Beyond the Estuary: An Extension of the Nomad Life History Strategy in Coho Salmon

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Displaced coho salmon fry known as "nomads" (Chapman 1962) enter estuaries and saltwater where early observers assumed they perished without contributing to the adult population (Chapman 1966; Crone and Bond 1976). However, a substantial body of evidence, summarized by Koski (2009), indicates that many nomads likely survive and grow in the estuary, returning to overwinter before migrating as smolts the following spring. Recorded movement of coded-wire tagged fish among streams separated by saltwater distances of 56–113 km in Lynn Canal and Stephens Passage, Southeast Alaska (Table 1) indicates that presmolts are able to overcome osmoregulatory challenges to achieve much to their growth in marine as well as estuarine waters before they re-enter freshwater in the fall to overwinter and move to the sea in the spring. Of a total of 13 recovered tags, two were from fish migrating upstream in Auke Creek in fall (September–October). The other tagged fish were captured in downstream migrant smolt traps in the spring, including 10 fish from the Berners River and one from Jordan Creek (Lum and Glynn 2007; Table 1).

Table 1. Inter-system movement of tagged presmolt coho salmon in Lynn Canal and Stephens Passage, Southeast Alaska, showing minimum saltwater distances traveled.

Number Recovered	Tagging Location	Tagging Date(s)	Recovery Location	Recovery Date(s)	Recovery Fork Length (mm)	Distance (km)
1	Berners R.	June 22−30, 1988	Auke Cr.	October 11, 1988	125	56
1	Chilkat R.	April 7−June 2, 1999	Berners R.	May 17, 2000	126	67
1	Chilkat R.	June 1−6, 1999	Berners R.	May 26, 2000	127	67
1	Chilkat R.	May 12−29, 2004	Auke Cr.	September 10, 2004	147	109
1	Chilkat R.	May 14−22, 2001	Jordan Cr.	May 13, 2002	−	113
8	Burro Cr. Hatchery	June 13, 2000	Berners R.	May 11−29, 2001	114−142	90

Otoliths from 11 of the fish listed in Table 1, including all 10 fish recovered from the Berners River and one fish from Jordan Creek (Lum and Glynn 2007), were microprobed along a transect from the primordium to the otolith margin to measure the Sr:Ca ratio, an indicator of exposure to freshwater, estuarine, and saltwater habitats (Campana 1999; Zimmerman 2005). Features evident in the growth history of the otolith were matched with the microprobe transect to pinpoint transitional movement between habitats. All of the samples showed elevated Sr:Ca ratios, marking the fish's exposure to estuarine and marine waters of Lynn Canal and Stephens Passage prior to smolting. However, one of the two wild Chilkat-Berners migrants was of particular interest because it displayed evidence of extended exposure to saline water during two periods, comprising 36% and 15%, respectively, of the smolt's total growth history as indicated by the distance from the primordium to the margin of the otolith (Fig. 1). A check was evident at emergence, with an apparent winter annulus appearing at the point where the Sr:Ca ratio began to decline in fall 1998, indicating a return to freshwater prior to initial capture and tagging in a section of the Chilkat River 5–26 km upstream from the mouth in spring 1999 (Ericksen 2001). A second marine-rearing period marked by an elevated Sr:Ca ratio is evident as the fish moved 67 km across Lynn Canal before swimming 8 km up the Berners River, where it was captured in May 2000 as a 126 mm migrant in a beaver pond. This was the only sample that displayed evidence of early departure from the river as a typical "nomad" fry, as defined by Chapman (1962), while otolith transects from the other fish indicated exposure to marine waters only after they were tagged as age-1 presmolts during the second spring period after emergence.

