A LITERATURE REVIEW RELEVANT TO JUVENILE FALL CHINOOK SALMON HABitat USE, MIGRATION BEHAVIOR, AND SURVIVAL IN THE LOWER SNAKE RIVER

Task 2 for Contract #W912EF-08-D-0005

Prepared by:
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College of Natural Resources
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Under subcontract to:
Normandeau Associates, Inc.

Prepared for:
U.S. Army Corps of Engineers
Walla Walla District

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1.0 INTRODUCTION

The primary objective of this review is to synthesize known information on fall Chinook salmon (*Oncorhynchus tshawytscha*) relevant to juvenile habitat use, behavior, and survival in lower Snake River reservoirs. The review will inform ongoing research projects and guide implementation of dredged sediment disposal plans as recommended by the Biological Opinion (BiOp) on operation of the Federal Columbia River Power System (FCRPS). The review is part of a multi-objective project that includes field sampling and tagging (i.e., PIT-tag and telemetry) to identify Snake River reservoir habitats used by juvenile fall Chinook salmon, and collection of a wide range of biological parameters (e.g., water temperature, dissolved oxygen, chlorophyll a, sediment type, macrophyte and algae abundance, invertebrate and zooplankton composition, predator abundance, etc.). Seasonal patterns are of particular interest because recent research has shown that some subyearling fall Chinook salmon overwinter in Snake River reservoirs (e.g., Connor et al. 2005). This behavior contrasts with the traditionally held belief that all fall Chinook salmon juveniles migrate seaward in mid-summer shortly after spring emergence (Healey 1991) and raises new FCRPS management questions for the Snake River population.

Snake River fall Chinook salmon were listed as threatened under the U.S. Endangered Species Act in 1992 (NMFS 1992) as a result of orders-of-magnitude population declines. The declines are primarily attributable to the significant loss of fall Chinook salmon spawning habitat in the Snake River main stem following construction of dams without fish passage facilities in the Hells Canyon reach (Waples et al. 1991; Myers et al. 1998). Construction and operation of eight dams on the lower Snake and Columbia rivers has also impacted Snake River fall Chinook salmon migration behaviors and survival (both adult and juvenile) by transforming riverine habitats to reservoir habitats (e.g. Raymond 1968, 1979; Bentley and Raymond 1976). In addition, in the portion of the unimpounded Snake River now accessible to fall Chinook salmon the river environment (i.e., river discharge, water velocity, water temperature, turbidity) is much different than what was encountered by adult and juvenile fall Chinook salmon in historical spawning and rearing areas. The combination of changes has resulted in a potential mismatch between fall Chinook salmon life history requirements and post-dam conditions in the lower Snake River.

A variety of mitigation efforts have been used to increase survival and productivity of Snake River fall Chinook salmon. The most substantive management strategies have included: water releases from upstream reservoirs in the Snake and Clearwater rivers that are timed to aid outmigrating juveniles by increasing water velocity and reducing water temperatures (‘flow augmentation’); juvenile collection at dams and subsequent transport downstream in barges or trucks (‘transportation’); and releases of hatchery-reared juveniles originally from genetically-similar brood stock (‘supplementation’). Large-scale creation of shallow-water rearing habitat in lower Snake River reservoirs, if found to contribute to system productivity, would be an additional significant mitigation effort as such habitats are currently limited in the reservoirs.

The U.S. Army Corps of Engineers (USACE) began experimental in-water disposal of sediment dredged from the navigation channel in the lower Snake River in 1988. Results of the evaluations were generally considered favorable, with the dredged sediment creating shallow water rearing habitat without apparent increases in predators, major changes in biotic
communities, or likely long-term reductions in reservoir productivity. Further evaluation of the sediment disposal plan and the associated mitigation potential for threatened and endangered Snake River salmonids is required as part of a Programmatic Sediment Management Plan Environmental Impact Statement (EIS).

For this review, literature on Snake and Columbia River juvenile salmonids was collected by searching in a peer-reviewed database (Web of Science) and through grey literature reports posted on the USACE and Bonneville Power Administration (BPA) websites. We then searched the citation lists in the most relevant papers and reports for additional reference material and attempted to locate electronic files using Google Scholar. Relevant unpublished and recent reports were also solicited from personnel at the various agencies conducting fall Chinook salmon research in the Snake River basin; relatively few preliminary results were included. Information from the reviewed papers and reports were organized into six basic categories, and these were used to frame the synthesis: (1) early life history; (2) juvenile migration behavior; (3) migration timing patterns; (4) downstream migration rates; (5) reach survival; (6) habitat use; and (7) ecological relationships. A final section includes a discussion of current information gaps relevant to managing juvenile Snake River fall Chinook salmon.

2.0 EARLY LIFE HISTORY

2.1 FALL VS. SPRING–SUMMER CHINOOK SALMON

The Snake River supports a diverse group of Chinook salmon populations with at least two distinctive life history types (Myers et al. 1998; Brannon et al. 2004). ‘Ocean-type’ and ‘stream-type’ Chinook salmon have divergent life history schedules and are phenotypically and genetically different from each other (e.g., Waples et al. 2004). Adult stream-type fish typically return to the Snake River basin from April through August (e.g., Myers et al. 1998; Keefer et al. 2004) and spawn in high-elevation headwater streams in late summer and early fall. These fish are often referred to as spring–summer Chinook salmon based on their adult migration timing. Juvenile stream-type fish typically emerge from late January to early May and parr rear in headwater streams before migrating seaward as yearlings (Chapman and Bjornn 1969; Bjornn 1971; Healey 1991). Notably, many subyearling spring–summer fish move long distances downstream and overwinter in large tributary or main stem Snake River habitats (Myers et al. 1998) and some subyearlings are present in these habitats from spring through winter (Achord et al. 1996; Marshall et al. 2000; Connor et al. 2001b).

Ocean-type adult Chinook salmon return to the Snake River from mid-August through November with fall spawning in lower reaches of large tributaries and in the Snake River main stem (Dauble et al. 1999; Groves and Chandler 1999; Garcia et al. 2003). Most ocean-type Chinook salmon emerge from April to June, and then rear in freshwater for several weeks to several months before migrating seaward as subyearlings (Lister and Genoe 1970; Healey 1991; Brannon et al. 2004). The recently identified ‘reservoir-type’ Chinook salmon are the progeny of fall-run fish that emerge relatively later in spring and then overwinter in reservoirs as subyearlings and migrate seaward as yearlings the following spring (Connor et al. 2005). This behavior has also been referred to as residualizing (Connor et al. 1996). Relatively little is
known about the behavior or survival of reservoir-type Chinook salmon relative to ocean-type fish. However, there is accumulating evidence that reservoir-type fish that successfully overwinter are more likely to survive to adulthood because they have some size- and timing-related migration advantages. For example, larger juvenile salmonids tend to survive passage through the FCRPS at relatively high rates across species and runs (e.g., Bugert et al. 1997; Bickford and Skalski 2000; Connor et al. 2005). In addition, early-timed migrants often outperform late-timed fish because they encounter more favorable river conditions (e.g., Giorgi et al. 1990; Connor et al. 2000; Smith et al. 2003).

Management of ocean- and reservoir-type Chinook salmon can be challenging because juveniles often mix with subyearling and yearling stream-type fish during rearing along shorelines and during both passive and active downstream migration (Marshall et al. 2000; Connor et al. 2001a, 2001b). In Snake River main stem samples of subyearlings, the spring–summer fish contribution ranged from 5–63% (Marshall et al. 2000) and from 15-44% (Connor et al. 2001a). This mixing confounds interpretation of many juvenile fall Chinook salmon studies and the use of subyearling passage indices at dams.

2.1.1 GENETIC SEPARATION

Despite mixing among life history types during rearing and migration, genetic studies have consistently shown that stream- and ocean-type Chinook salmon are reproductively isolated in the Snake River (Waples et al. 1991; Marshall et al. 2000). Narum et al. (2007) collected ocean-type fish at Lyons Ferry Hatchery, the Nez Perce Tribal Hatchery, and from the lower Clearwater River and stream-type fish from 22 Snake River basin populations. Genetic distance between ocean- and stream-type Chinook salmon was highly significant, suggesting nearly complete reproductive separation since at least the last glaciation event (Narum et al. 2007). In contrast, the three ocean-type groups were genetically similar, with no significant differences from each other. These authors also found significantly higher genetic diversity in ocean- versus stream-type Chinook salmon in the Snake River, which they attributed to potentially larger founding populations or episodic colonization events for the ocean-type group.

Marshall et al. (2000) also found highly significant allozyme allele frequency differences among Snake River ocean- and stream-type Chinook salmon and little difference between hatchery and wild-origin ocean-type fish. Samples collected by Marshall et al. (2000) were subyearling fish from main stem habitats, and ocean-type fish were the target group. Notably, the authors emphasized that it was difficult to physically or visually differentiate stream- from ocean-type fish, as the two were “cryptically intermingled.” Subyearling stream-type fish in the main stem Snake River apparently originate from a variety of upstream wild-origin and hatchery sources, with relatively large contributions from the Imnaha, Grande Ronde, and Salmon rivers and from naturalized fish from Rapid River Hatchery (Connor et al. 2001b).

Using genetic tests to differentiate stream-type Chinook salmon from ocean-type (or reservoir-type) fish is somewhat impractical for in-season management decisions. However, genetic results have been used to back-calculate emergence dates (e.g., Connor et al. 1991) and for post-hoc evaluations of size differences among life history types (e.g., Connor et al. 2001a). Results of these analyses have been used for some in-season applications.
2.1.2 MORPHOLOGICAL SEPARATION

Phenotypic characteristics have also been compared in efforts to differentiate stream-, ocean-, and reservoir-type Chinook salmon juveniles in the Snake River. Body morphology was used to successfully distinguish subyearling ocean-type fish from yearling stream-type Snake River fish by Tiffan et al. (2000b). The subyearling ocean-type (fall-run) fish had relatively smaller heads and eyes, deeper bodies, and shorter caudal peduncles than yearling spring-run Chinook salmon; discriminant analyses correctly classified ~80% of the fish in these categories, as confirmed by genetic analysis (Tiffan et al. 2000b). In contrast, body morphology did not effectively separate subyearling ocean- and stream-type fish that were collected in main stem Snake River habitats. Tiffan et al. (2000b) speculated that the morphological similarities among subyearlings of both life history types were due to their shared low-gradient, warm-water rearing environment; in other words phenotypic plasticity masked genetic differences. Juvenile growth opportunity in the Snake River main stem is believed to be high compared to in colder, high-gradient tributary habitats, and these environmental differences have been similarly associated with variability in Chinook salmon morphological traits in other systems (e.g., Taylor 1990).

