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The Fate of Coho Salmon Nomads: The Story of an Estuarine-Rearing Strategy Promoting Resilience

K V. Koski[1]

[1]The Nature Conservancy Alaska Field Office, Juneau, Alaska, USA

NOMAD LIFE-HISTORY STRATEGY

Adult coho salmon (*Oncorhynchus kisutch*) typically enter small coastal streams or tributaries of larger rivers in fall and usually ascend to the headwaters to spawn enabling their progeny to fill habitats throughout the system. Conventional understanding of coho salmon life history presumes that, following emergence from the redd in spring, coho fry take up residency in the stream for a year or more before migrating to sea in spring as smolts (Sandercock 1991). However, large numbers of fry (age 0, 1st year of life), typically move downstream following emergence. Chapman (1962) first coined the term “nomads” referring to those coho fry moving downstream between emergence and October. The movement of nomads downstream following emergence was interpreted as normal behavior, and this movement is still observed in streams from Oregon to Alaska (Salo and Bayliff 1958, Chapman 1962, Crone and Bond 1976, Hartman et al. 1982, Harke and Lucey 1999). The movement in spring often accompanied freshets, although fry were observed moving downstream even during periods of stable flow. This downstream movement was considered a result of either a physical displacement because of streamflow and fry size (Hartman et al. 1982, Tschaplinski 1987), a behavioral response to aggression and territorial space (Chapman 1962, Mason and Chapman 1965), or a result of habitat limitations

(Ruggles 1966, Fraser et al. 1983). In an intensive study of the comparative ecology of stream and estuarine-rearing coho, Tschaplinski (1987) found no evidence of density-dependent causes for this migration and concluded from his observations that the fry were physically displaced by rapid currents associated with freshets.

Though their fate was not known, nomads were often considered surplus to the stream, and it was thought they did not survive (Crone and Bond 1976, Hartman et al. 1982). Following emergence in spring, coho fry are generally in a colonization phase in which they are moving to other areas within the system in search of rearing habitat (Au 1972). Conventional wisdom suggested that displaced or nomadic fry kept moving downstream until they were able to find and defend a territory (Ruggles 1966, Hartman et al. 1982, Fraser et al. 1983). Chapman (1966) presented data indicating that the production of downstream migrating fry was a function of the number of spawning females, and that the carrying capacity for fry was exceeded when female spawner abundance was high; thus, nomads represented surplus fry. The concept of surplus fry became an accepted characteristic of coho salmon life history.

Quinn (2005) posed a question pertinent to understanding nomad behavior: “Does the presence of migrating fry indicate that the carrying capacity of the stream has been reached, or does it represent an alternative life-history pattern?" Reimers (1971) was one of the first to demonstrate that salmon are capable of developing different life-history strategies to take advantage of diverse habitat opportunities. He described five different life-history strategies for Chinook salmon (*O. tshawytscha*) in the Sixes River, Oregon. The most successful strategy involved a combination of both freshwater and estuarine rearing that allowed the Chinook to migrate to sea at age 0. Kahler et al. (2001) observed that movement of coho fry reflected habitat choice rather than failure to compete. Several studies in Alaska river systems documented different life-history strategies used by Chinook, sockeye (*O. nerka*), and coho juveniles that reflected habitat choice and resulted in a greater capacity for survival of these species (Murphy et al. 1984, 1989, Heifetz et al. 1989, Johnson et al. 1992, Koski and Lorenz 1999, and Halupka et al. 2003).

In this paper, I discuss some recent studies and insights showing that nomads are generally not surplus or involuntarily displaced by freshets as speculated, rather a specific life-history strategy has evolved from what Thorpe (1986) calls their opportunistic behavior. This general behavior of salmon and coho, in particular, allows these species to take advantage of more productive habitats downstream resulting in an adaptive capacity to be more ecologically resilient (Healey 2009). In addition to being opportunistic, salmonids are phenotypically plastic generalists, with highly variable life-history strategies within species (Thorpe 1986, Waples et al. 2009). life-history strategies are the means by which animals are ultimately able to reproduce and sustain their populations under varying environments (Thorpe 1994*a*). The nomad estuarine-rearing life-history strategy is one of the means or attributes that coho have evolved to cope with environmental uncertainties providing an increased capacity for survival and success (Healey 2009).