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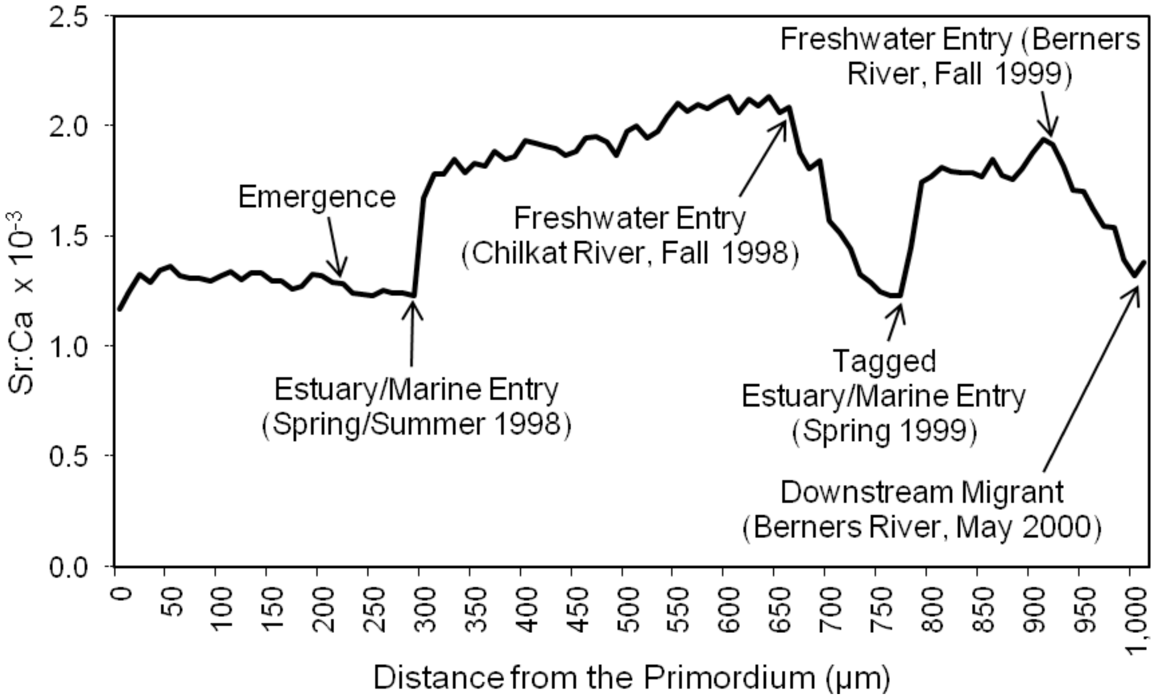

Fig. 1. Changes in the Sr:Ca ratio measured across an otolith from a coho salmon tagged in the Chilkat River between April 7 and June 2, 1999 (Ericksen 2001) and recaptured from the Berners River at a length of 126 mm on May 17, 2000.

In addition to freshwater, there is evidence that some juvenile coho salmon in Alaska over-winter in estuarine habitat (Hoem Neher 2012). An otolith Sr:Ca transect from a fish tagged in the Chilkat River in May 2001 (Ericksen 2003) and captured the following May in a downstream migrant trap located on Jordan Creek, situated at the margin of the estuarine Mendenhall wetlands (Lum and Glynn 2007), shows evidence of overwinter exposure to brackish water until just prior to capture (Fig. 2; Table 1).