2.1.3 DEVELOPMENTAL SEPARATION

Spring–summer Chinook salmon emerge as fry as early as January in some Snake River tributaries, and most fish have emerged by May (Bjornn 1971; Howell et al. 1984). This is an earlier emergence schedule than that for most fall Chinook salmon, and as a result spring–summer fish that emigrate to the Snake River as subyearlings can be larger than newly-emerged fall-run fish. In mixed-race subyearling collections in the Snake River main stem, Connor et al. (2001a) found spring–summer fish were rearing along shorelines slightly earlier and were larger on average (85 vs. 73 mm; ~16%) than fall fish. Working backwards from genetic data, Connor et al. (2001a) developed models to separate spring–summer subyearlings from fall subyearlings from combinations of capture date, fish length, and capture location data; these models correctly classified 75-85% of the subyearlings. However, as in the morphological comparisons of Tiffan et al. (2000b), subyearling life history attributes for the two races overlapped substantially. Connor et al. (2001a) concluded that the presence of spring–summer subyearlings in the main stem Snake River would tend to skew fall Chinook salmon rearing and migration timing estimates towards earlier dates and that fall Chinook salmon abundance would be overestimated.

The various efforts to improve separation of stream- and ocean-type subyearlings (i.e., genetic, morphological, and developmental) have differed in accuracy and in their usefulness for in-season applications. Continued development of reliable tools to separate life history types is needed, because the presence of stream-type fish confounds many fall Chinook salmon evaluations.

2.2 CHARACTERISTICS OF OCEAN- AND RESERVOIR-TYPE FISH

The timing of many early Chinook salmon life history events — including incubation, emergence, growth, development, downstream migration, and smoltification — is strongly tied
to water temperature (Metcalfe and Thorpe 1990; Groot and Margolis 1991; Connor et al. 2002; Richter and Kolmes 2005). As a result, juvenile fall Chinook salmon life history stages can progress at different times (i.e., early vs. late) and at different rates (i.e., rapid vs. slow growth) as a function of prevailing temperatures. For example, reach-specific winter and spring temperature patterns can be used to predict emergence timing (e.g., Hanrahan 2007) and whether fall Chinook salmon juveniles migrate seaward in summer (i.e., ocean-type) or residualize and become reservoir-type fish (e.g., Connor et al. 2002). Temperature differences among spawning and rearing reaches in the Snake River basin therefore have important implications for fall Chinook salmon management and shape many of the behavioral patterns described in subsequent sections.

Historically, most Snake River fall Chinook salmon spawned in the lower reaches of major tributaries and in the main stem Snake River, primarily in a reach near Marsing, Idaho (Connor et al. 2002). This reach is more than 200 river kilometers (rkm) upstream from Hells Canyon Dam (built in 1967), which along with Brownlee (1958) and Oxbow (1961) blocked anadromous fish passage (Dauble et al. 2003; Hanrahan et al. 2005). Currently, most fall Chinook salmon spawning occurs in the ~165 rkm stretch of unimpounded Snake River between Lower Granite Reservoir and Hells Canyon Dam (hereafter: Hells Canyon reach). Water temperature and flow in the Hells Canyon reach are partially controlled by the upstream dams, and the upper portion of the reach is generally warmer in winter and spring than the section closer to Lower Granite Reservoir (Connor et al. 2002). Notably, the most productive historic spawning reach is believed to have been warmer than any current fall Chinook salmon spawning areas in the Snake River basin (Connor et al. 2002; Connor and Burge 2003). This suggests that fall Chinook salmon fry emergence in the currently available habitat is likely later, and that parr and subyearling growth rates are likely lower than historically (Connor and Burge 2003). Changes in these life history stages have important implications for outmigration and smoltification timing (i.e., a likely shift towards later timing, when river conditions are less favorable) and survival (i.e., smaller fish are less likely to survive).

On average, about 25-35% of redd construction upstream from Lower Granite Dam occurs in the Clearwater River (Connor et al. 2002; Garcia et al. 2003). As a result of cold-water releases from Dworshak Reservoir on the North Fork Clearwater River, the lower Clearwater River spawning reach is typically several degrees cooler than the main stem Snake River (e.g., Arnsberg et al. 1992) and cool compared to historic conditions. In comparisons of Snake and Clearwater River fall Chinook salmon populations, the pervasive effects of temperature on life history type (ocean- or reservoir-) and a range of life history events are clearly evident.

2.2.1 EMERGENCE TIMING

Fall Chinook salmon fry emergence timing varies among reaches and years (Figure 1). Emergence by most fish in the Hells Canyon Reach occurs from mid-March through early June. Estimated median and/or peak emergence dates in the Hells Canyon Reach have ranged from 9 April to 23 May (Connor et al. 1991, 1993b, 1997, 1998a, 2001c, 2002; Connor 2003) with fish in the upper section of the reach generally emerging earlier than in the lower reach by a few days to about two weeks. In the cooler Clearwater River, fry emergence was primarily in May and
June, with estimated median and/or peak dates ranging from 21 May to 27 June (Connor et al. 1991b, 2001c, 2002; Arnsberg et al. 1992).

Figure 1. Emergence timing distributions (median and range) for fall Chinook salmon collected upstream from Lower Granite Dam as reported by Connor et al. (2002). ● = lower Hells Canyon reach; ● = upper Hells Canyon reach; ● = lower Clearwater River reach.

The several-week difference in emergence timing between Snake and Clearwater populations is believed to reflect the cooler incubation temperatures experienced by Clearwater River fish. Similar differences among populations presumably existed historically, as suggested by Connor et al. (1997) who used temperature data to estimate historic mean emergence dates of 23 April (± 7 d) in the Snake River near Marsing and 4 June (± 13 d) in the lower Clearwater River. Notably, these historic estimates fall on the early end of the range reported in recent years in the current system.

2.2.2 GROWTH TO PARR SIZE

Connor et al. (2002) used a 45 mm cutoff to separate fall Chinook salmon fry from parr, and reported that growth to parr size was earlier in reaches and years with warmer water temperatures. In that study, parr size was achieved earliest in the upper Hells Canyon Reach (annual median dates = 23 April to 28 May), followed by the lower Hells Canyon Reach (median dates = 14 May to 8 June), and Clearwater River (median dates = 19 June to 2 July) (Figure 2). Growth from fry to parr size is both food and temperature dependent, with some interactive effects (Thorpe 1989; Healey 1991). Parr growth rates in the Snake River, estimated at approximately 1.1 mm/d overall, were significantly higher in warmer study reaches (Connor and Burge 2003). While these growth rate estimates are high compared to many ocean-type Chinook salmon populations across their geographic range, Connor and Burge (2003) concluded that they
are probably lower than historic rates in the Snake River. Slower growth compared to historic rates suggests that smoltification and emigration also occur later now.

![Figure 2. Growth-to-parr size (> 45 mm fork length) timing distributions (median and range) for fall Chinook salmon collected upstream from Lower Granite Dam as reported by Connor et al. (2002). ● = lower Hells Canyon reach; ▪ = upper Hells Canyon reach; ◼ = lower Clearwater River reach.](image)

2.2.3 OVERWINTERING / RESIDUALIZING

Emergence timing, growth rates, and rearing temperatures combine to generate fall Chinook salmon trajectories towards either ocean-type or reservoir-type life histories. Connor et al. (2002) estimated that ~2% of the subyearlings from the upper Hells Canyon Reach overwintered in lower Snake River reservoirs versus ~11% of subyearlings from the lower Hells Canyon Reach and 53% from the Clearwater River. The likelihood of expressing the reservoir-type life history appears to be inversely proportional to rearing temperature and growth opportunity (Connor et al. 2005). Across years and rearing sites, overwintering rates tended to be higher in years with cooler spring water temperatures (Connor et al. 2002). Notably, few if any Chinook salmon juveniles were captured during winter fish sampling in the reservoirs in historic surveys (e.g., Bennett et al. 1988), perhaps because there were fewer subyearling of Clearwater River origin.

Most residualized Chinook salmon from the Hells Canyon reach have been detected at lower Snake River dams in April, with similar median dates across dams (Connor et al. 1996). The PIT tag-based timing data suggest that these fish were fairly widely distributed across reservoirs during the winter months. By comparison, reservoir-type fish from the Clearwater River appeared to mostly overwinter upstream from Lower Granite Dam and then move downstream in a more cohesive group, with sequentially later detection dates at downstream dams in spring.
These estimates will be somewhat biased, however, because the juvenile collection facilities are not monitored during some winter months.

In recent years, combined radio telemetry and PIT-tag studies have provided some additional behavioral information for overwintering subyearlings (e.g., Tiffan et al. 2005, 2006; Kock et al. 2007). (Note: in the first year of this study, an acoustic telemetry approach had poor fish detection rates; Haskell et al. 2004.) In these studies, subyearlings believed to be fall Chinook salmon were collected by hook-and-line in Lower Granite Reservoir from October–February and were then monitored through the winter and spring as they moved downstream. Some fish were recorded passing dams in all months and at all times of the day. Passage nadirs occurred in mid-winter and passage increased in April. Fish were distributed throughout the lower Snake River, but a relatively large percentage of the fish overwintered in the Little Goose Reservoir. The telemetry data suggested many fish resided in dam forebays for extended periods (e.g., weeks to months) (Kock et al. 2007). Behaviors overall were quite variable, with some salmon showing directed downstream movements while others increased movement during runoff events from winter rainfall.

Reservoir-type fish that survive overwintering appear to have relatively high likelihood of survival to adulthood. Connor et al. (2005) estimated that 41% (14-52%) of adult wild fall Chinook salmon and 51% (31-82%) of adult hatchery adults appeared to be reservoir-type, based on scale analysis, and some reservoir-type fish were present in all brood years (adults collected from 1998–2003). Preliminary analyses of additional scale samples from adult fall Chinook salmon collected at Lower Granite Dam suggest that about 60–80% of the returning adults had entered the Pacific Ocean as yearlings (Sneva and Connor 2004; Marsh et al. 2007). In the Marsh et al. study, about a third of the returning fish that entered the ocean as yearlings were ‘conclusively’ shown to have spent their first winter in reservoirs, while the remainder reared in unknown freshwater locations, potentially including estuarine waters. Marsh et al. (2007) also concluded that juvenile migration history was strongly associated with whether fish entered the ocean as subyearlings or yearlings: 65% of those transported from the Snake River in summer, 39% of those transported in fall, and 21% of those that migrated in-river entered the ocean as subyearlings (Marsh et al. 2007). Yearling ocean entrants in both studies were somewhat more likely to return as precocious males (e.g., jacks or mini-jacks) though a full range of adult ages were identified.

The timing of life history events of subyearling fall Chinook salmon can have a large impact on subsequent behavior and survival. In general, the reviewed studies indicate that the trajectories of early- versus late-timed fish are quite different. Fish that emerge early tend to migrate sooner and to emigrate from the lower Snake River in-season, while late-timed fish are far more likely to residualize. The early- and late-timed groups experience different river conditions and differ in size through the season. As a result, behaviors, spatial and temporal habitat use patterns, and mortality risks presumably vary among groups.
3.0 JUVENILE MIGRATION BEHAVIOR

A relatively large number of studies have examined subyearling fall Chinook salmon migration behaviors and migration rates in both the Snake and Columbia rivers. These projects have generally used mark-recapture techniques (e.g., PIT tags, freeze brands, coded-wire tags) or stratified sampling designs (e.g., seining, trapping, electrofishing). There have also been some laboratory tests to evaluate physiological and proximate influences on some behaviors.

