

Residence Time and Seasonal Movements of Juvenile Coho Salmon in the Ecotone and Lower Estuary of Winchester Creek, South Slough, Oregon

BRUCE A. MILLER*

Oregon Department of Fish and Wildlife,
Post Office Box 5430,
Charleston, Oregon 97420, USA

STEVE SADRO

South Slough National Estuarine Research Reserve,
Post Office Box 5417,
Charleston, Oregon 97420, USA

Abstract.—The juvenile life history of coho salmon *Oncorhynchus kisutch* in the stream–estuary ecotone of Winchester Creek, South Slough, Oregon, was investigated in 1999–2001. Seines and a rotary screw trap were used to capture fish for dye-marking, and residence time within the ecotone was determined for recaptured marked fish. In the lower estuary, ultrasonic transmitters were used to document residence time and patterns of movement for smolts migrating to the ocean. Nearly half of each brood year moved to the estuary as subyearlings. A portion of age-0 juveniles that moved downstream during spring lived in the ecotone through summer for up to 8 months, then most moved back upstream to overwinter. Fish that moved to the ecotone during fall and winter had mean minimum residence times of 48 d in 1999 and 64 d in 2000. Some of the fish that moved to the ecotone during fall and winter moved into an off-channel beaver pond and resided there for a mean of 49 d. Spring age-1 smolts had a mean minimum residence time in the ecotone of 18 d for both years and used recently restored salt marshes and other off-channel habitats. Smolts implanted with ultrasonic transmitters lived in the lower estuary for an average of 5.8 d, during which their direction of movement corresponded to the direction of tidal flow.

The period of estuarine residence of migrating juvenile coho salmon *Oncorhynchus kisutch* is generally assumed to be an important component of their life history. Estuaries provide the spatial salinity gradient necessary during the physiological adaptation from freshwater to salt water as well as a rich foraging environment that offers a last opportunity for growth before ocean entrance (Healey 1982). For other salmonids, faster growth in the estuary and larger size at ocean entrance have been shown to account for higher marine survival (Reimers 1973; Macdonald et al. 1988; Levings et al. 1989; Solazzi et al. 1991; Northcote 1997; Percy 1997; Trotter 1997). For coho salmon, these benefits are usually inferred; juveniles are found in the estuary for a period of at least several weeks, during which time they may experience faster growth (Tschaplinski 1982) and potentially higher marine survival.

Although there is agreement that estuaries may be important in the life history of juvenile coho salmon, there is limited information on the sea-

sonality and duration of estuarine residence or on specific habitat use. In most cases, the estuary is treated as a single habitat, with little or no distinction between lower and upper reaches characterized by different tidal ranges, salinity regimes, types of marsh communities, and levels of accessibility to various habitat types by juvenile fish. It is reasonable to expect that different suites of estuarine habitats receive differential use by juvenile coho salmon.

Although few studies have focused on the estuary as rearing habitat for juvenile coho salmon, a small number of studies have identified the importance of the transition zone, or ecotone (Odum 1971), between freshwater and brackish water in the upper estuary. Merrell and Koski (1978) have defined the stream–estuary ecotone, and we adapt their definition to include the area extending from the upper limit of tidal influence downstream to the area where the channel becomes bordered by tidal mudflats. This definition of the ecotone includes all tidal channels and fringing marsh habitats that are accessible to fish for at least some portion of the tidal cycle.

Numerous studies have documented the down-

* Corresponding author: millerb@fsl.orst.edu

stream migration of subyearling (age-0) coho salmon to the stream–estuary ecotone or lower main-stem reaches. These migrations have been attributed to both density-dependent (Chapman et al. 1961; Chapman 1962; Hartman et al. 1982; Murphy et al. 1984; Rodgers et al. 1987) and density-independent (Au 1972; Tschaplinski 1982, 1988; Kahler et al. 2001) causes. The regular and widespread occurrence of early emigration suggests that a portion of juvenile production in many systems may take advantage of rearing opportunities provided by the stream–estuary ecotone. Merrell and Koski (1978) have further suggested that the benefits (to juvenile production) of rearing in the ecotone are proportional to the extent of this habitat within a system.

Within the northern portion of the range of coho salmon, Murphy et al. (1984) showed that the stream–estuary ecotone is an important habitat for age-0 coho salmon in Porcupine Creek, Alaska. Crone and Bond (1976) found that some coho salmon moved to the estuary soon after emergence in Sashin Creek, Alaska. In British Columbia, work in Carnation Creek has also shown that the “upper intertidal zone” is an important rearing habitat for age-0 coho salmon (Tschaplinski 1982, 1988).