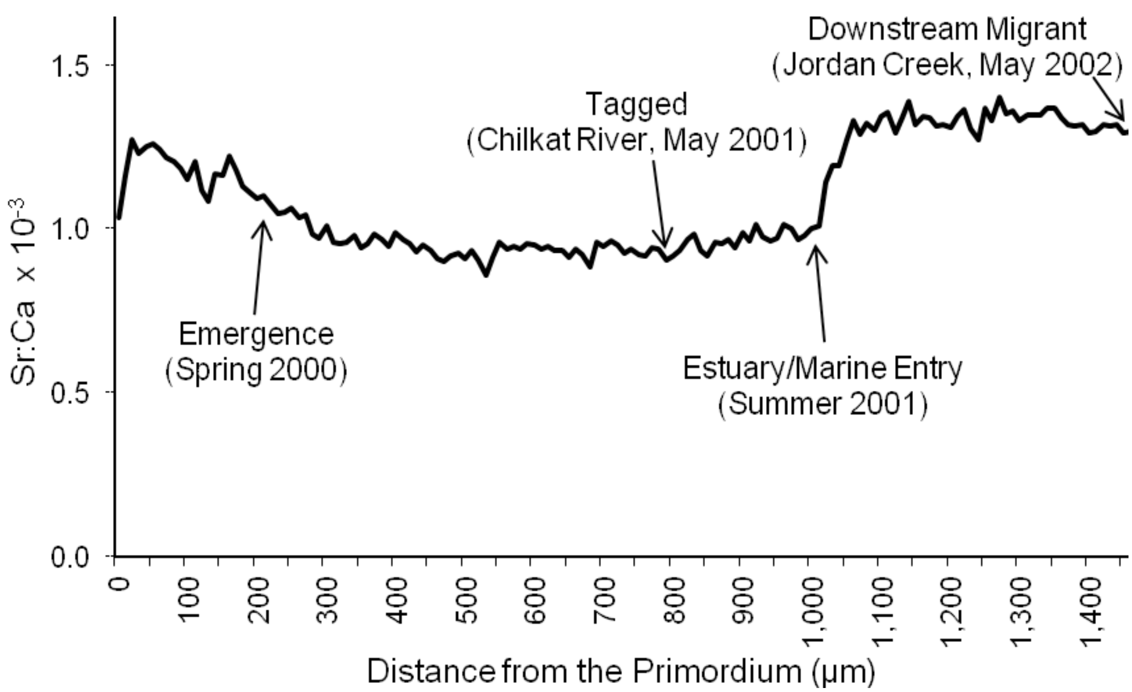

Fig. 2. Changes in the Sr:Ca ratio measured across an otolith from a coho salmon tagged in the Chilkat River between May 14 and May 23, 2001 (Ericksen 2003) and recaptured from Jordan Creek on May 13, 2002 (Lum and Glynn 2007).

Although seldom documented, a fall upstream migration of immature coho salmon juveniles returning to streams from estuaries and marine waters appears to be a common occurrence in Southeast Alaska. These migrations begin as early as mid-summer, peak from mid-September to mid-October during the return of adult spawners, and can continue at least until early November (Harding 1993; Shaul et al. 2011). Harding (1993) found fall immigrants varied widely in fork length from 38 to 235 mm (average 83 mm) with most resembling migrating smolts in color and some with attached sea lice (*Caligus* spp.), suggesting recent immigration from marine water. Several of the largest immigrants (> 200 mm) were dissected and confirmed not to be precocious males. The weir at Auke Creek was modified to capture small immigrants during four years (Taylor and Lum 2003, 2004, 2005; Taylor 2006). Minimum seasonal counts (through late-October) of immigrant juveniles comprised 12.5%, 6.8%, 2.1%, and 6.8% (average 7.0%), respectively, of subsequent downstream smolt migrations from the system the following spring (Taylor and Lum 2004, 2005; Taylor 2006, 2007; Shaul et al. 2011).

Do nomadic juveniles that overwinter in distant freshwater systems and estuaries imprint on the streams from which they eventually smolt, or do they return to spawn in their natal stream? The latter possibility is supported by recovery of four adult spawners in the Chilkat River that had been tagged in the Berners River (3) and Jordan Creek (1) and had moved in the opposite direction between the smolt and adult stages. These recoveries were compared with four fish tagged as apparent presmolts in the Chilkat River that were later recaptured as smolts migrating from the Berners River (2) and Jordan Creek (1) and as a fall immigrant into Auke Creek (Shaul et al. 2011; Table 1). Although imprinting is commonly associated with the parr-smolt transformation, a surge in production of plasma thyroxine associated with imprinting has also been documented in coho salmon during earlier stages involving migration (Dittman et al. 1996), supporting the possibility of imprinting on a natal stream despite subsequent prolonged exposure to a non-natal water source prior to smolting.