These various approaches have had different strengths and weaknesses. For example, the PIT-tagging studies have provided relatively precise estimates of point-to-point migration rates, while trapping and seining projects have helped more clearly define fish presence and absence at a variety of spatial and temporal scales. Significant limitations to these types of studies have included low recapture rates that often limit the interpretation of results, and difficulty identifying specific habitats used or environmental conditions encountered by individual fish. There are also concerns about the selectivity of recapture methods with these studies that may bias results. More recently, a small number of studies have used acoustic or radio telemetry approaches, and results from these projects have provided more detailed migration histories, though for comparatively few fish. Interpretation of the telemetry results is confounded somewhat by the size of tags that could be used with subyearlings, with generally unavoidable tagging bias for larger-than-average fish.

3.1 MIGRATION PHASES

Connor et al. (2003b) described four general migration phases for subyearling fall Chinook salmon collected in the Hells Canyon reach of the Snake River: (1) discontinuous downstream dispersal along shorelines in the unimpounded river, (2) abrupt and mostly continuous downstream dispersal in the main river channel, (3) passive, discontinuous downstream dispersal offshore in Lower Granite Reservoir, and (4) active and mostly continuous downstream movement. Individual fish will likely exhibit more than one phase reflecting changes in fish size, physiological development (i.e., smoltification), and environmental cues (e.g., river environment, photoperiod). There are reasonably well-defined correlations between seasonal river conditions and subyearling behavior patterns, as indicated by peaks in subyearling passage indices at lower Snake River dams (e.g., FPC 2007). However, the early life history differences among populations (see Section 2.2) suggest that the timing of migration phases differ among groups of subyearlings within year.

In the mid-Columbia River, distinct subyearling populations (Hanford wild, Hanford hatchery, upriver wild) are at least partially separated temporally and spatially as they pass through the Hanford Reach and through downstream reservoirs (Dauble et al. 1989; Tiffan et al. 2000a). Migration behaviors by subyearlings from the much larger populations of Columbia River ocean-type Chinook salmon generally support the ‘phase’ hypothesis of Connor et al. (2003b), with increasingly downstream- and offshore-oriented movement through time. In the Hanford Reach, a similar migration behavior hypothesis has been referred to as ‘spiraling-rearing’, whereby subyearlings alternate between relatively stationary rearing in shoreline areas alternated with downstream movement in the main river channel (Independent Scientific Group 2000; Tiffan et al. 2006b). A spiraling hypothesis is also partially supported by the work of Venditti and
Garland (1996), who found subyearlings showed high site fidelity during rearing near shorelines in the Hanford Reach, including more upstream than downstream movement during daytime feeding. Giorgi et al. (1994) also described upstream movements by subyearlings in the John Day Reservoir; motivation for the behavior was unclear.

Taken together, the ‘phase’ and ‘spiraling’ migration hypotheses suggest that there is considerable behavioral variability by subyearlings, with pre-migrant, passive migrant and active migrant components and likely differences between day and night. This variability affects interpretation of migration rates and habitat use evaluations. Tagging studies that use active transmitters may provide some insight into the mechanics of migration and offer evidence for one (or both) of the current hypotheses.

### 3.1.1 DEVELOPMENTAL CUES

A general pattern in juvenile salmonid behavior is that fish select higher velocity, deeper habitats as they grow larger (e.g., Everest and Chapman 1972; Hillman et al. 1987). Juvenile size is also closely linked with migration readiness and behavior. Larger juvenile fall Chinook salmon both initiate migration earlier (e.g., Connor et al. 2004) and move downstream more rapidly (Giorgi et al. 1997; Tiffan et al. 2000a) than their smaller counterparts. This is supported both by direct sampling, such as the collection of larger fish in offshore versus nearshore Hanford Reach habitats (Dauble et al. 1989), and by results from several migration rate studies (e.g., Connor et al. 1991, 1993b; Giorgi et al. 1997). Growth is also linked with physiological development, and larger fish have generally survived seawater challenges at higher rates than smaller fish in experimental tests (e.g., Tiffan et al. 2000a).

Subyearling growth and physiological/osmoregulatory development occur concurrently, and the combination appears to create a “window of migration opportunity” (Tiffan et al. 1997). In tests using subyearlings from the Hanford Reach and collected at McNary Dam, fish showed the greatest seawater preference in late June to mid-July (Tiffan et al. 1997, 2000a). This is a period of rapid subyearling growth that coincides with peak gill ATPase activity, increasing osmoregulatory competence, and increasingly directed downstream movement (Tiffan et al. 1996, 1997). Full seawater competence (i.e., smoltification) was noted only after fish had started active migration, after which gill ATPase levels declined (Tiffan et al. 2000a). This research group inferred that the initiation of downstream movement by Hanford Reach subyearlings occurred when fish were approximately 70 mm long.

A similar size threshold associated with the initiation of downstream movement was reported for Snake River subyearlings. In beach seine collections, average fork lengths were 56-61 mm in May when subyearling abundance was at its peak in rearing habitats, and 86-92 mm in July after the majority of the fish had moved downstream into Lower Granite Reservoir (Connor et al. 2003b).

### 3.1.2 ENVIRONMENTAL CUES

It is difficult to separate environmental migration cues (i.e., water temperature or photoperiod) from physiological and growth-related cues because these variables tend to be inter-correlated.
In fall Chinook salmon literature cited in Connor et al. (2003b), rapid growth, smolt development, and migratory tendencies all increased as water temperatures rose from approximately 9°C to 17°C. Bennett et al. (1998) reported that Snake River subyearling Chinook salmon moved away from shoreline rearing habitats in reservoirs when water temperatures reached approximately 16°C, suggesting this may be a cue for active downstream migration. At temperatures higher than about 20°C, however, juvenile growth can be disrupted along with normal metabolic and smoltification activities (Mesa et al. 2002). This is supported by field studies that show decreasing subyearling migration rates at higher temperatures.

Photoperiod has been shown to affect juvenile salmonid gill ATPase activity, the timing of migration initiation, and downstream migration rates. Experiments with Clearwater River yearling Chinook salmon (stream-type) showed that artificially advancing photoperiod accelerated smolt development and downstream migration despite rearing at ambient temperatures (Muir et al. 1994). In this study, a treatment combination of increased water temperature and advanced photoperiod had the largest effect on physiological and behavioral metrics. A similar combination presumably affects smoltification timing and behaviors of subyearlings.

3.2 DIEL BEHAVIORS

Tiffan et al. (1996) used a series of day- and night-time tests in an experimental tank to evaluate seasonal, time-of-day, and water velocity effects on downstream movement by subyearling Chinook salmon. In this study, few fish moved downstream without some velocity through the tank. The highest net downstream movement occurred during the day at the highest velocity treatment (45 cm/s), and overall downstream movement was greatest in May and June. Movement at night was almost exclusively downstream, in contrast to during the day, when fish actively moved upstream and downstream. Across treatments, subyearlings were far more active during the day, while nighttime behaviors were more passive and downstream-oriented.

A large-scale subyearling and yearling salmonid sampling project in the Hanford Reach found that most fish moved downstream at night (Dauble et al. 1989). Peak fyke net catches for subyearlings were just after darkness (2200–2400 h), while yearling catches were highest between midnight and dawn (2400–0400 h). Relatively more subyearlings than yearlings were caught during daylight hours along shorelines. In electrofishing samples, diel catch patterns varied seasonally, with peak subyearling catches from 1600–2200 h in April and May, from 0400–1000 h in June, and from 2200–0400 in late summer. Dauble et al. (1989) attributed these differences to seasonal size-related distribution differences and feeding/rearing behaviors; notably, stock-of-origin also differed among time periods. In the Snake River reservoirs, juvenile Chinook salmon were captured almost exclusively at night (Bennett et al. 1988).

Venditti and Garland (1996) also reported seasonal differences in diel catch rates of Hanford Reach subyearlings, with a shift from more daytime to more nighttime catch from early to late in the season. Diel abundance estimates were significantly different seasonally and spatially, with evidence for different behaviors in nearshore and offshore habitats (Venditti and Garland 1996).
During daylight hours, subyearlings tended to use the water column, presumably for feeding; at night, subyearlings were primarily associated with the bottom substrate.

As with migration phases, the combined research on subyearling migration behaviors and migration cues suggest that fish likely respond to a variety of environmental, ecological, and physiological stimuli. There does not appear to be a consensus on which factors are the best predictors of migration initiation or subsequent migration behavior. Instead, it is likely that subyearlings are affected by a combination of factors and that the reported behaviors represent a complex set of responses.

4.0 MIGRATION TIMING PATTERNS

Estimating migration timing for Snake River subyearling fall Chinook salmon is complicated by two primary factors: (1) the presence of spring–summer subyearlings (see Section 2.1), and (2) identifying when fish are actively migrating. The latter challenge is especially difficult in the Hells Canyon reach and in Lower Granite Reservoir, where subyearling show a mixture of rearing, discontinuous downstream movement, passive, and active migration (e.g., Connor et al. 2003b). The transition from rearing to migration appears to be gradual, and the timing of this transition is highly variable among individuals (Smith et al. 2002, 2003) and populations (i.e., Hells Canyon vs. Clearwater River). Migration timing distributions become more clearly defined once subyearlings reach the lower Snake River dams, both because fish can be collected more efficiently and with less bias, and because there is a general consensus that most subyearlings that reach the dams have entered a more active migration phase.

4.1 UNIMPOUNDED REACHES

Subyearling rearing in shoreline areas of Hells Canyon peaks in May–June and continues into July in most years (Connor et al. 1993b, 2002, 2003b; Smith et al. 2003). Estimates of emigration timing in this reach have generally been back-calculated from dates PIT-tagged fish were captured at Lower Granite Dam or by inferring emigration dates from catch-per-unit-effort (CPUE) patterns in beach seine sampling. Recapture rates of PIT-tagged fish in shoreline samples have typically been quite low (i.e., ≤ 15%). They indicate that some fish hold position for days to weeks following tagging (medians = 7–9 d, range = 1-42 d, Connor et al. 2003b). In contrast, very few (< 5%) subyearlings have been recaptured in shoreline sampling upstream or downstream from their tagging location, perhaps because fish move downstream to Lower Granite Reservoir relatively quickly after leaving shoreline areas. These patterns suggest that shoreline CPUE may be a useful metric to approximate population-level emigration timing, indicated by CPUE declines following peak catches.