DOWNSTREAM MOVEMENT OF NOMADS

The number of nomads leaving a stream often greatly exceeds the number of smolts produced (Salo and Bayliff 1958, Chapman 1962, Tschaplinski 1987, Harke and Lucey 1999). Migration has been explained as a general response to adversity. If an animals' needs are being met, it stays where it is. If they are not, it moves until they are (Taylor and Taylor 1977). The carrying capacity of coho fry in a small stream increased 6- to 7-fold when the natural food supply was supplemented (Mason 1976). Coho nomads transferred to natural stream areas barren of other coho remained there, whereas nomads added to resident populations tended to move downstream (Chapman 1962). These studies indicated that food and perhaps space affected the fry's response to migrate.

When one considers the minimal food resources in a stream environment and the requirements of rearing salmonids, alternative life-history strategies make ecological sense. Stream-rearing salmonids are in what Quinn (2005) called an "egg-fry conflict," in which cold streams are ideal environments for egg incubation, but not for rearing of fry because of the scarcity of food. Allan (1969) noted that the physiographic conditions in the Pacific Northwest with relatively short high gradient streams are likely to be unfavorable to rearing salmonids and that this region would favor the development of species with very short or minimal freshwater life. Chapman (1966) presented evidence that the availability of food and space were indeed factors regulating the rearing density of salmonids in streams. Chapman (1962) showed that aggressive behavior was a factor in downstream migration of coho, and it acted as a population spreader, but he also thought that some fry may have an innate urge to migrate downstream.

Thus, it is not surprising to see life-history patterns evolve to maximize feeding and survival opportunities. The development of the "ocean-type" life-history strategy, i.e., migrate to sea at age 0 without overwintering in freshwater (Healey 1983), appears to be an ecologically appropriate response to adversity and a consequence of an inadequate riverine environment. This strategy is also the basis for Thorpe's (1994*a*:106) question "What is lacking in the riverine habitat which causes salmon to smolt and migrate from that environment?" By using the protected habitat of streams for reproduction, salmonids have selected a relatively unproductive environment for their progeny to develop. Consequently, salmonids have developed smolting as a life-history strategy for obtaining their sustenance (Thorpe 1994*b*). In addition to pink (*O. gorbuscha*) and chum (*O. keta*) salmon, both Chinook (Reimers 1971, Healy 1983, Johnson et al. 1992) and sockeye (Heifetz et al. 1989) are capable of migrating to the ocean as age 0 juveniles and survive to adults as shown by ocean-type scale pattern and tag returns (Thedinga et al. 1998). Food availability and rapid growth are thought to be the key mechanisms for ocean-type life history patterns in sockeye and Chinook in Alaska. Coho nomads used the estuarine habitats for rearing in ways similar to those of sockeye and Chinook, but differed in that coho nomads returned to freshwater to overwinter before migrating to the ocean (Murphy et al. 1984, 1997, Harding 1993, Koski and Lorenz 1999, Miller and Sadro 2003).

SALTWATER ADAPTATION OF COHO

A number of studies with differing results have been conducted on the effect of salinity on survival and growth of juvenile salmon to better understand their transition to the ocean. Crone and Bond (1976) observed that some coho fry in Sashin Creek, Alaska, migrated to the estuary during their first spring or summer as fry. They conducted salinity tolerance bioassays, which indicated that coho fry could survive in salinities of 10–15, and that fry could survive salinities as high as 29 provided that they had been able to acclimate to lower salinities for 35 d. Contrary to some of their findings, Kennedy et al. (1976) observed that when coho fry were put into saltwater, they died prematurely, and nonsmolted fingerlings either died immediately or grew slowly and then subsequently reverted to their parr condition and died. Weisbart (1968) showed that salinity tolerance was not a function of age, but rather of size. Coho fry up to 5–6 cm in length and 5-mo-old did not survive in seawater; the threshold size for survival seemed to Weisbart to be about 7–8 cm. Conte et al. (1966) found that the transformation of coho to the marine environment was size-dependent, that it began shortly after completion of embryonic development, and that the hypo-osmoregulatory mechanism was not completely functional until a size of about 9 cm was reached.