In the southern portion of the range in Washington and Oregon, studies that have evaluated the use of the estuary by juvenile coho salmon have been more limited in scope and have not differentiated the stream–estuary ecotone from other habitats. These studies describe ranges of possible residence time in the entire estuary for age-1 smolts (Healey 1982; Myers and Horton 1982) or time that age-0 coho salmon spent in specific marshes or sloughs (Ryall and Levings 1987). It is not clear from these studies whether the importance of such behaviors as age-0 migration and estuarine rearing ascribed to northern populations of coho salmon may also apply in the southern portion of the range.

In this study, we describe aspects of the juvenile life history of coho salmon for two consecutive brood years in a small estuarine system along the southern Oregon coast. Components include seasonal movements, change in mean length and condition factor within specific reaches or habitats, residence times within the stream–estuary ecotone, and patterns of movement and residence times in the lower estuary.

Methods

Study Area

South Slough forms a 7,800-ha subbasin of Coos Bay along the southern Oregon coast (Figure 1).

This slough is located near the mouth of Coos Bay, and tidal influx is characterized by mixed, high-salinity waters rather than lower-salinity waters found in sloughs further upstream in the Coos River system. Winchester Creek, draining 1,600 ha, forms the principal tributary to South Slough. The upper reaches of Winchester Creek are terrace constrained and have an average gradient that ranges from less than 1.0% in the lower portions to 3.7% in the uppermost portion. The gradient downstream from a point 0.5 km above head of tide is very low, and the channel is unconstrained within an active, broad floodplain. Stream substrate is predominantly silt and sand throughout most of the watershed, and beaver ponds are common in upper reaches. Spawning habitat for coho salmon is limited to a 1-km reach of West Fork Winchester Creek, one of three principal forks. Other resident salmonid fishes include sea-run cutthroat trout *O. clarki clarki* and small numbers of winter steelhead trout *O. mykiss*. Mean monthly discharge, measured at a gauge located 0.5 km above head of tide, ranges from less than 0.05 m³/s during summer to over 5.7 m³/s during winter. Water temperature ranges from 6°C to 16°C.

The uppermost 3 km of Winchester Arm of South Slough, the transition zone between the freshwater of Winchester Creek and the saline water of the estuary, forms the stream–estuary ecotone. Within this ecotone, two reaches (A and B) characterized by distinct habitat types were sampled.

Reach A extends from the head of tidal influence to approximately 1 km downstream and forms a narrow, deeply entrenched stream channel with embedded large wood debris (Figure 1). Riparian vegetation is composed primarily of slough sedge *Carex obnupta* and bulrush *Scirpus microcarpus*, and widely spaced sitka spruce *Picea sitchensis*. Tidal flux ranges up to approximately 1 m, and physical parameters vary seasonally and are a function of freshwater input. The water column is mixed, and salinity at high tide ranges from 0‰ during high winter flows to approximately 10‰ during low spring and summer flows. Water temperature ranges from 6°C in winter to 16°C in spring, but may reach 20°C during summer as flood tidal flows move over extensive mudflats further downstream.

Reach B extends for 2.3 km downstream of reach A and has a channel width that varies between 10 and 25 m with tidal height. Tidal height ranges up to 3.3 m above mean lower low, the water column is mixed, and salinity ranges from