Connor et al. (2003b) estimated mean subyearling residence times for fish tagged in the upper and lower sections of the Hells Canyon reach of 10–15 d and 9-13 d, respectively. Importantly, emigration from Hells Canyon did not appear to indicate the active seaward migration typical of
smolts, as these authors estimated that subyearlings spent an additional 20–42 d and 38–57 d rearing in Lower Granite Reservoir.

Among subyearlings from Hells Canyon and lower River reaches, those from the upper Hells Canyon Reach begin migrating earliest and those from the Clearwater River are latest, reflecting the importance of water temperature effects (Connor et al. 2002). In all reaches, migration was significantly earlier in years with warmer spring water temperatures. A clear temperature threshold for migration initiation has not been established in the free-flowing rivers upstream from Lower Granite Reservoir. However, 16–18°C temperatures have been associated with subyearling dispersal offshore in Lower Granite Reservoir (Curet 1994; Bennett et al. 1998) and in Columbia River reaches (Key et al. 1993). At Lower Granite Dam, the 18°C threshold is generally reached in late June or early July (Smith et al. 2003; Columbia River DART), coincident with rapidly decreasing CPUE in Hells Canyon (Connor et al. 2003b). In the cooler Clearwater River, the 18°C threshold is less predictable and is not reached in some years; in this reach, temperatures depend in part on water releases from Dworshak Reservoir, which potentially alter the timing of life history events. It is highly likely that temperature units accumulated (growth potential) will have a higher effect on rearing duration than a temperature threshold date.

4.2 TIMING AT DAMS

The subyearling passage indices compiled by the Fish Passage Center (FPC) show subyearlings passing Lower Granite, Little Goose, and Lower Monumental dams from approximately mid-May into September (Figure 3). Timing distributions at the three dams are relatively consistent within year, but year-to-year variability is quite high. In the last decade (1998-2007), median dates have ranged from early June to mid-July, inter-quartile ranges span from late May into early August, and some late migrants continue to pass well into September in some years (Figure 3). The later migrants are presumably dominated by Clearwater River subyearlings, though this has not been conclusively demonstrated. During these years, there was also a trend towards earlier timing, but it is not clear whether this can be explained by river environment or some other factor (e.g., demographics). Importantly, the FPC indices do not differentiate among spring–summer and fall-run fish and the presence of spring–summer subyearlings (depending on their relative abundances) would tend to skew distributions early.
Timing distributions at Lower Granite Dam for fall Chinook subyearlings PIT-tagged in Hells Canyon and in the Clearwater River by Connor and colleagues show that peak passage generally occurred from late June through mid- to late July (Figure 4). Few subyearlings were recorded at the dam prior to about 15 May. In contrast, many distributions were right-skewed, with some fish recording in the juvenile bypass system into early November. Clearwater River fish arrived at Lower Granite Dam one month to about six weeks later, on median, than fish from the Hells Canyon reach (Connor et al. 2002).

In a multi-year PIT-tagging study by Smith et al. (2003), wild and hatchery-reared subyearlings released in weekly batches in the Hells Canyon Reach had peak passage at Lower Granite Dam from 6-19 July (1998), 13-26 July (1999), and 29 June-12 July (2000). In 2001, a very low flow year, two peaks were observed, with the first from 1-14 June and a second from 29 June-12 July (Smith et al. 2003).
Figure 4. Timing distributions (median and range) for subyearling Chinook salmon detected at Lower Granite Dam. All data were reported in Connor et al. (2000; 2002; 2003a). Data from the 2000 paper (●) included a mix of fall and spring–summer subyearlings collected in the Snake River. The remaining fish were all fall Chinook, with the following collection sites: ● = lower Hells Canyon reach (2002 paper); ● = upper Hells Canyon reach (2002 paper); ● = lower Clearwater River reach (2002 paper); ● = lower Hells Canyon reach (2003 paper); ● = upper Hells Canyon reach (2003 paper).

5.0 DOWNSTREAM MIGRATION TIMES AND RATES

Point-to-point passage times (d) and rates (km/d) have been calculated for subyearling fall Chinook salmon through a variety of Columbia and Snake River reaches. These metrics are generally less subjective than attempts to define migration phases or migration timing distributions. Most estimates have relied on PIT-tagging studies, with subyearlings collected using a variety of techniques (i.e., seining, trapping, electrofishing, or collection in juvenile bypass facilities at dams). For the most part, downstream detections have been at dam bypass systems.

Many of the reviewed studies used univariate or multivariate regression analyses to evaluate environmental and/or physiological effects on fish migration speed. In most cases, results of these analyses have been mixed or inconclusive, in large part because it has been difficult to clearly separate biological from environmental effects. In both the Snake and Columbia rivers, flow (discharge) and water temperature during the summer tend to be strongly negatively correlated, while water velocity also tends to decrease as discharge decreases. Most analyses have used river discharge data — which are readily available — rather than flow velocity, which may be the more biologically important variable. In addition, all of the environmental variables
tend to be correlated with subyearling growth rates, fish size, and physiological changes such as ATPase activity and osmoregulatory competence.

As a general rule, subyearling migration rates (km/d) have been shown to increase as fish move downstream through the Snake and Columbia rivers, but rates were highly variable among years and among individuals (Connor et al. 2003; Giorgi et al. 1997). Effects of environmental conditions were often inconsistent across reaches and years, reflecting both biological differences among fish as they transitioned from rearing to active migration and likely non-linear responses to environmental conditions (i.e., changes in river discharge or water temperature may affect migration rates only until some threshold level is reached) (Berggren and Filardo 1993; Giorgi et al. 1994; Smith et al. 2003).

5.1 HELLS CANYON TO LOWER GRANITE DAM

Travel time estimates for subyearlings PIT-tagged in Hells Canyon have included time spent in both the unimpounded reach and Lower Granite Reservoir. Connor et al. (2003b) attempted to partition the time spent in these migration segments by using recapture data from beach seine sampling in the riverine portion (see below). However, most travel time studies have estimated times and/or rates that included the combined riverine and reservoir residence times, and therefore reflect a combination of rearing and migratory behaviors.

In the Connor et al. (2003b) study, subyearlings spent an annual average of 10–15 d in the Hells Canyon reach after initial tagging before recapture in beach seines. Median migration rates for the relatively small number of fish that were recaptured were 5.5 km/d ($\text{range} = 0.2–25.2 \text{ km/d}$) for fish tagged in the upper Hells Canyon reach and 0.3 km/d ($\text{range} = 0.1–31.0 \text{ km/d}$) for fish tagged in the lower portion of the reach. These rates are much lower than would be expected for even passive downstream movement, suggesting fish were rearing for much of the elapsed time.

In studies by Smith et al. (2003) and Connor et al. (2003b), mean subyearling migration rates from release in Hells Canyon through the combined riverine and reservoir reaches to Lower Granite Dam ranged from 3.1–6.6 km/d for fish released in the upper Hells Canyon and from 1.8–3.3 km/d for fish released in the lower Hells Canyon (Figure 5). The fastest fish moved through the combined reach at rates of 20–45 km/d. Median migration rates for weekly release groups from the Hells Canyon reach and the Clearwater River (Smith et al. 2002) were 1.8–7.1 km/d across several years; median residence times in this study were 13–66 d.

In earlier studies summarized by Connor et al. (1991, 1993b, 1996), subyearling Chinook salmon annual migration rates ranged from 2.1–3.6 km/d from the Hells Canyon reach to Lower Granite Dam. Migration rates were higher for larger subyearlings. The size-migration rate relationship was confirmed in an experiment with hatchery-reared yearling and subyearling fall Chinook salmon of different size classes (Connor et al. 2004). In that study, PIT-tagged fish were released in Hells Canyon and detected at Lower Granite Dam, and yearling fish migrated approximately 2–6 times faster than subyearlings. In addition, large subyearlings migrated significantly faster than medium and small subyearlings (Connor et al. 2004).
The Nez Perce Tribe monitored hatchery-reared yearling fall Chinook salmon released in the Snake and Clearwater rivers for several years (e.g., Rocklage 2005). Migration rates to Lower Granite Dam ranged from 5.5–17.6 km/d. Travel times were 13–16 d from the release locations in the Clearwater River to Lower Granite Dam and were 23–29 d from release to McNary Dam. Migration rates were positively correlated with river discharge and negatively correlated with temperature (Rocklage 2005), patterns also observed for subyearling fish.

![Subyearling fall Chinook salmon migration rates](image)

**Figure 5.** Subyearling fall Chinook salmon migration rates (km/d) reported in the combined reach that included Lower Granite reservoir and the Snake River upstream from the reservoir. Data are from Connor et al. (2003) and Smith et al. (2003). ○ = mean and range, fish released in the Snake River between the Lower Granite reservoir and the Salmon River; ● = mean and range, fish released in the Snake River upstream from the Salmon River; ▪ = median, 20th, and 80th percentiles, fish released in the Snake River at Pittsburg Landing; ■ = median, 20th, and 80th percentiles, fish released in the Snake River near Billy Creek.

Subyearling passage times (d) in the Hells Canyon–Lower Granite Dam reach tend to increase later in the year with decreasing flow (discharge), increasing temperature, and increasing water clarity (Smith et al. 2003). Similar patterns have been recorded in a variety of reports and papers (Connor et al. 2003b, and several annual reports by Connor and colleagues), and have been attributed to lower velocity at low discharge, reduced likelihood of smoltification at high temperatures (i.e., > 20°C, Marine 1997), and collinearity among these predictor variables. Among-fish variability in migration rates was generally higher in this combined reach when compared to rates in downstream reservoirs in the Snake and Columbia rivers (Smith et al. 2003), presumably because of differing levels of active migration versus rearing and potentially a weeding out effect. Fish behavior patterns were also somewhat unpredictable in years with unusual environmental conditions. For example, Smith et al. (2003) speculated that some subyearlings were flushed out of Hells Canyon and Lower Granite Reservoir early in 1997, a
year with very high spring and summer discharge, while others remained for longer-than-average periods in upriver rearing locations.

5.2 LOWER SNAKE RIVER RESERVOIRS

5.2.1 LOWER GRANITE RESERVOIR

Few studies have directly estimated subyearling migration rates in Lower Granite Reservoir, though the overall subyearling rearing period was estimated at 75–112 d by Bennett et al. (1998). As much as a third of the total reservoir residence time reported in the Bennett et al. (1998) study was in pelagic rather than shallow littoral areas.

In PIT-tagging studies, Connor et al. (2003b) used a combination of recapture and downstream detection data to estimate that fish from Hells Canyon spent an annual average of 20–42 d in Lower Granite Reservoir, with travel rates of <1–3.5 km/d. These estimates were calculated by subtracting the estimated time subyearlings spent in the free-flowing Snake River from the total time from Hells Canyon to Lower Granite Dam. The times and rates incorporated feeding and rearing behaviors as well as active migration. Active migration, once initiated, was presumably at substantially higher ground speeds than suggested by the median rates. The authors also noted that passage times were likely inflated (i.e., rates were slower) for many fish due to slow passage through the apparently challenging environment in the Lower Granite forebay, as has been described at other dams (e.g., Venditti et al. 2000).