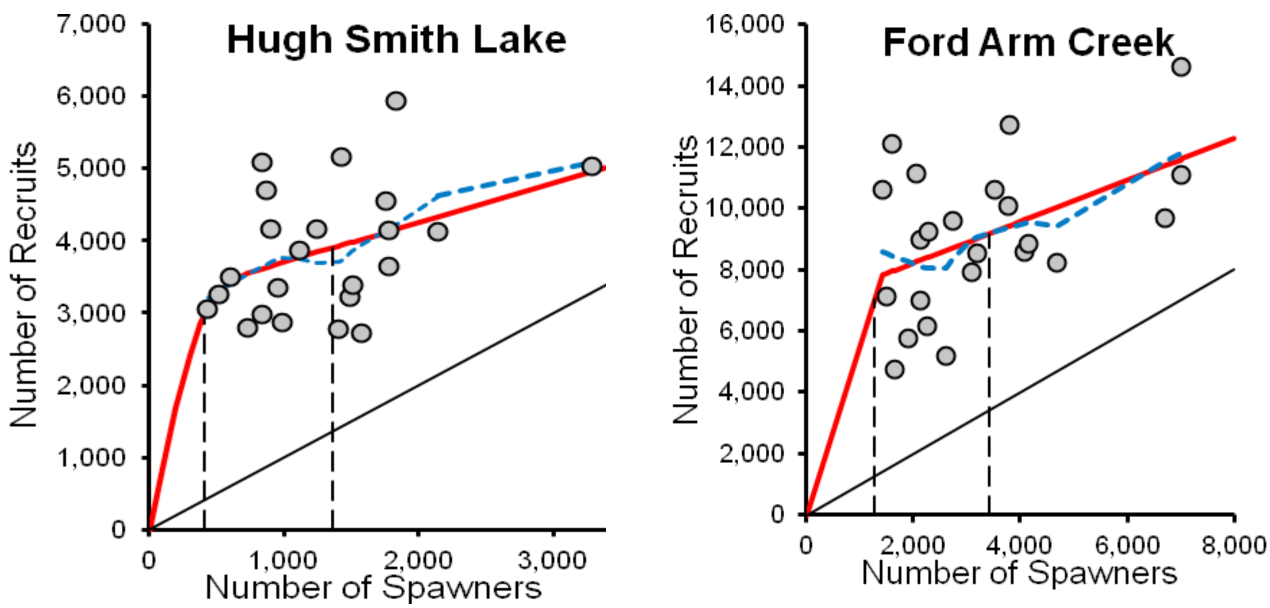

Fig. 3. Bent hockey stock (BHS) spawner–recruit relationships for Hugh Smith Lake coho (1982–2004 brood years) and Ford Arm Lake coho salmon (1982, 1983, and 1985–2005 brood years) showing a 0.75 LOESS trend (blue dashed line), the replacement line (black solid), and the escapement range estimated to produce 90% or more of maximum sustained yield (black dashed lines).

The marine-rearing strategy allows fish that are surplus to the summer carrying capacity of freshwater habitat to attain a high growth rate on estuarine and marine food resources (Murphy et al. 1984; Tschlapinski 1988) before returning in the fall to suitable overwintering habitat. Although estuarine and marine waters present osmoregulatory challenges and increased predation risk, growth and survival in those environments appears to be far less compensatory than in freshwater (Tschaplinski 1988). The successful contribution by nomads to coho salmon smolt and adult populations provides a plausible explanation for the significant positive linear slope observed in the spawner-recruit relationships (parent escapement versus smolts x average marine survival) for Southeast Alaska coho populations in Hugh Smith Lake (slope = 0.60, $p = 0.04$) and Ford Arm Creek (slope = 0.68, $p = 0.02$; Fig 3). We propose a modification to the logistic hockey stick (LHS) model (Barrowman and Myers 2000; Bradford et al. 2000) in which nomads entering estuarine and marine waters contribute to smolt and adult production at a constant proportion of the increase in the number of spawners, at escapements above the level needed to maximize smolt production from freshwater habitat (K_F). A conceptual representation, the bent hockey stick (BHS) model, is depicted in Fig. 4 with an initial slope (α), smoothness parameter (θ), and the secondary slope (representing the nomad contribution within and above in the inflection region), based on average parameter estimates for the populations in Hugh Smith Lake and Ford Arm Creek. Although the indicated lower escapement goal bound (13% of K_F) and escapement at maximum sustained yield (E_{msy}; 17% of K_F) differ very little from the LHS model, the escapement range predicted to produce 90% or more of MSY based on the BHS model encompasses a 74% broader range with an upper bound at 38% of K_F instead of 27% of K_F for the LHS model. A positive population response to increasing escapement allows imprecisely but conservatively managed mixed-stock fisheries to achieve a high percentage of theoretical MSY, with a low yield penalty for variable escapements above E_{msy} (Shaul et al. 2011).