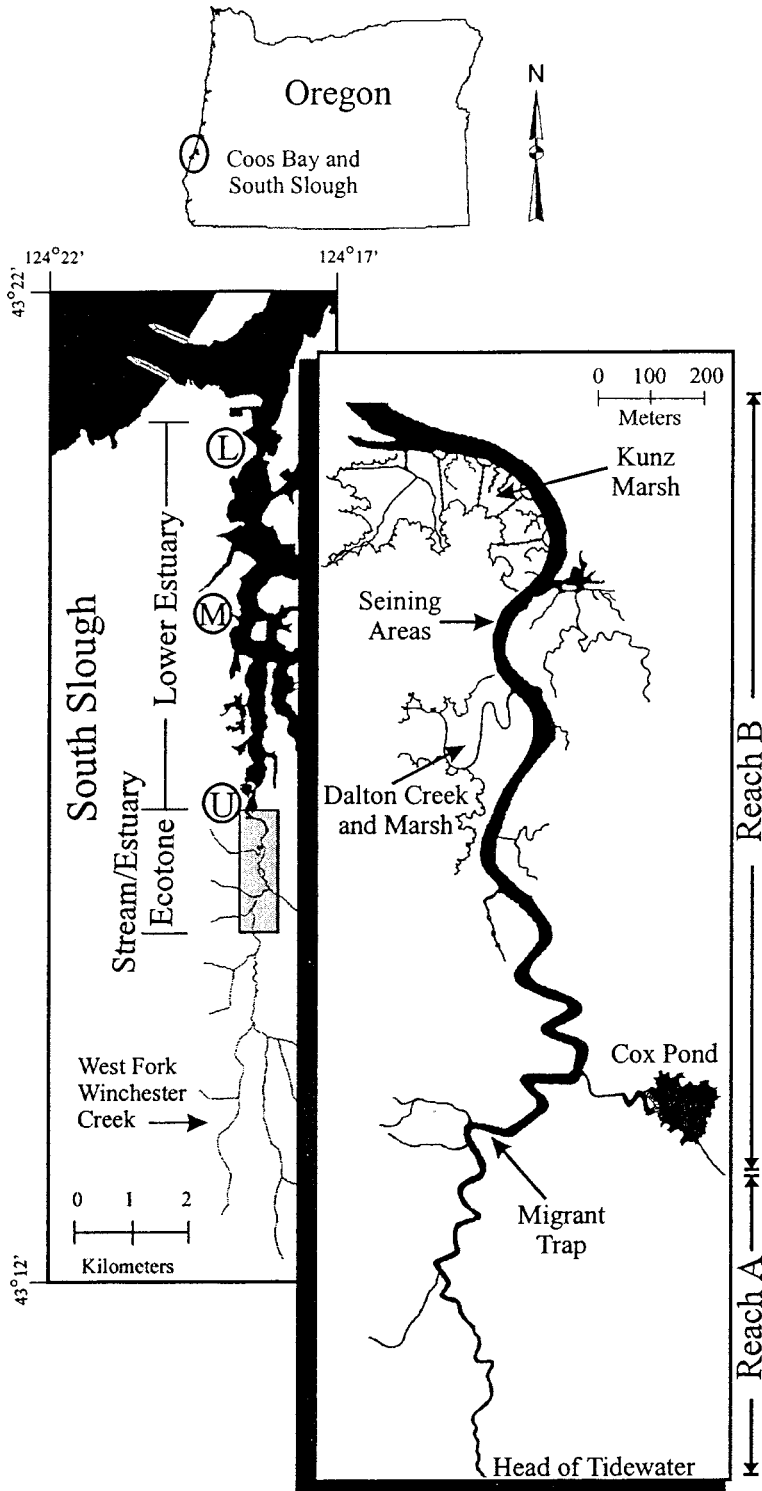


FIGURE 1.—Location of the Winchester Creek stream–estuary ecotone within the South Slough estuary. Letter codes in the left panel denote the locations of ultrasonic tag receivers in the upper (U), middle (M), and lower (L) reaches of the estuary. Upland boundaries are only shown for study marshes.

0% during winter freshet events to approximately 32% during lower spring and summer flows. Temperatures range from 6°C to 22°C. Four sample sites located within reach B were the main channel, Dalton Marsh, Kunz Marsh, and Cox Pond (Figure 1). Dalton Marsh is a restored salt marsh that has been reconnected to the main channel by removal of a dike and tide gates. The tidal channel in Dalton Marsh has been reconstructed to facilitate drainage of Dalton Creek through the marsh. This channel is bordered primarily by Lyngby's sedge *Carex lyngbyei* and alkali bulrush *Scirpus maritimus*. Kunz Marsh has also been restored by removal of a dike and tide gate, but there is little freshwater input. The tidal channels in Kunz Marsh extend only a short distance from the main channel of Winchester Creek and are bordered primarily by Lyngby's sedge, salt-marsh sand spurry *Spergularia marina*, sea arrowgrass *Triglochin maritimum*, and dwarf spike-rush *Eleocharis parvula*. Cox Pond is a large beaver pond (~5,600 m²) located in a tributary within reach B. There is no spawning habitat for coho salmon above Cox Pond or in Dalton Creek.