5.2.2 LITTLE GOOSE RESERVOIR

Mean annual migration rates from Lower Granite Dam to detection at Little Goose Dam ranged from 10–20 km/d for fish released in the upper Hells Canyon and 7–18 km/d for fish PIT-tagged and released in lower Hells Canyon (Figure 6). Median rates for weekly release groups differed from year-to-year and week-to-week, but generally ranged from about 8–20 km/d, with a few exceptions when fish migrated more slowly (mostly in weeks with small sample sizes) (Smith et al. 2002).

Connor et al. (2003b) found little correlation between subyearling migration rates in the Little Goose Reservoir and either river flow (discharge) or water temperature. Fish from the lower (and cooler) Hells Canyon reach continued to migrate relatively more slowly in Little Goose Reservoir after at least partial mixing with upper Hells Canyon fish in Lower Granite Reservoir (Connor et al. 2003b). This may reflect lingering effects of temperature-related size differences among cohorts.

5.2.3 LOWER MONUMENTAL RESERVOIR

Migration rates from Little Goose Dam to Lower Monumental Dam have been calculated using PIT tags in several years (Smith et al. 2002, 2003), radiotelemetry in three years (Venditti et al. 2000), and acoustic telemetry in one year (Cook et al. 2007). Weekly median migration rates ranged from < 5 to more than 30 km/d, with considerable week-to-week and among-year
variability (Figure 7). Rate estimates were affected by the downstream endpoints (e.g., Lower Monumental forebay, tailrace or juvenile bypass system) because many fish pass relatively slowly through the forebay area (Venditti et al. 2000). (Note: comparison across studies and methodologies should be qualitative only, because start and endpoints differed and some fish recorded in the forebay were not recorded passing the dam.)

Using radiotelemetry, Venditti et al. (2000) partitioned the Lower Monumental Reservoir into several reaches. They found that subyearling migration rates differed among reaches, with slower rates in each successive downstream reach: estimates ranged from ~26 km/d in the uppermost portion of the reservoir, to ~14 km/d in lower reaches and < 1 km/d in the Lower Monumental forebay. Differences among reaches were attributed, in part, to reduced velocity in downstream reaches and possible route-searching behaviors in the forebay. Between 10–20% of the tagged fish spent a week or more in the forebay and/or lower reservoir, and many fish moved upstream or laterally across the reservoir multiple times (Venditti et al. 2000). Median residence times in this study were 1.8–2.3 d in the upper reservoir (~46 km) and 1.0–1.4 d in the lower reservoir (~15 km).

In the acoustic telemetry study of Cook et al. (2007), there were significant behavioral and biological differences among subyearling Chinook salmon that were or were not recorded passing Lower Monumental Dam after release below Little Goose Dam. The authors defined
these two groups as ‘non-migrant’ and ‘migrant’. (Note: acoustic arrays were in place through late September, so overwintering fish were not detected). Fish that passed through the reservoir tended to be larger and moved more rapidly than fish that were last detected upstream from Lower Monumental Dam, including in the forebay. The percentage passing the dam dramatically decreased with migration date, from > 80% passage for fish released in mid-June to < 10% in mid-July (Cook et al. 2007). Migration rates varied through time, with the slowest fish recorded early and late in the study period, and the fastest fish in the middle release group in early July. Median reservoir residence times from release to the Lower Monumental forebay detection array ranged from 1.4–4.4 d and averaged about 2.1 d; median times from release to the Lower Monumental tailrace ranged from 1.6–3.4 d (mean = 2.4 d, ‘migrant’ fish only). These residence time estimates were similar to, or slightly lower than the 3–6 d medians reported for PIT-tagged fish in Smith et al. (2003) from Little Goose Dam to Lower Monumental Dam.

![Figure 7. Subyearling fall Chinook salmon migration rates (km/d) reported in Lower Monumental reservoir.](image)

5.2.4 LOWER MONUMENTAL DAM TO MCNARY DAM

Subyearlings migrated more rapidly from Lower Monumental Dam to McNary Dam (the next downstream juvenile collection site) than through any of the upstream Snake River reaches. Based on weekly release groups, median annual migration rates through this reach were mostly 20–40 km/d (Smith et al. 2002). Sample sizes were small for many weekly releases, but there
was a general pattern of faster migration in years with higher river discharge (i.e., rates were generally slowest in low-flow 2001 and highest in moderately high-flow 1998).

5.3 UPPER COLUMBIA RIVER

Subyearling migration rates in the Columbia River are shown for comparison, and the larger research effort provides some additional context. In the upper Columbia, ocean-type Chinook salmon subyearlings were collected and PIT-tagged at Rock Island Dam from 1992-1995 and migration rates were calculated from Rock Island Dam downstream ~261 km to McNary Dam (Giorgi et al. 1997). Mean migration rates during the four years averaged 15.6 km/d (range = 0.8–50.9 km/d). Larger fish were more likely to be detected at McNary Dam, and fish size was the best single-variable predictor ($r^2 = 0.59$) for migration rate. The combination of fish size and mean river flow (discharge) explained more of the variation in migration rates than any other combination of variables, which included water temperature and date of fish release (Giorgi et al. 1997). These authors concluded that subyearlings were relatively insensitive to changes in river flow or temperature in this migration reach.

5.4 LOWER COLUMBIA RIVER RESERVOIRS

There has been a considerable research effort to understand subyearling ocean-type Chinook salmon migration behaviors and passage times through John Day Reservoir. These studies have targeted fish from the Hanford Reach (wild- and hatchery-origin) and from summer-fall ocean-type stocks upstream from Priest Rapids Dam. Most fish have been collected in the juvenile bypass system at McNary Dam, though fish have also been tagged or marked at a variety of upstream locations.

In the early 1980s, Giorgi et al. (1994) used freeze branding to mark groups of subyearlings collected at McNary Dam and then recaptured approximately 123 km downstream at John Day Dam. Median travel times for 49 branded groups ranged from 6–26, 9–46, and 7–29 d in three study years (median migration rates = 5–20, 3–14, 4–18 km/d). Individual migration rates were highly variable within release groups. In addition to collection at John Day Dam, some fish were recaptured in mid-reservoir purse seines. This sampling indicated that many fish (60–67%) moved upstream within the reservoir, often for considerable distances (9–82 km) and for extended periods (6–104 d). Efforts to model subyearling migration rates using water temperature, release date, and a flow variable were mostly inconclusive, with low explanatory power; different ‘best’ models were selected in each year and with all years combined (Giorgi et al. 1994).

Berggren and Filardo (1993) used the Giorgi et al. (1994) data plus data from an additional three years of subyearling marking at McNary Dam. This expanded study built a model that accounted for approximately 65% of the variability in subyearling passage times through the John Day Reservoir. The model included date, change in flow, and the reciprocal of average flow (i.e., flow$^{-1}$). The reciprocal flow term explained the highest proportion of the variability, and was interpreted as shorter fish passage times at higher flow. Migration date was negatively correlated with passage time, with later fish migrating more slowly. The ‘change in flow’ flow
variable was also significant, which the authors attributed to longer migration times as flow (discharge) rapidly decreased in summer.

In the early 1990s, several hundred thousand subyearling Chinook salmon were collected and tagged with coded wire tags at McNary Dam, in a total of 130 brand groups (e.g., Nelson et al. 1991; Tiffan et al. 1996, 2000a). Median migration times through John Day Reservoir varied seasonally, with faster migrants generally early and late in the migration and the slowest fish in mid-migration (note: the 1994 results showed an opposite pattern; Tiffan et al. 1996). Mean travel times were 9.3, 19.8, and 14.1 d (rates = 6–13 km/d) in the three ‘typical’ years. In multiple regression analyses by Tiffan et al. (2000a), the reciprocal of minimum flow (i.e. \( \text{flow}_{\text{min}}^{-1} \)) and mean fork length produced the best model \( r^2 = 0.47 \). This finding was consistent with the subyearling results of Giorgi et al. (1997) in the Rock Island to McNary reach. Tiffan et al. (2000a) also evaluated the effects of gill ATPase activity, and found it was not useful for explaining the variability in subyearling travel time. In fact, some of the highest ATPase levels were associated with the slowest migrants (Tiffan et al. 2000a).

In the John Day Reservoir reach, population effects likely influence the results of subyearling travel time models. Fish size- and timing-related differences among Hanford Reach wild fish, Priest Rapids Hatchery fish, and Snake and upper Columbia River stocks affect arrival timing of these groups at McNary Dam (Dauble et al. 1989; Nelson et al. 1991), and may explain the somewhat counterintuitive pattern of relatively slow migrants in mid-migration described by Tiffan et al. (2000a).

Few subyearling studies have been designed to directly evaluate migration rates downstream from John Day Dam, but a few ancillary results have been collected. Nelson et al. (1991) reported that fish moved more rapidly through the The Dalles and Bonneville reservoirs than through the John Day Reservoir. Similarly, in the Smith et al. (2003) study of Snake River subyearlings, migration rates between McNary and Bonneville dams were much faster (\( \text{median} = 43 \text{ km/d} \)) than through any Snake River reservoir (\( \text{median} \approx 11 \text{ km/d} \)) or through the reach from Lower Monumental Dam to McNary Dam (\( \text{median} = 27 \text{ km/d} \)).

The combined Columbia River subyearling studies of Nelson et al. (1991), Berggren and Filardo (1993), Giorgi et al. (1994,1997), and Tiffan et al. (1996, 2000a) — along with the annual reports for these studies — present some disagreement about the effects of river discharge on migration rates. There was a general sense that fish moved downstream more rapidly when discharge was higher, but analyses were often confounded by population effects, physiological and size differences among fish, and collinearity among tested predictor variables.

### 6.0 REACH SURVIVAL

A variety of studies have estimated subyearling Chinook salmon survival rates through the lower Snake River. Most of the research has focused on reach-scale survival and therefore includes effects of river, reservoir and dam passage. PIT-tag studies have predominated, substantially limiting the ability to partition mortality among migration environments or passage routes. Collectively, the survival studies have examined seasonal patterns, correlations with river
conditions (e.g., discharge, water temperature, turbidity), and among-population differences (e.g., Hells Canyon vs. Clearwater, wild- vs. hatchery-origin).

Estimation methods have changed over the years, with more recent work estimating ‘joint probabilities of survival and detection’ at the dam bypass systems (PIT-tag studies). The joint approach was partially an effort to address the fates of overwintering fish, which were typically excluded in traditional survival estimates. Joint probability estimates have generally differed little from traditional estimates for subyearling groups with relatively low overwintering rates (i.e., upper Hell’s Canyon fish), but have had a larger effect on the interpretation of Clearwater River fish. The joint probability approach produces conditional survival estimates, as they incorporate the probability of migration in-season, the probability of detection (reduced when bypass systems are shut down), and survival. These conditions would tend to produce survival underestimates, particularly for the PIT-tag studies given their dependence on the dam bypass systems.