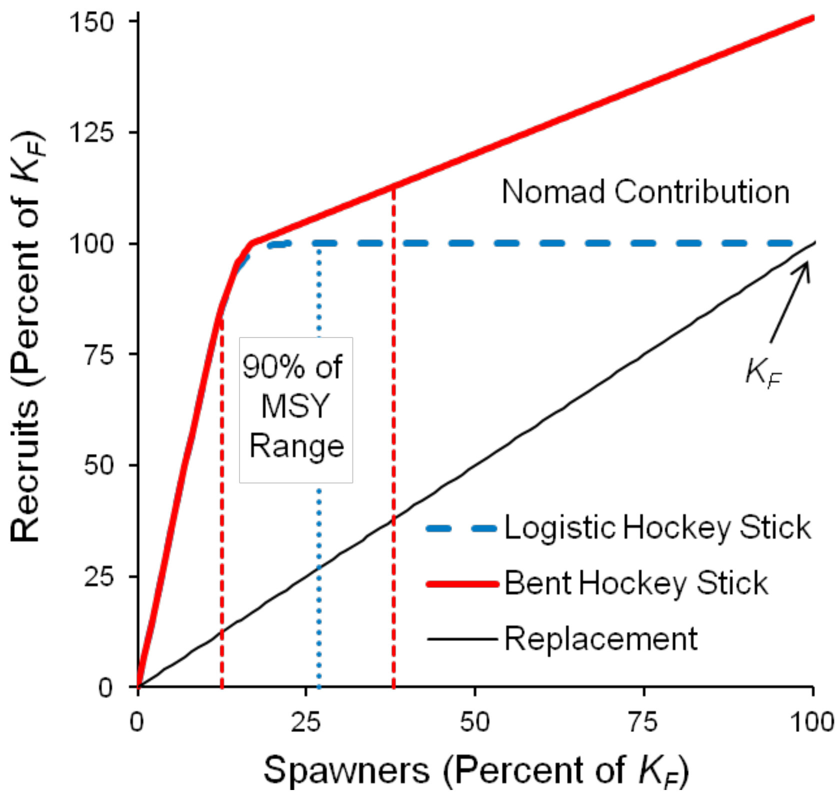

Fig. 4. Conceptual bent hockey stick (BHS) model based on average spawner-recruit parameters (including α, θ, and secondary slope) for the Ford Arm Creek stock and the Hugh Smith Lake stock compared with the logistic hockey stick (LHS) model. Axis scales are shown as a percent of freshwater carrying capacity (KF) indicated by the LHS model.

If we attribute the slope of the BHS relationship above estimated E_{msy} entirely to nomad production, then the contribution by nomads to adult returns from average brood year escapements of 1,305 spawners at Hugh Smith Lake and 3,275 spawners in Ford Arm Creek is predicted at 12% and 14%, respectively, of combined total production (Shaul et al. 2011). These theoretical proportionate contributions by nomads are similar to the highest minimum count of immature fall coho salmon immigrants into Auke Creek as a percent of the smolt migration the following spring (12.5%), and somewhat above the average for four years (7.0%). While we hypothesize that growth and survival in estuarine and marine waters has an important influence on the spawner-recruit relationship (and optimal fishery management strategy), it is clearly secondary in importance to production of smolts reared entirely in freshwater. Although their survival may be low on average and variable, nomads' use of a different, less density-limiting environment for summer growth benefits populations with life history diversification and a potential population buffer. The strategy enables populations in wet coastal regions like Southeast Alaska to efficiently access diverse habitats for growth and overwinter refuge, connecting thousands of small anadromous streams where coho salmon populations would otherwise remain isolated and vulnerable to population shocks.

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