782–794.
- Zaugg, W. S. 1982. A simplified preparation for adenosine triphosphate determination in gill tissue. *Canadian Journal of Fisheries and Aquatic Sciences* 39:215–217.
- Zaugg, W. S., E. F. Prentice, and F. W. Waknitz. 1985. Importance of river migration to the development of seawater tolerance in Columbia River anadromous salmonids. *Aquaculture* 51:33–47.
- Zimmerman, M. P. 1999. Food habits of smallmouth bass, walleyes, and northern pikeminnow in the lower Columbia River basin during out-migration of juvenile anadromous salmonids. *Transactions of the American Fisheries Society* 128:1036–1054.