A general pattern, especially upstream from Lower Granite Dam, is that subyearling survival has steadily decreased within year, with very low survival for the latest release groups in late June through early July. This migration timing effect is correlated with a suite of environmental and physiological (i.e., size-related) changes, and researchers have had difficulty clearly separating effects within year. Earlier in the outmigration period discharge and turbidity tend to be higher, and water temperatures tend to be lower; these variables have had relatively strong correlations with subyearling survival estimates and migration rates. Year-to-year differences also suggest higher survival in cooler, high-flow years.

Downstream from Lower Granite Dam, survival patterns have been somewhat less predictable. Correlations with environmental conditions were mostly in the same direction, though with lower explanatory power, than in the reach upstream from Lower Granite Dam. This may reflect differences in migratory behavior, as fish that passed Lower Granite Dam were more likely to be active migrants. River conditions also tended to be considerably less variable during summer when fish are passing through the lower three reservoirs, making it more difficult to detect differences; this challenge has been compounded by relatively smaller sample sizes downstream from Lower Granite Dam.

In all study reaches, there has been uncertainty about subyearling mortality agents, with migration delay, disorientation, metabolic costs, and predation all posed as potential explanatory variables. Low flow and high temperature indirectly affect each of these potential mortality types, by either slowing migration, increasing predation exposure time, or through metabolic effects on both subyearlings and predators. In general, larger subyearlings have tended to survive at higher rates, perhaps as a result of greater swimming abilities and/or size-selective predation on smaller fish. Predation studies suggest smallmouth bass (*Micropterus dolomieu*), northern pikeminnow (*Ptychocheilus oregonensis*), walleye (*Stizostedion vitreum*), and channel catfish (*Ictalurus punctatus*) become more active as water temperatures rise and these predators tend to be more efficient in less turbid conditions. Combined, these factors suggest that elevated predation rates late in the season likely contribute to the low survival during this time, though a combination of slow passage, developmental effects, and predation effects is likely. (See Section 8.2 for additional description of predation studies.)
6.1 SURVIVAL TO LOWER GRANITE DAM

Among the Snake River reaches, survival studies have emphasized the reach upstream from Lower Granite Dam for several reasons. These include the relatively longer residence times and higher mortality rates in this reach compared to the downstream reservoirs. In addition, the majority of untagged subyearlings are collected (when possible) at the Snake River dams during the summer and are transported downstream in barges (Smith et al. 2003; Muir et al. 2004).

Several of the larger-scale subyearling survival studies (e.g., Muir et al. 1998, 1999, 2004; Smith et al. 1997, 2002, 2003; Connor et al. 1998b, 2000, 2003b) reported greater hatchery and wild subyearling survival to Lower Granite Dam with higher river discharge, lower temperature, and with increased water transparency. These patterns were also clearly demonstrated in high survival estimates early compared to late in most annual migrations (e.g., Figure 8). Survival for weekly release groups was > 70% early in the migrations in some years, and often dropped to < 10% late in the season. Variability in annual survival estimates to Lower Granite Dam was quite high among years, with some of the lowest survival rates recorded in 2001, a year with near-record low-flow conditions.

In experiments with subyearling and yearling fall Chinook salmon, fish size was a strong predictor of survival from release in the Snake River to the Lower Granite Dam tailrace (Connor et al. 2004). Modeled survival probabilities suggested a rapid increase in survival after fish length reached approximately 110 mm. Survival estimates in two experimental years were 42–43% for ‘small’ subyearlings, 65–72% for ‘medium’ subyearlings, 73–82% for ‘large’ subyearlings, and 89–92% for yearling fish (Connor et al. 2004). The yearling survival estimates were nearly identical to the rates reported for yearling spring-summer Chinook salmon as they passed through Lower Granite Reservoir (Muir et al. 2001).

Subyearlings from the Clearwater River have typically survived to Lower Granite Dam at rates that were lower (i.e., up to ~75% lower) than fish from the Snake River (e.g., Connor et al. 1997; Connor 2001), though estimates have been similar for some hatchery-reared releases of similar-sized fish (e.g., Connor et al. 1998b). This presumably reflects both later emergence timing and subsequent size-related survival differences among the populations. The higher likelihood of overwintering behavior by Clearwater fish may also play a role, as these fish may be less likely to be detected. However, Connor and colleagues have concluded that mortality in the emergence year is probably more consequential than during the overwintering period.
Figure 8. Examples of estimated subyearling fall Chinook salmon survival probabilities, from sites where fish were released upstream from Lower Granite Reservoir to Lower Granite Dam. Open symbols represent data reported in Smith et al. (2002), where release sites were: \(\Delta = \text{Billy Creek}; \circ = \text{Pittsburg Landing}; \Box = \text{Big Canyon Creek (Clearwater River)}; \) inverted \(\Delta = \text{Asotin}.\) Solid symbols represent data reported in Connor et al. (2003b), wherein all fish were released in the Hells Canyon reach. Symbol colors: black = 1998; blue = 1999; red = 2000; green = 2001. Error bars = +/- 1 SE.

6.2 LOWER SNAKE RIVER RESERVOIRS

6.2.1 LITTLE GOOSE RESERVOIR

Muir et al. (2004) reported weekly hatchery subyearling survival rates from Lower Granite Dam to Little Goose Dam ranging from 87–94% in 2003 (Figure 9). These estimates were based on weekly release dates at the upstream sites. When calculated based on detection dates at Lower Granite Dam, weekly estimates ranged from 60–95%. In earlier years of this research, weekly estimates ranged from 30–93\% (means = 50–70\%) (Muir et al. 1998).

A recent comparison among rearing types (wild origin, hatchery surrogates for wild fish, and hatchery production fish produced survival estimates to Little Goose Dam ranging from 60–97\%, with most estimates between 70–80\% (Connor et al. 2008). Hatchery production fish generally performed better than either the wild or surrogate fish, largely because production fish were larger upon release.
Figure 9. Examples of estimated subyearling fall Chinook salmon survival probabilities, from Lower Granite Dam to Little Goose Dam. Symbols represent data reported in Smith et al. (2002), where colors: black = 1998; blue = 1999; red = 2000; green = 2001. Error bars = +/- 1 SE.

6.2.2 LOWER MONUMENTAL RESERVOIR

Annual survival estimates through the combined Little Goose and Lower Monumental reservoirs ranged from 41–77% (mean = 64%; Figure 10) through August for the hatchery fish released upstream from Lower Granite Dam by Smith et al. (2002, 2003). After early August, survival estimates for these fish dropped to 25–50% (mean = 35%). Results in the Muir et al. (1998, 1999) studies were similar.

Muir et al. (2004) estimated weekly hatchery subyearling survival rates from Little Goose Dam to Lower Monumental Dam ranging from 0.83–0.96 in 2003. These estimates were based on weekly release dates. When calculated based on detection dates at Lower Granite Dam, weekly estimates ranged from 0.76–1.00. The Connor et al. (2008) comparison among rearing types produced survival estimates for this reach that were mostly 80–90% in 2006.

Survival estimates (joint probability of survival and detection) in the acoustic telemetry study of Cook et al. (2007) varied substantially within a single year. In this study, three periods were identified, one where fish were considered ‘active migrants’ in the second half of June, a second ‘transitional period’ in early July, and a third ‘non-migrant’ period in mid-July. Survival from the release site downstream from Little Goose Dam to the Lower Monumental tailrace declined from > 80% in the first period, to < 70% in early July, and then dramatically to about 11% in mid-July (Cook et al. 2007). These patterns were attributed to possibly high predation during the warmer, later period plus behavioral differences that included, potentially, overwintering.
Figure 10. Examples of estimated subyearling fall Chinook salmon survival probabilities, from Little Goose Dam to Lower Monumental Dam. Symbols represent data reported in Smith et al. (2002), where colors: black = 1998; blue = 1999; red = 2000; green = 2001. Error bars = +/- 1 SE.

6.2.3 MULTI-DAM REACHES

Several studies have included survival estimates over multi-dam reaches, including Smith et al. (2002) and Muir et al. (1997, 1998, 2004). In the Muir et al. studies, survival from release sites in the Snake and Clearwater rivers to Lower Monumental Dam (i.e., through three reservoirs) ranged from < 5% for fish released in July to as high as 35–40% for fish released in early to mid-June. Mean estimates in 1996, a relatively cool, high-flow year, were about 18% (Muir et al. 1998). In 1995, estimates for Hells Canyon releases to Lower Monumental Dam were somewhat higher (25–45%), considerably higher than for Clearwater River fish (~5%) (Muir et al. 1997).

Survival estimates from Lower Granite Dam to Lower Monumental Dam varied among years, but were mostly 50–80% during weekly estimates from the middle of the run (i.e., June-July), and then typically dropped off to 25% or less by late August (Smith et al. 2002). Muir et al. (2004) reported weekly hatchery subyearling survival rates from Lower Monumental Dam to McNary Dam ranging from 73–85% in 2003, based on weekly release dates. When estimates were calculated based on detection dates at Lower Granite Dam, weekly values from 36–99% and estimates were lower later in the migration.

6.3 ENVIRONMENTAL EFFECTS

Many of the analyses related to environmental effects on subyearling survival in the lower Snake River have focused on the effects of summer flow augmentation from Dworshak and Brownlee
reservoirs. Releases from these sites increase both flow volume and velocity, particularly in Lower Granite Reservoir, which has been associated with higher juvenile survival rates. The releases also increase water turbidity, which researchers believe reduces predation rates. Finally, cooler water released from Dworshak Reservoir is believed to provide some potential survival benefits at the warmest times, though there is some tradeoff with reduced subyearling growth rates in the lower Clearwater River and possibly Lower Granite Reservoir.

The general survival pattern reported in several studies is that subyearling survival increased as flow increased and temperature decreased (Muir et al. 1999, 2004; Connor et al. 1998b, 2003a; Smith et al. 2003). These river environment variables are typically highly correlated during summer (i.e., \( r > 0.9 \)), making it difficult to separate effects. However, somewhat atypical conditions in 1998–2000, when correlations were substantially lower, indicated that flow and temperature independently affected survival rates (Connor et al. 2003a).

Muir et al. (2004) suggested that a temperature threshold of approximately 19°C was associated with a substantial decrease in subyearling survival. Similarly, substantial survival decreases were associated with temperatures reaching between 18–19°C in a temperature exposure index described in Connor et al. (2003a). While increasing temperature was consistently associated with lower survival rates, Smith et al. (2003) cautioned that the relationship was not necessarily constant from year-to-year, probably because of the effects of other factors like discharge.