Downstream of reach B, the predominant habitats include fringing pocket salt marshes and broad tidal mudflats with extensive beds of eelgrass *Zostera* spp. For this study, we define the area downstream of reach B as the lower estuary.

Seasonal Movement

The juvenile coho salmon sampled in this study ranged in age from newly emerged fry to yearling smolts. We use the terms "age-0" for subyearlings and "age-1" for yearlings. No fish older than age 1 were found, based on scale analysis of smolts sampled during spring. These age groups are further defined by the season during which they were sampled (for example, fall age-0 or spring age-1). We limit the term "migration" to spring age-1 fish, which are generally considered to be smolts moving seaward. The term "movement" is used when referring to the behavior of age-0 fish, which may leave natal reaches and move seasonally between summer and winter habitats.

The downstream movement of juvenile coho salmon in Winchester Creek was monitored daily with a 1.53-m-diameter rotary screw trap from February 1999 through May 2000 and November 2001 through May 2001. The trap was located 1 km below the head of tidal influence, at the transition point between reaches A and B (Figure 1), and the trap drum turned an average of 11.9 h/d, primarily during ebb and low tide. During very

low flows in late spring 2001, the trap drum was powered with a 12-V motor that was controlled with float and photovoltaic switches to operate only during nighttime ebbing and low tides.

Independent measurements of trap efficiency for age-0 and age-1 fish were determined by releasing marked fish 110 m above the trap and measuring the rate of recapture. Spring age-0 fish were marked with a small clip on the caudal fin. Fall age-0 and older fish were given a dye-mark via a needleless dental injector containing alcian blue (a copper phthalocyanine derivative) at a concentration of 6.4×10^{-2} g/mL water (Arnold 1966; Hart and Pitcher 1969). Total number that moved past the trap each week (N_T) was calculated as total catch divided by trap efficiency. Variance was calculated by use of a bootstrap method with 1,000 iterations (Thedinga et al. 1994).

Few marked spring age-0 fish released above the trap were recaptured; thus, trap efficiency and the estimated number that moved to the ecotone could not be determined for this age-group. Numbers of spring age-0 fish captured are reported to show timing of movement past the trap.

A subpopulation of fish that lived in reach A during summer was also dye-marked to document seasonal movement in the ecotone. During August and September 2000, 117 fish in reach A were given unique dye-marks of alcian blue. Fish were recaptured at the trap and the numbers of marked fish were expanded by calculation of weekly trap efficiency.

Determination of Residence Time

Stream-estuary ecotone.—Minimum residence time in the ecotone was determined from recapture of dye-marked fish. Fish larger than 60 mm were dye-marked on the ventral surface with a combination of marks applied from just anterior to the pectoral fins to just posterior to the pelvic fins. Fish were dye-marked with either alcian blue or India ink, and the combination of marks was changed at 3-d intervals. Dye-marked fish were also given a unique mark each time they were recaptured. The number of days since initial capture for fish subsequently recaptured was calculated from the midpoint of the 3-d period assigned to each dye-mark. Spring age-0 fish sampled in Dalton Marsh were smaller than 60 mm and were given a dye-mark on either the dorsal or ventral lobe of the caudal fin, resulting in two mark groups.

Minimum residence times were plotted as the percent of total recaptures that resided for increasing numbers of days since first capture. Because

residence times varied seasonally, cumulative values of the percentages of residence time were plotted for two periods, fall/winter and spring. Plots of cumulative percentages were then used to project the proportion of the population that resided for different lengths of time.

All fish over 60 mm sampled at the migrant trap were dye-marked. Four sites within reach B were also sampled to mark and recapture fish, including:

(1) The main channel, 1.5 km downstream of the trap, was sampled at low tide with a 25-m \times 2-m, 6-mm-mesh beach seine at 1-week intervals between January and June of 2000 ($n = 190$ marked) and 2001 ($n = 290$).

(2) Dalton Marsh, 1.4 km below the trap, was sampled with a 2-m \times 1-m, 4-mm-mesh seine at 1–2-week intervals during spring 1999 to monitor spring age-0 fish that migrated from Winchester Creek into the reconstructed channel of this salt marsh. A total of 71 fish were dye-marked on April 19 and 27.

(3) Kunz Marsh, 1.8 km below the trap, was sampled monthly over three consecutive nights during the spring tide series to capture age-1 coho salmon that entered from the adjacent main channel during high tide. Sampling occurred in February through May of 2000 ($n = 51$ marked) and 2001 ($n = 25$). A 0.59-ha low-marsh portion of Kunz Marsh was sampled by placing the bag of a modified 50-m \times 2-m, 6-mm-mesh seine over the principal drainage channel, creating a complete barrier to fish passage. Fish became trapped in the bag as water drained from the marsh during ebb flow.