The large numbers of migrating nomads and the idea of estuarine rearing inspired Otto (1971:347) to investigate the effect of salinity on the survival of pre-smolt (age 0) coho. He conducted salinity tolerance tests on coho and concluded that "underyearling coho were poorly equipped physiologically to survive emigration to the sea before smolt transformation." He also thought that "pre-smolt emigrants would not be expected to contribute substantially, if at all, to the fishery for adult salmon." However, he qualified his conclusions by saying that his experimental stock of coho may not have been representative of pre-smolt emigrants genetically, and he also referenced work by Otto and McInerney (1970), which showed that survival of coho fry may be possible when they have the ability to select salinities within the range of tolerance and, indeed preferred those salinities when growth, food intake, and food conversion efficiency were maximized. Canagaratnam (1959) performed an experiment with several species of fish including coho salmon fry (36–42 mm) to determine if they could grow better in environments of different salinities in which temperature and food were controlled as compared to freshwater. The coho fry survived and grew well in all the salinities tested, i.e., 6, 12, and 18, and exhibited the fastest growth in the highest salinity environment (18) tested. He speculated that the coho grew better in saltwater than than they did in freshwater because they expended less energy to maintain osmotic equilibrium. Tschaplinski (1987) performed salinity tolerance experiments with both stream and estuary-rearing coho fry from Carnation Creek and demonstrated that complete adaptation was a gradual process. Estuary fry could regulate their plasma sodium concentrations after achieving acclimation to brackish water. However, regardless of body size, short-term, (72 hr) adaptation was not possible for fry that had not previously been exposed to brackish water.

The equivocal results from studies on the salinity tolerance of age 0 coho may have been due to genetic differences among the stocks of coho tested or the particular experimental design, in which fish were either restricted to a specific salinity or given a choice. When given the opportunity to select the preferred salinity, coho in some studies were able to grow and survive in the estuarine environment as also shown by Tschaplinski (1987).

ESTUARINE HABITAT REARING

Salmon use a variety of habitats in the estuarine environment. Merrell and Koski (1978) described a rearing habitat in the transition zone between freshwater and saline water of Porcupine Creek, southeast Alaska, as the stream-estuary ecotone, i.e., ecotone, following Odum's (1971) definition of a transition zone or ecotone between ecotypes. This salmon habitat in the upper estuary extended from the head of tide downstream to the area within the intertidal zone where the channel was bordered by marsh vegetation and mudflats (Fig. 1). The 0.64-ha brackish estuarine ecotone included all tidal channels, sloughs, and fringing salt marsh dominated by the sedge, (*Carex* spp.) and rye grass, (*Elymus* spp.), which were accessible to salmon. Whigham et al. (1988) refers to this area of the estuary as the tidal-fresh to tidal-brackish transition region. This habitat was characterized by low salinity, warm temperature in the summer, and an abundance of food, e.g., isopods and amphipods (Koski 1984, Kirchhofer 1984). The ecotone also serves as the habitat for salmon to make the osmotic transition to the ocean as well as a productive habitat with more food. Miller and Sadro (2003) also described a stream-estuary ecotone with diverse habitats in South Slough, a 7800-ha sub-basin of Coos Bay in southern Oregon, in which coho spent an extended time rearing before heading back upstream for the winter. The uppermost 3 km of Winchester Arm of South Slough formed the stream-estuary ecotone between Winchester Creek and the saline waters of the estuary.

Observations from southern Oregon to southwestern Alaska, (Fig. 2) have documented the rearing of nomad coho in the estuary or ecotone: South Slough, Oregon, (Miller and Sadro 2003), Lint Slough, Oregon, (Garrison 1965), Salmon River, Oregon, (Cornwell et al 2001), Carnation Creek, British Columbia, (Tschaplinski 1987), Porcupine Creek, Alaska, (Merrell and Koski 1978, Murphy et al. 1984), Kake Bake Creek, Alaska, (Harding 1993), Sashin Creek, Alaska, (Crone and Bond 1976), Duck Creek, Alaska, (Koski and Lorenz 1999), Situk River, Alaska, (Thedinga et al. 1993), and Cook Inlet, Alaska, (Larry Engle Alaska Department of Fish and Game, Anchorage, *personal communication 2005*). Other observations of coho rearing in estuarine habitats along the Pacific Coast have been made, but references were not readily available. These wide-ranging observations point to a high genetic diversity and phenotypic plasticity, which allows coho to respond to varying environmental conditions throughout their range (Waples et al. 2009, Healey 2009). The nomad life-history strategy is not just a local adaptation but a strategy or tactic of the species that provides an important measure of resilience. These observations have also shown that estuaries play a very important role in the early life history of coho by providing them with increased food and growth, expanding their nursery area, increasing the overall production from the watershed, and facilitating repopulation of depressed stocks.