The relationship between river discharge and survival has been modeled in several ways, including using indices during subyearling rearing and migratory phases. In the Connor et al. (2003a) study, regression models suggested that survival increased by approximately 3% for each 100 m³·s⁻¹, with a relatively linear relationship between about 1,000–2,400 m³·s⁻¹. In Smith et al. (2003), the relationship between flow and survival was non-linear, with relatively large survival increases with flow increases until a threshold of about 2,000 m³·s⁻¹; above this level, survival rates were more constant. These authors note, however, that survival results in the unusually high-flow 1997 study year may have affected modeling results because subyearling behaviors were different (i.e., many apparently moved downstream early) and passage conditions at the dams were difficult.

### 6.4 WINTER SURVIVAL

Dam-to-dam survival estimates for the radio-tagged subyearlings in Tiffan et al. (2005, 2006c) and Kock et al. (2007) were quite variable among years and reaches. Importantly, these estimates were limited by radio tag battery life and were therefore more likely to be underestimates of true survival because overwintering fish and those with long passage times would be undetected. Fish were released in the Lower Granite Dam forebay in all years, and 81–85% were detected in the Lower Granite tailrace. Percentages detected in downstream tailraces were 32–60% at Little Goose, 16–52% at Lower Monumental, and 6–31% at Ice Harbor dams. Estimates for individual reservoir reaches were 38–74% through the Little Goose Reservoir, 52–86% through Lower Monumental Reservoir, and 35–76% through Ice Harbor Reservoir (Tiffan et al. 2005, 2006c; Kock et al. 2007).
7.0 HABITAT USE

Much of the research on subyearling Chinook salmon habitat use in lower Snake River reservoirs was conducted by Bennett and colleagues in the late 1980s through the 1990s. The work was part of several integrated studies that examined subyearling habitat associations, ecological relationships (i.e., community structure, predator and prey relationships), and benthic invertebrate evaluations. The studies were mostly designed to inform dredge sediment disposal options being considered at that time.

Subyearling fall Chinook salmon habitat associations have also been extensively studied in the Hanford Reach of the Columbia River and, to a somewhat lesser degree, in McNary and John Day reservoirs. Across Columbia and Snake River research projects, a reasonably cohesive set of substrate, water velocity, slope, depth, and temperature associations have been identified for subyearling rearing and feeding behaviors in summer. In contrast, habitat use patterns during active migration, during the ‘spiraling’ or discontinuous downstream movement phases, and during winter have been relatively incompletely described.

Most of the regional subyearling habitat evaluations have relied on seining or electrofishing to collect fish. Such projects were typically shoreline-oriented, which introduced an initial bias into sample collection. There has also been uneven day- and night-time sampling effort, and diel habitat use patterns have not been fully described (but see Venditti and Garland 1996 and Venditti et al. 1997). There has been little—if any—effort to describe habitat use patterns by individual fish over longer time scales (i.e., for days to weeks).

7.1 FEEDING / REARING

7.1.1 SUBSTRATE

In the Bennett et al. (1988-1998) and Curet (1994) studies in Snake River reservoirs, subyearling Chinook salmon were primarily collected in beach seines and trawls over sand substrate (> 80% of most annual catch), especially during early rearing. More limited use of sand/talus and sand/cobble substrates was also reported, while strong avoidance of rip-rap habitat. These patterns were consistent across all study years, and habitat associations were similar in all four reservoirs. The apparent preference for sand substrates may have been at least partially a function of several other habitat characteristics. Sandy areas were predominantly low-velocity and low-slope and were common in the slightly warmer nearshore areas. Each of these habitat conditions are favored by subyearlings and many of their prey.

Notably, larger Chinook salmon juveniles (potentially including stream-type fish) were associated with more complex habitats in the lower section of Lower Granite Reservoir in the sampling by Bennett et al. (1988). These areas had more cover and more substrate diversity than sites in the upper reservoir. However, Bennett et al. (1988) cautioned that the apparent preference for these sites may have simply reflected more downstream-oriented movements by the larger fish.
Most subyearlings collected in the Hells Canyon reach have been from areas with fine or sandy substrates (Key et al. 1993; Connor et al. 2001b). Such habitats are spatially restricted in this relatively high-gradient section of the Snake River, but their use by subyearlings appears to be extensive.

Results from studies in McNary Reservoir were consistent with the Snake River reservoir results, as subyearlings were 8–10 times more likely to be collected in relatively unaltered shoreline habitats dominated by sand and gravel than in areas with rip-rap (Garland et al. 2002). In this study, subyearlings were collected by electrofishing at 277 sites, and fish were present in ~14% of sampled rip-rap habitats versus ~46% of unaltered shoreline habitats. This distribution suggests that fish were patchily distributed, even in apparently suitable areas. In contrast with the Snake River and McNary Reservoir results, Tiffan et al. (2006b) reported that subyearlings in the Hanford Reach of the Columbia River were most associated with intermediate-sized gravel and cobble substrates. Fine sands and silts were relatively less used, as were boulder-sized substrates. Subyearling avoidance of rip-rap was also described by Li et al. (1984) in the Willamette River. As in the Snake River reservoir studies, avoidance of rip-rap habitats at these additional sites may have been partially a function of high water velocity and the presence of predators.

Earlier studies by Key et al. (1993, 1996) found fewer clear patterns of subyearling use of specific substrate types in either the Columbia or Snake rivers, although subyearling abundance was highest over coarse gravel in the McNary Reservoir and fish there avoided large boulders. These authors concluded that substrate associations in the Hanford Reach were primarily a function of other habitat features, including water velocity and temperature, and the relatively opportunistic drift feeding behaviors of subyearlings.

### 7.1.2 WATER VELOCITY

In the Columbia River, rearing subyearling Chinook salmon appeared to avoid habitats where water velocity exceeded approximately 0.4 m/s (Garland et al. 2002; Tiffan et al. 2002, 2006b). This threshold was identified in both the free-flowing Hanford Reach and in McNary Reservoir. In Hanford Reach studies, most subyearlings were captured in sites where water velocities were < 0.26 m/s (Key et al. 1993; Tiffan et al. 2002, 2006b), consistent with juvenile Chinook salmon preferences reported in other river systems (e.g., Johnson et al. 1992; Scrivener et al. 1994). Almost no fish (< 1%) were caught in velocities > 0.7 m/s in the Tiffan et al. (2002) study.

Use of low-velocity habitats is believed to be at least partially a function of fish size, as small subyearlings may not be able to maintain position at higher velocity. Field support for this idea was shown in the distribution of larger subyearlings in deeper, faster water in the Hanford Reach (Dauble et al. 1989; Venditti et al. 1997; Tiffan et al. 2006b) and in many studies in smaller rivers (e.g., Everest and Chapman 1972; Hillman et al. 1987). Beechie et al. (2005) also described velocity-based microhabitat selection in the large Skagit River system, with smaller fish selecting low-velocity sites. Sampling bias may also have affected these habitat evaluations since it is logistically more difficult to collect fish by seine and electrofishing in faster flowing water.
7.1.3 WATER TEMPERATURE

In at least one study, the temperature difference between shoreline and offshore habitats was the most important predictor of subyearling use of shoreline rearing habitats in the Hanford Reach of the Columbia River (Tiffan et al. 2006b). In this electrofishing study, each 0.1°C increase in the temperature differential increased the likelihood of subyearling presence by 5.3 times. Abundance was especially higher when the temperature difference was > 0.51°C. The authors attributed the preference for warmer water to likely feeding and growth-related advantages, particularly during spring and early summer when temperatures were relatively low. Temperature patterns were also presumably correlated with other habitat features, including water depth and velocity.

In the Snake River reservoirs, fish reportedly became more pelagically oriented after shoreline water temperatures reached 18–20°C, coincident with increased downriver movement (Bennett et al. 2000). Many habitat studies in both the Columbia and Snake rivers collected temperature data. In general, fish were present in shoreline habitats that were slightly warmer than the main channel. The relationships between water temperature and peaks in subyearling abundance tended to track seasonal patterns, with longer residence times in cooler years (e.g., Connor et al. 2003) (also see Section 3.1). One of the few studies to track temperature associations for individual fish (using temperature-recording radio transmitters) showed that subyearlings in Little Goose Reservoir mostly used habitats with ambient temperatures (Tiffan et al. 2003). The study tagged relatively large (> 120 mm) fish that were actively migrating, and there was no evidence for thermal refugia use as the reservoir was largely homothermic.

7.1.4 DEPTH

Although subyearling Chinook salmon have primarily been captured in shallow, near-shore areas, they have been collected throughout the water column in both the Columbia and Snake rivers (Bennett et al. 1988; Dauble et al. 1989). In Snake River reservoirs, fish were mostly concentrated in the upper portion of the water column (Bennett et al. 1988), whereas fish were collected at all depths in the Hanford Reach (Dauble et al. 1989).

Additional Hanford Reach studies indicated that most subyearlings were captured in areas where water depths were between 0.5–1.75 m (Key et al. 1993; Tiffan et al. 2002, 2006b). Few fish in the Key et al. study were captured at sites with extensive areas of very shallow water (i.e., where depth was < 0.25 m at ~15 m from shore), which may reflect avian predator avoidance. Tiffan et al. (2002) concluded that depth was relatively unimportant as a predictor variable in models, likely because the lateral gradient term (which incorporates depth) was a strong predictor of subyearling presence.

7.1.5 SLOPE

Lateral shoreline slope was a significant predictor of subyearling presence in the Hanford Reach (Tiffan et al. 2006b). Subyearling presence was most likely in point samples where lateral slope was < 20% (75-85% of samples included subyearlings), and the likelihood steadily decreased
with increasing slope: 37% of samples included fish at slopes of 30-40% and 23% of samples included fish at slopes > 40%. Few subyearlings were collected in areas with slopes > 40% in this study or in earlier work (Tiffan et al. 2002). In McNary Reservoir, lateral gradient was also an important predictor of subyearling presence, with the highest numbers of subyearlings captured where slopes were 20–25% (Key et al. 1996).

The combined Columbia River studies concluded that slope was a good surrogate for overall habitat suitability, as it was predictive of shallow water, is important in shaping velocity and temperature patterns, and may be a good indicator of predator presence. By comparison, lateral slope was not identified as important in the Garland et al. (2002) study in McNary Reservoir, perhaps because there was little variability in this metric in the studied areas.

In their final dredged sediment disposal analysis, Bennett et al. (1998) recommended that shallow shorelines with lateral gradients of 3–5% slope would be the most suitable created habitats for subyearling Chinook salmon in the Snake River reservoirs.

Overall, results presented in the several habitat studies suggest that shoreline rearing areas for subyearlings are characterized by shallow, low-velocity, low-slope-angle habitats with substrate ranging from sand (especially in Snake River reservoirs) to small cobbles. There was some evidence that shoreline areas with higher water temperature relative to nearby mid-channel habitats were also preferred. A general consensus was that subyearlings avoided developed shorelines (i.e., with rip-rap), probably for a variety of reasons that include unfavorable velocity and water depth and greater predator abundance at these sites. There was also some evidence that subyearlings may use open water habitats to feed on zooplankton, though these habitats have been less frequently sampled. Less is known about the habitats subyearling use during active migration, though fish appear to use higher velocity, main-channel areas during active (or passive) downstream movement.