(4) Cox Pond, 315 m downstream of the trap, was sampled with a 25-m \times 2-m, 6-mm-mesh beach seine at 1-month intervals from November 1999 to May 2000 ($n = 244$ marked) and from November 2000 to February 2001 (no fish marked).

Lower estuary.—Movement and residence time of age-1 fish that emigrated during spring was followed in the lower estuary by tracking fish that were implanted with ultrasonic transmitters. Migrating smolts from the 1999 brood year were captured between April 5 and May 5, 2001, in the main channel of reach B or in Kunz Marsh. Twelve of the largest individuals, ranging between 131 and 151 mm fork length, were tagged to minimize the effects of transmitters on fish behavior (Moore et al. 1990; Adams et al. 1998). An ultrasonic transmitter (Vemco, Ltd., Nova Scotia: 8 mm \times 20 mm, 3.1 g) was surgically implanted in the peritoneal

cavity of each fish (Jepsen et al. 2001). Fish were allowed to recover for 5–24 h in a mesh flow-through container moored in the channel prior to release 0.7 km above the lower end of reach B.

Four submersible ultrasonic receivers (Vemco, Ltd., Nova Scotia: VR2 single channel) with a detection range of 300–500 m were positioned at three stations. To determine when fish left the stream–estuary ecotone, one receiver was deployed at the lower end of reach B, 6.8 km above the mouth of South Slough (upper reach in Figure 1). To track movement of coho salmon in the lower estuary, one receiver was deployed 2.8 km upstream of the mouth of South Slough (middle reach in Figure 1). To determine when fish left the estuary, two receivers were deployed near the mouth of South Slough, 2.2 km from the ocean entrance (lower reach in Figure 1). An ultrasonic transmitter was used to confirm signal detection from bank to bank at all receiver locations to ensure no fish would pass undetected.

Migration rate was calculated by dividing the distance between receivers by the time it took a smolt to travel that distance. A lack of movement detected by a fixed receiver for at least 1 h was defined as holding behavior (Moser et al. 1991).

Length and condition factor.—Fork lengths of fish caught at all sample sites in the ecotone were recorded, and beginning February 2000, wet weights were measured to the nearest 0.1 g. Condition factor (CF) was calculated as $[\text{weight}/(\text{length})^3] \cdot 10^5$. West Fork Winchester Creek was sampled by electrofishing at 1-month intervals from April 1999 to May 2001 to measure mean length and CF of fish ($n \geq 15/\text{month}$) in the upper watershed. Few marked fish were recovered that could be individually recognized based on mark combinations, precluding calculation of mean growth rates within specific reaches or habitats; therefore, mean lengths and CF for cohorts are reported.

Age-1 fish captured in Kunz Marsh during April 2001 ($n = 36$), the month of peak catch, were held for 24 h in a flow-through container moored in the tidal channel near the marsh. This allowed for evacuation of gut contents and measurement of change in CF. Condition factor of fish held for 24 h was compared with CF of the subpopulation of fish sampled in the main channel in reach B. Difference in mean CF between groups was then used as a proxy for comparison of foraging success.

Results

Seasonal Movement

A total of 242 age-0 fish of the 1998 brood and 177 fish of the 1999 brood were trapped during

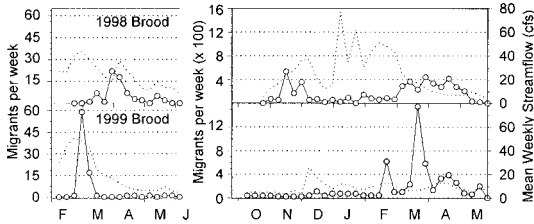


FIGURE 2.—Migration timing of the 1998 and 1999 broods of juvenile coho salmon (open circles) and weekly streamflow (dotted line) in Winchester Creek, South Slough. Months, shown on the x-axis, are abbreviated to their first letters. Only the numbers of spring age-0 fish caught are shown; the numbers of fall age-0 and older fish are expanded estimates based on rotary screw trap efficiency.

spring, but because few of the fish that had been marked to measure trap efficiency were recaptured, the total number of age-0 fish that moved to the ecotone could not be estimated. The peak in downstream movement of spring age-0 fish for the 1998 brood did not correspond with particularly strong streamflows but followed several weeks of diminishing flow. Conversely, spring age-0 fish of the 1999 brood entered tidewater in association with moderately strong streamflows (Figure 2).