The high productivity of some estuarine habitats in Alaska allows the full expression of the classic ocean-type life history pattern described by Healey (1983). This life-history strategy was exemplified by Chinook and sockeye salmon in the Situk River, Alaska, (Heifetz et al. 1989, Johnson et al. 1992, Thedinga et al. 1993, 1998). Following emergence, both sockeye and Chinook fry moved downstream to the lower reaches of the Situk River, in an ecotone in which they fed and grew rapidly in the warmer environment. When these age 0 fry reached a threshold size of about 50 mm for sockeye (Heifetz et al 1989) and about 80 mm for Chinook (Johnson et al. 1992) they migrated to the ocean. Two life history patterns or strategies were shown by age 0 sockeye in the Situk River. There was an early migration of newly emerged fry into the estuary in March and April and a later migration of larger fry through the lower river in May. Neither group spent much time in the estuary and were gone when they reached the threshold size for survival (Thedinga et al 1993). A similar migration of two groups of age 0 sockeye was observed in the Taku River (Murphy et al 1997). These variants of life history patterns appear to be adaptations of sockeye attempting to maximize their survival, and these patterns reflect the plasticity and opportunistic behavior of salmon. Coho nomads, in contrast, were present in the Situk River estuary and tidal sloughs for about 6 mo from March through August and coinhabited some of the same habitats with sockeye and Chinook. Coho were not present in samples from the estuary in August, and were presumed to have moved upstream (Thedinga et al. 1993). Though it appeared that these nomads did not complete the ocean-type life-history strategy, no further investigation was conducted to determine their presence upstream or to examine scales of smolts or adults for evidence of estuarine rearing.

Coho nomads in Porcupine Creek (Murphy et al. 1984) and Carnation Creek (Tschaplinski 1987) showed similar migrations downstream to the ecotone and had rapid growth, becoming larger than their siblings upstream, similar to the findings of Reimers (1971) for Chinook salmon in the Sixes River, Oregon. Tschaplinski (1987) found that coho fry in the estuary outgrew fry in the stream in both length and weight; the estuary biomass grew 1.8 to 2.3 times faster than the stream biomass; and by autumn about 50% of all estuary fry were as large as the one-year-old smolts leaving Carnation Creek. Studies of coho rearing in estuarine habitats clearly show that these fry grow and survive in this environment and can contribute substantially to the overall production of the system.

OCEAN SURVIVAL OF AGE 0 COHO

Documentation of age 0 coho migrating to the ocean and surviving to adults is limited. Scientists have generally been unaware of the use of estuaries by coho and as a result there have been few tagging studies that targeted estuarine-rearing fry. One of the earliest experiments to examine the survival of age 0 coho migrating to the ocean, Garrison (1965) demonstrated that coho fry, reared to smolt size in 90 d in a brackish water impoundment with salinities of up to 32, migrated to sea and survived. The fish fed naturally on the dominant organism, *Corophium spinicorne* in the impoundment and were marked and released into the estuary in June at an average size of 50.7/kg (estimated length, 113 mm). These age 0 coho returned after 15 mo at sea as mature 2-yr-old adults at a survival rate of about 2.1%. In an experiment to determine the effects of time-and-size-of-release of juvenile hatchery coho salmon on returns at maturity, Bilton et al. (1982) found that age 0 coho released on the same day as 1-yr-old juveniles of slightly larger sizes had considerably lower returns. Because the two age groups were released on the same day, and the ranges of the average release weights of the three releases overlapped, they suspected that factors other than time and size were important in determining success of returns. In the Salmon River estuary in Oregon, Cornwell et al. (2001) found that a substantial portion of sub-yearling coho fry used the estuary marshes. Scale patterns among returning adults showed evidence of sub-yearling ocean migrant, a life history type that accounted for 3%-18% of the coho adults returning to Salmon River (L. Borgerson, or Department of Fish and Wildlife, *unpublished data*). Preliminary information from tagging of estuary fry in Carnation Creek in autumn indicated that the estuary could contribute some spawners for the following generation although those that returned were sexually-mature juveniles (Tschaplinski 1987).

All of these observations agree that coho fry, reared in the estuary, can survive in the ocean and can contribute to the next generation of spawners. However, the studies do not confirm that these fry migrated directly to the ocean following tagging, and it is possible that some of these fry may have overwintered somewhere in freshwater. Some studies indicate that at least some of the estuarine-reared fry migrate back into freshwater before smolting (Murphy et al. 1984, 1997, Harding 1993, Koski and Lorenz 1999, Miller and Sadro 2003).