8.0 ECOLOGICAL RELATIONSHIPS

8.1 DIET

The feeding ecology of subyearling Chinook salmon is relevant to this review because the types, availability, and distribution of preferred prey potentially affect salmon habitat selection and use, residence times, growth rates, and survival. As might be expected, subyearling feeding studies have shown that diet changes seasonally, with fish size, and among riverine versus reservoir environments. For example, in rearing areas of the Hanford Reach of the Columbia River, subyearling diets were predominated by midges (Diptera) and caddisflies (Trichoptera), but then shifted to zooplankton (i.e., *Daphnia* species), midges (Diptera) and terrestrial insects (Hymenoptera, Hemiptera, and Homoptera) in downstream reservoir reaches (Rondorf et al. 1990). This switch largely reflected prey availability differences in the two habitat types, though there were also seasonal differences in the relative abundance of the various prey types.

Dauble et al. (1980) similarly reported a subyearling Chinook salmon preference for Dipterans, especially *Chironomidae* (midges) larvae and pupae, in the Hanford Reach. Midges were the
predominant diet item in spring and early summer, after which caddisfly (Trichoptera) adults and cladocerans (Daphnia species) became important. The authors concluded that changes in prey items reflected seasonal abundance patterns but also some selective feeding by subyearlings (Dauble et al. 1980). Availability also appeared to be an important driver of prey choice in Snake River and lower Columbia River reservoirs (Craddock et al. 1976; Muir and Coley 1996). In the lower river, where zooplankton availability can be very high, zooplankton were the most prevalent item in juvenile Chinook salmon diets (Craddock et al. 1976). Diet patterns in the Snake River were similar to those in the Hanford Reach, with a predominance of Dipterans (Muir and Coley 1996).

8.2 PREDATION

Predation has been implicated as a major source of juvenile salmonid mortality in the Columbia and Snake River basins (Rieman et al. 1991; Vigg et al. 1991; Tabor et al. 1993; Beamesderfer et al. 1996; Roby et al. 2003; Wiese et al. 2008) and has therefore been the focus of a relatively large research effort. Both native and non-native predators are abundant in some reaches in the system, and there is evidence that piscivorous fishes and birds can target juvenile salmonids, particularly in reservoirs and areas where fish are concentrated such as juvenile bypass system discharge sites. Important piscine fishes in the system include northern pikeminnow (Ptychocheilus orogonensis), smallmouth bass (Micropterus dolomieu), walleye (Stizostedion vitreum vitreum), and channel catfish (Ictalurus punctatus). Piscivorous birds include gulls (Larus species), Caspian terns (Hydroprogne caspia), double-crested cormorants (Phalacrocorax auritus), common mergansers (Mergus merganser), American white pelicans (Pelecanus occidentalis), belted kingfisher (Megaceryle alcyon), and others.

In many Columbia River reservoirs, northern pikeminnow are the most abundant predator. In contrast, in the lower Snake River non-native smallmouth bass are relatively abundant (Zimmerman and Parker 1995) and smallmouth predation on subyearling Chinook salmon has been estimated to be greater than predation by northern pikeminnow (April–June; Curet 1993). Smallmouth bass in the studies of Curet (1993), Tabor et al. (1993), Poe et al. (1991), and Naughton et al. (2004) appeared to select smaller subyearlings over yearling salmonids, also somewhat in contrast with northern pikeminnow (Zimmerman 1999). Smallmouth bass have been associated with shoreline habitats more than northern pikeminnow and relatively high densities have been reported in dam forebays (e.g., Zimmerman and Parker 1995; Naughton et al. 2004). These spatial distributions may have important impacts on Snake River subyearlings given their shoreline orientation during rearing and generally slow passage in forebay environments.

The general distribution and abundance of piscivorous predators in the lower Snake River described by Zimmerman and Parker (1995), Ward et al. (1995), and Bennett and colleagues indicated that northern pikeminnow tended to be most abundant in tailrace areas (i.e., in more riverine environments) while smallmouth bass were most abundant in forebays and in mid-reservoir sites. Channel catfish were distributed more evenly among habitat areas, whereas walleye were largely absent in the lower Snake River (Zimmerman and Parker 1995).
Avian predation on juvenile salmonids (and especially subyearlings) in the Snake River has not been as well documented as in other portions of the Columbia basin (e.g., Collis et al. 2001, 2002; Roby et al. 2002, 2006). Antolos et al. (2005) reported on Caspian tern predation on PIT-tagged yearling Chinook salmon and steelhead from colonies near the confluence of the Snake and Columbia rivers. Predation rates in this study varied among species and years, and the authors hypothesized that avian predation rates were higher in low-flow years because smolts had longer passage times and therefore longer exposure to surface-feeding terns. Subyearling vulnerability to avian predation presumably differs among migration phases, with greater predation risk during rearing in shallow habitats, and reduced risk during active downstream migration in the main channel. Foraging birds also congregate in dam tailrace areas, including near outfalls from juvenile bypass systems.

A consistent theme in the predation research and in the subyearling survival research is that as water temperatures rise, predator metabolic demands and predation rates also increase (Vigg and Burley 1991; Connor et al. 1998b; 2003a; Smith et al. 2003, 2004; Marine and Cech 2004). Similarly, low-flow and low-turbidity conditions may increase the risk of avian predation. The combination of high temperature, low flow, and low turbidity may be especially important with regards to subyearling Chinook salmon survival in the Snake River reservoirs.

9.0 INFORMATION GAPS

► To date, relatively few data have been collected on subyearling Chinook salmon mortality agents through time. Correlative studies have consistently shown that survival rates change seasonally, but most of the research has been only speculative with regards to allocations among mortality sources (i.e., predation, starvation, turbine passage, etc.). A better understanding of the sources of subyearling loss is needed to determine what management options can realistically improve production for the Snake River population. In addition, separating natural background mortality from loss associated with the Hydrosystem (e.g., dam-related mortality, barging effects, reduced travel rates, bioenergetic costs, increased non-native predators, etc.) will be informative. Studies that could potentially address these questions include fish condition evaluations, active tag studies to help determine individual fish fates, predator and subyearling stomach content analyses, and continuing PIT-tag evaluations.

► There is a need for more individual-based habitat use studies. Most of the historic subyearling Chinook salmon habitat work has relied on stratified sampling approaches, and have concentrated on near-shore environments. It is unclear, however, to what extent individual fish use multiple habitat types (including pelagic waters) and/or move between habitats at various spatial and temporal scales. Such information is necessary to identify critical habitat features and to more conclusively establish where a shortage of preferred habitats is limiting survival or production. Active tag study designs that can collect detailed locations of individual fish over extended periods (rather than point samples) would be informative. Methods are also needed to evaluate when and where fish use shallow versus deep-water habitats, and to determine why fish select different habitat types at different times (i.e., during the diel cycle, during different migration phases, or seasonally).
There continues to be considerable uncertainty about wintertime subyearling Chinook salmon habitat use, behavior, dam passage rates, routes, and survival. Given evidence for disproportionate contribution of reservoir-type fish to adult fall Chinook salmon returns, more data are needed on all aspects of the winter ecology of these juveniles. More specifically, data are needed on how juvenile fall Chinook behave during winter and which habitats they use. For example, it would be useful to identify whether fish are sedentary versus active, particularly with regards to winter dam passage. Similarly, better information on winter feeding behaviors, movement patterns, and mortality would help identify potential management actions. Operating PIT-tag detection systems during winter and active tag studies would each add some resolution to these questions.

Researchers have identified a variety of broad-scale environmental effects on subyearling Chinook salmon life history events (i.e., emergence and migration timing), behavior, and survival. These studies have demonstrated temperature and flow effects, particularly evident across years. However, fine-scale fish responses to environmental conditions remain poorly understood, particularly regarding potential threshold levels for migration initiation, various rearing/migration behaviors, and survival. Addressing questions of environmental variability is possible within-year using a variety of monitoring approaches, including both active and passive tag studies, particularly when in-river conditions are variable within season. However, many of the flow and temperature-related associations with subyearling behavior and survival have been identified in multi-year comparisons and therefore continuing baseline monitoring projects should be continued to provide time series data.

More data on potential among-population differences are needed. Results described in this literature review have predominantly been for subyearling Chinook salmon collected and/or tagged in the Hells Canyon reach of the Snake River or the lower Clearwater River, with some additional fish outplanted from hatchery programs. However, subyearlings are also produced in lower reaches of the Grande Ronde, Salmon, and Imnaha rivers and, to a limited extent, tailraces of lower Snake River dams. There are probable differences in emergence, growth, and behaviors of these groups. Identifying fish source is potentially critical to interpreting results and making management decisions. If there are genetic or microchemical differences among populations, these markers could be used to identify if critical habitats differ among groups, if hatchery and wild fish should be managed separately, and if actions can be taken to improve production from specific river reaches. It would also be useful to determine the relative contribution of different spawning groups to overall Snake River production, including the contribution of reservoir/tailrace spawners.

Many (a majority in some years) of the subyearling fall Chinook salmon collected at Snake River dams during summer are subsequently transported downstream in barges. The implications of this management strategy have not been fully explored. Potential areas of interest include delayed juvenile mortality after release downstream from Bonneville Dam, adult return rates of barged versus in-river and reservoir-type migrants, inter-basin straying of transported fish, among-population effects, and selection biases in collection efforts. It will also be important to evaluate whether survival benefits differ among collection and transport locations.
Although subyearling Chinook salmon prey does not appear to be limiting in the lower Snake River reservoirs, there has been little evaluation of possible competition for resources between subyearlings and other species in any season. Ecological relationships are especially poorly understood during winter. For example, it is unknown whether food availability in winter can limit subyearling growth or survival, or whether there is competition between subyearlings and juveniles of either native (e.g., northern pikeminnow) or non-native (e.g., American shad) species.

The relationship between flow augmentation and overwintering does not appear to have been studied. Research that can establish whether increased summer flows from either Dworshak Reservoir or Hells Canyon complex dams affect the likelihood of overwintering (and/or subyearling survival) would augment management decisions about this mitigation approach.

There is a continuing need to develop reliable methods to differentiate stream-type from ocean-type subyearlings. Accurate separation of these groups will improve overall abundance estimates, increase the utility of subyearling passage indices, and improve the resolution and utility of life history, migration timing, and survival studies.

If dredged materials are used to create shallow near-shore habitats for juvenile salmonids in the Snake River reservoirs, it will be important to test whether these habitats are having the expected impacts. Depending on the scale of the habitat creation effort, detecting differences in metrics like reach survival may be difficult, and responses may be complex. Therefore, study designs that carefully test the outcomes of the habitat actions, including BACI designs (before-after-control-impact) and the collection of multi-year time series data, will be important for detecting the type and magnitude of effects. Potential population-level benefits should be considered in all habitat evaluations.
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