Part of the problem in assessing the contribution of nomad coho to adult production in the wild may be attributed to the difficulty in interpreting estuarine growth from scales. In one of the few intensive investigations of coho age from scales, Pritchard (1940) found that only 22 of the 6312 wild adult coho examined from British Columbia had migrated to sea as fry and had returned as 2-yr-old adults. Crone and Bond (1976) noted that the scale patterns developed by fry reared in saltwater were indistinguishable from those of smolts that spent a year in freshwater. They concluded, however, that survival of wild age 0 coho at sea is apparently low and/or may not be recognized from their scales. Tschaplinski (1987) was not able to distinguish estuary fry from stream fry from scales. In some size classes of coho, estuary fry had slightly larger scales and wider circuli spaces, which suggested more rapid growth; however, he concluded that scale features in coho fry were not consistently useful in distinguishing individuals that rear in estuaries from stream-dwellers, because variation in growth in the stream was high and movements of stream coho to the estuary occurred throughout the summer. However, Harding (1993) who monitored age 0 coho migrating upstream after rearing in the ecotone of Kake Bake Creek in southeast Alaska found that their scales showed widely spaced circuli depicting estuarine growth. Scale patterns indicative of a period of estuarine growth were also observed from returning adult coho in Jordan Creek, a tributary to the Mendenhall ecotone near Juneau, Alaska (Briscoe 2004). The use of otolith strontium (Sr) or strontium-to-calcium (Sr:Ca) ratios is a relatively new and powerful tool for reconstructing the migration of salmon between freshwater and saltwater habitats (Zimmerman 2005). The use of this tool may help to confirm the use of estuarine habitats by coho nomads, aid in age determination, and elucidate if some coho actually migrate to the ocean at age 0.

MOVEMENT TO OVERWINTER HABITAT

If for some reason nomads rearing in the estuary are not capable of adapting the ocean-type life-history strategy and migrating directly to the ocean, then they may migrate to freshwater habitat to overwinter. Mason (1976) found that food rather than space limited the stream production of juvenile coho during summer, but habitat and behavior probably limited carrying capacity in winter. Similarly, coho rearing-density is less in streams where preferred winter habitat has been reduced following riparian logging (Toews and Moore 1982, Tschaplinski and Hartman 1983, Heifetz et al. 1986, Murphy et al. 1986). As water temperature begins to decline and streamflow increases in the fall, coho begin seeking habitat that will protect them in winter from freshets, ice scour, predation, and other sources of mortality. The preferred overwinter habitat in freshwater for juvenile coho salmon consists of low stream velocity, pools with woody debris cover, side channels, and beaver ponds and lakes (Bryant 1984, Murphy et al. 1984, Heifetz et al. 1986). Freshets and declining temperatures appear to be the principal factors affecting the timing and intensity of the movement of these juveniles into winter habitat.

Skeesick (1970) first documented a fall movement of juvenile coho into a small spring-fed tributary of the Wilson River on the northern Oregon coast, and he observed the migration of these same fish out in the spring as smolts. These immigrants migrated out as smolts at a larger size than those that resided in the stream. He speculated that these fish moved into the tributary to escape high flows. He also documented a fall and winter upstream migration of coho juveniles into two other streams on the Oregon coast: Munsel Creek and Elk River. A fall migration of juvenile coho salmon into more suitable or preferred winter habitat has since been documented by several investigators (Bustard and Narver 1975, Cederholm and Scarlett 1981, Peterson 1982, Tschaplinski and Hartman 1983, Murphy et al. 1984, McMahon and Holtby 1992, Harding 1993, Koski and Lorenz 1999, Ebersole et al. 2006). Scarlett and Cederholm (1984) observed that marked coho in the Clearwater River, Washington, moved as far as 38 km downstream from summer-rearing areas before entering tributaries for overwintering.

Harding (1993) documented an upstream movement of coho into Kake Bake Creek, in southeast Alaska, from the ecotone or estuary between August and November (mean date: September 25); these immigrants averaged 83 mm in length, were bright silver in appearance and several had sea-lice attached near the anal fin. Although some were over 200 mm in length, none were mature. In the following spring, 29% of the smolts from the stream were fall immigrants. Murphy et al. (1997) studying the large glacial Taku River in Southeast Alaska, found that age 0 coho moved downstream from the upper River in large numbers from May through November, but only a small number were caught in the estuary. Coded-wire tag recoveries from adults in the fisheries indicated that many of these age 0 fry had remained in freshwater habitats of the lower river for 1–2 yr before smolting.

Murphy et al. (1984) reported that the stream-estuary ecotone in summer provided roughly 30% of the rearing habitat for age 0 coho in Porcupine Creek, southeast Alaska, but by November these fry had left the ecotone and moved upstream, apparently to avoid lower temperatures, higher salinities, and less cover. In Winchester Creek, South Slough, Oregon, Miller and Sadro (2003) found that a portion of age 0 coho having migrated to the ecotone in spring, had lived there for up to 8 mo before moving upstream to overwinter. However, some of the juvenile coho moved to an off-channel beaver pond in the lower part of the ecotone to overwinter. Tschaplinski (1987) reported that the estuary population of fry in the Carnation Creek estuary ranged from 9.1% to 12.1% of the total system population. The proportion of fry remaining in the estuary at the end of summer varied from 22.8% in 1979 to 8.9% in 1980. They assumed that these fish had left the estuary in November, but they stated that the fish did not overwinter in Carnation Creek (Hartman 1981, Tschaplinski 1982). In a later report, Hartman and Scrivener (1990) reported that by October, some of the coho that used the Carnation Creek estuary for rearing had entered an adjacent stream, One that had been dry in summer.

CASE STUDY OF NOMADS IN DUCK CREEK, ALASKA

A stream restoration project on Duck Creek provided additional insights into the probable fate of nomad coho and their role in the resilience of the species (Koski and Lorenz 1999). Duck Creek, located in the Mendenhall Valley near Juneau, Alaska, is a small, 4.8 km-long, second-order stream with an annual flow of about 0.142 m^3/s. Except for being impacted by urbanization, it is similar to hundreds of small coho salmon streams in southeastern Alaska. The stream originated from glacial outwash of the Mendenhall Glacier, is supplied primarily by groundwater, and flows into the Mendenhall stream-estuary ecotone, which is part of the Mendenhall Wetlands State Game Refuge. The Mendenhall ecotone covers 1523 ha and extends for 14.5 km along the Gastineau Channel between Douglas Island and the mainland near Juneau. The ecotone has a very low gradient and is subjected to two high-tide cycles daily with a mean range of 4.3 m and an extreme range of 8.1 m. Seventeen freshwater streams, two of which are glacial, flow into this ecotone. Consequently, the salinity is highly variable throughout the ecotone because of the large freshwater input, ranging from about 0 to 30. An extensive salt marsh community composed of *Carex* sp., *Puccinellia* sp., and *Elymus* sp. characterizes this ecotone, which is used by all five species of

Pacific salmon as well as numerous marine species.

Duck Creek is impaired by urban residential development, e.g., road runoff, inadequate culverts, and riparian encroachment, which has caused problems with streamflow, sedimentation, and water quality. The stream once supported up to 10,000 adult chum salmon annually, but that run was extirpated, and currently only hatchery strays of chums use the stream (Baker et al. 1996). Coho numbered about 500 spawners annually in the 1960s and have declined to fewer than 100 fish/yr today (Bethers et al. 1993, Koski and Lorenz 1999). Coastal cutthroat trout also spawn and rear in the stream.

When coho smolts were being enumerated during baseline development for the restoration project, coho fry were not caught or observed in the stream; consequently, additional studies were conducted to determine the reasons for their absence. Spawning success was suspected and evaluated by excavating redds to determine egg survival and by assessing eyed-egg survival using Vibert-Whitlock boxes buried in known spawning areas (Koski and Lorenz 1999). These studies showed a 100% mortality of eggs, which was attributed to the high level of fine sediment and the low concentration of dissolved oxygen in the streambed. The egg mortality confirmed that natural reproduction was not occurring and explained the absence of fry.

The paradox in this system was the relatively high number of coho smolts emigrating from the stream each spring. The smolt-yield from Duck Creek in the mid 1990s ranged from fewer than 1000 to about 4000 smolts annually. These smolts originated as nomads that had migrated from the Mendenhall ecotone to Duck Creek to overwinter. Studies using underwater video cameras and upstream traps documented the movement of juvenile coho into Duck Creek with the onset of fall freshets. Enumeration of upstream and downstream migrants near the mouth of Duck Creek revealed a small upstream movement of nomads in the spring, but most entered the stream in the fall. Smolts leaving Duck Creek were tagged with coded wire tags in 1994–1997. Adults recovered in the local fisheries and in the stream indicated that these smolts had a marine survival up to 6.5% and contributed to the local fisheries (Koski and Lorenz 1999). No information, however, was reported on whether these fish strayed into other streams. During an estuarine assessment study in 1998, coho fry were also observed rearing in the Mendenhall ecotone during the spring and summer months (Gerke et al 1999).

Documentation of the fall migration of coho juveniles to Duck Creek was fortuitous in that it demonstrated that age 0 juvenile coho with the nomadic life-history strategy could provide resilience by repopulating a non-natal stream with fry that would emigrate as smolts in spring. The Duck Creek coho population was entirely dependent on recruitment of nomads from the ecotone because of its impaired spawning habitat with no natural reproduction. The nomads probably immigrated into Duck Creek because they were attracted to the warmer temperature of this stream as a result of groundwater influence. Because imprinting likely occurred during smolt transformation, in Duck Creek (Scholz et al. 1976), adults probably returned to spawn there even though it was not their natal stream. Because imprinting may not be developed in nomads, those fry rearing in the ecotone would probably migrate into any stream that provided the appropriate cues to overwinter habitat. This behavior of rearing in estuaries and then migrating back into freshwater streams for overwintering before migrating as smolts the following spring is consistent for other estuaries (Murphy et al. 1984, Harding 1993, Miller and Sadro 2003).

Jordan Creek, a stream located adjacent to Duck Creek in the Mendenhall watershed also drains into the Mendenhall ecotone and is used by nomads seeking overwinter habitat. This stream is similar in size to Duck Creek but has not been extensively impacted by urban development, and it has more natural overwinter habitat because of extensive beaver ponds. The smolt yield for Jordan Creek has ranged from about 8000 to 26,000 fish annually and is largely attributed to these nomads (Briscoe 2004).

Based on this case study and the other observations presented, coho nomads that have connectivity to an ecotone or estuarine habitat will probably rear there in summer, and in the fall will migrate to a natal or non-natal stream that provides overwinter habitat.

CONCLUSIONS

Coho salmon nomads are not surplus fry and do not inevitably perish at sea as previously thought. The downstream migration of coho nomads to estuarine habitats is a life-history strategy that is not well known. The nomad life-history strategy and estuarine rearing appear to be widespread throughout the range of coho and are likely factors in the resilience of coho populations in some systems. The nomad strategy appears to have developed as a result of food limitations in streams and because of foraging success found in estuarine habitats. Though both Chinook and sockeye fry have developed ocean-type life-history strategies, which enable them to migrate to the ocean at age 0, evidence that coho naturally migrate to the ocean and use this age 0 strategy is inconclusive. The contribution of nomads to the total watershed production of coho smolts can be substantial and may be important in repopulating both natal and non-natal streams. Several studies indicate that the coho nomad life-history strategy includes spring/summer rearing in estuarine habitats as age 0 fry, and an upstream migration in fall to freshwater habitats for overwintering before smolting. The nomad life-history strategy represents a variation on the classic ocean-type life-history strategy; however, there may be a component of these nomads that develop the ocean-type life history. Accurate determination of estuarine residence from scales and/or otoliths may be required for the final interpretation of their life-history strategy or strategies. Nomads obscured their presumed fate because their life-history strategy enabled them to select preferred salinities, acclimate, grow, and survive in estuarine habitats and then return to overwinter in either natal or non-natal freshwater habitats before smolting the following spring. The stream-estuary ecotone located in the upper reach of the estuary is one of the habitats specifically used by nomads. Ecotones at the lower reaches of streams appear to have similar characteristics of low gradient, long stream channels connected to estuary basins, extensive emergent salt marsh vegetation, and diluted salinities. Estuarine habitats including ecotones, tidal sloughs, and estuary basins must be restored to fully functional condition to maintain both habitat diversity and the coho nomad strategy required to help recovery of depressed coho stocks.

MANAGEMENT IMPLICATIONS

The majority of the human population in the Pacific Northwest lives near the coastal shoreline, and growth in this area is expected to increase. This growth will probably continue to alter the marine, estuarine, and freshwater habitats that are essential for the production and condition of the salmon resources. Estuarine habitats are inherently complex and variable because of their tremendous temporal and spatial variability in physical and chemical characteristics. Because of these characteristics, they form a continuum of diverse habitats from the river mouth to the ocean that salmon encounter in their transition to the ocean.

Diking, draining, and filling of estuarine wetlands and riverine floodplains have been done worldwide over the centuries for urban and industrial development (NRC 1996). The draining of estuarine wetlands in the Pacific Northwest began approximately 200 years ago (Dahl 1990), and the salt marshes close to urban centers were particularly impaired by this conversion, with losses of 50% to 90% in many Oregon and Washington estuaries (NRC 1996). Gregory and Bisson (1997) reported that over 95% of the tidal wetlands in parts of Puget Sound have been lost to dikes and landfills. Tide gates are often used in dikes to control the flow of upland water through streams and sloughs into estuaries, and the physical, chemical, and biological effects of tide gates on migratory fish can be profound (Giannico and Souder 2004). The loss of this estuarine habitat and connectivity by diking, tide gates, and culverts has probably had a major impact on coho salmon. We know from studies on the effect of logging that a loss of quality winter habitat in freshwater streams can reduce coho production (Bustard and Narver 1975, Tschaplinski and Hartman 1983, Heifetz et al. 1986, Beschta et al. 1987).

The availability of ecotones and estuarine habitats to coho is likely a critical habitat and limiting factor for some populations. The simplification of these estuarine habitats may have already altered some of the unique life-history strategies that coho have evolved to adapt to their environment. Because coho nomads have evolved to exploit additional rearing habitat in stream-estuary ecotones and estuaries, the loss or impairment of these habitats may diminish the benefits of the nomad strategy and may actually limit or prevent the recovery of coho in some systems. Thus, diking, draining and filling of estuarine habitats represent essentially a permanent disruption of connectivity between habitats leading to reduced life history diversity and perhaps less resilience through rapid evolution and an altered nomad strategy (Waples et al. 2009). Managers should know that the nomad strategy for rearing in estuarine habitats is essential to the sustainability of some coho populations and that in order to maintain this life-history strategy and resilience, protection and restoration of habitats in the lower reaches of rivers, ecotones and estuaries is critical. The recovery of coho salmon abundance will require breaching of dikes, removal or modification of tide gates, and the replacement of culverts to restore tidal inundation and connectivity between estuarine habitats and natal and non-natal stream habitats.

Coarse woody debris is an important part of estuarine and oceanic habitats, from upper tidewater of coastal rivers to the open surface of estuaries. The amount of woody debris in the mid-1800s significantly exceeded present amounts in the lower reaches of rivers and beaches (Gonor et al. 1988). Streams were the major supplier of wood with most of it transported to the estuary during high flows. Most of the wood for estuaries and beaches along the Oregon-Washington coast came from river corridors and was exhausted by 1920. Wood removal operations for channel navigability also played a major role in the depletion of wood from rivers and estuarine habitats. Woody debris in estuaries creates a diverse and spatially complex habitat by providing a ready source of detritus produced by invertebrate wood degraders, providing heavy solid objects and firm substrates in an environment with typically fine sediment, providing refuge for salmon in tidal rivers and sloughs (Murphy et al. 1989), affecting waterflow and sediment accumulation, stabilizing sand bars and mud banks, and creating diverse habitats in salt marshes (Gonor et al. 1988). Restoring the function and diversity of many estuarine habitats for rearing salmon will require the addition of large wood as is often done in stream restoration projects.

Creation of winter habitat in streams will help in the recovery of depressed coho populations by providing critical habitat for stream rearing, and for nomadic coho returning to freshwater to overwinter. Koski and Lorenz (1999) developed overwinter habitat in Duck Creek by building a stream channel that meandered through created wetlands containing deep pools. Several hundred coho nomads migrated from the stream-estuary ecotone into these wetlands for overwintering annually during 2004–2007 (Koski, *unpublished data*). In many larger river systems, side channels, natural ponds, and beaver ponds provide important winter habitat. Cederholm et al. (1988) developed methodology for creating pond habitat in the Clearwater River, Washington that successfully allowed juvenile coho to overwinter. Small ponds or alcoves excavated adjacent to the stream channel increased juvenile coho salmon densities and overwinter survival in Oregon streams (Nickelson et al. 1992). Managers should maintain and/or restore freshwater overwinter habitats and their connectivity to downstream estuarine habitats.

Because of southeast Alaska's mountainous, fiord topography with thousands of streams and estuaries in relatively pristine condition, salmon abundance is at near-record levels. The diversity of freshwater and estuarine habitats and their connectivity, which has resulted in the resilience exhibited by coho nomads and age 0 species, can be sustained through conservation strategies that protect and maintain these habitats.

RESEARCH NEEDS

The coho nomad life-history strategy is a relatively new concept that needs further research and documentation. Additional research is needed to fully explain the veracity and importance of this concept for developing and managing programs to maintain resilience and sustainability of coho populations. Some of the research needs include:

1. Determine the occurrence of this nomad strategy in other estuarine areas throughout the range of coho;
2. Develop or apply methodologies, e.g., strontium otolith analyses, that will confirm estuarine residency for coho juveniles and adults suspected of rearing in estuarine habitats;
3. Determine if the ocean-type life-history strategy exists in any coho population;
4. Determine why coho nomads rearing in saltwater migrate back to freshwater to overwinter before smolting;
5. Determine if age 0 coho have been generally misinterpreted and not recognized in scale analyses throughout their range; and
6. Determine if other life-history strategies or variants of the nomad strategy exist in coho populations.

RESPONSES TO THIS ARTICLE

Responses to this article are invited. If accepted for publication, your response will be hyperlinked to the article. To submit a response, follow this link. To read responses already accepted, follow this link.

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Address of Correspondent:
K V. Koski
416 Harris Street, Suite 301
Juneau, Alaska 99801
kkoski@tnc.org