An estimated 5,116 fish of the 1998 brood and 5,490 fish of the 1999 brood moved into the stream-estuary ecotone from October to June (Table 1). A portion of the 1998 brood moved to tidewater during fall, corresponding with high streamflow events, then continued to move downstream all winter in low numbers (Figure 2). Juveniles of the 1999 brood moved to tidewater in lower numbers during fall and winter, when low precipitation resulted in relatively low streamflows.

In both years, catch at the trap increased substantially at the beginning of March as age-1 fish moved downstream (Figure 2). Fish sampled after March 1 comprised 61.2% to 70.9% of the total fall age-0 and older migrants each year (Table 1).

Subpopulations of fish in the ecotone displayed a variety of seasonal and short-term movements. An estimated 62.6% of fish marked above the trap in reach A during summer subsequently moved past the trap. Most of these recaptures (71.4%) were caught after March 1. None of the fish marked in reach A were found while seining in either reach of the ecotone after November, indicating most of these fish overwintered above reach A.

Fish marked in reach B during winter and spring also made short-term upstream movements. In 2001, recapture of marked fish at the trap indicated that 8.6% of fish that used the main channel in reach B subsequently moved upstream of the migrant trap, then back downstream within 1 week of initial capture.

In 2000, 7.3% of fish marked in Cox Pond during fall and winter were subsequently recaptured upstream at the migrant trap. There was continuous immigration into this habitat during winter and spring: in early February, 10% of marked fish in Cox Pond were initially marked at the trap, but this proportion increased to 62.5% by May. The following year, few juvenile coho salmon appeared to use Cox Pond during fall and winter, possibly due to the difficulty of ascending the beaver dam into the pond during lower-than-average streamflows.

Residence Time

Stream-estuary ecotone.—Residence times of fish marked at the migrant trap and recaptured downstream in the main channel of reach B and in Kunz Marsh varied seasonally. Fish marked at the trap before March 1 had the longest residence times, with means (\pm SE) of 64.4 ± 6.82 d for the 1998 brood and 48.3 ± 8.55 d for the 1999 brood (Figure 3). In contrast, spring age-1 migrants marked after March 1 had shorter residence times, with means of 17.5 ± 2.24 d and 18.0 ± 1.45 d for the two brood years. The mean residence times

TABLE 1.—Actual catch and estimated number \pm SD of juvenile coho salmon that moved to the stream-estuary ecotone, Winchester Creek, South Slough, Oregon, 1999–2001. Low trap efficiency for age-0 fish in both broods precluded estimation of total migrants for this age group.

Brood	Sample period	Efficiency	Number caught	Estimated migrants
1998	Feb 5–May 23, 1999		242	
	Nov 9, 1999–Feb 29, 2000	0.124	246	$1,987 \pm 346$
	Mar 1–Jun 1, 2000	0.190	593	$3,129 \pm 296$
1999	Mar 22–Jun 1, 2000		177	
	Oct 17, 2000–Feb 28, 2001	0.133	213	$1,598 \pm 463$
	Mar 1–May 27, 2001	0.150	585	$3,892 \pm 467$

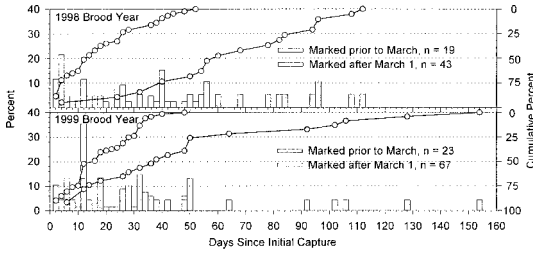


FIGURE 3.—Minimum residence time of juvenile coho salmon in reach B that were dye-marked at the trap and recaptured 1.4–1.8 km downstream in the main channel and in Kunz Marsh. Cumulative values of individual percentages of residence time are plotted to describe the proportions of the populations that resided in the ecotone for increasing lengths of time. These values appear in reverse order to express the minimum time that a proportion of the population was present.

between the pre- and post-March 1 groups were significantly different in both years (*t*-test, $P < 0.001$), whereas the within-group means of residence time were not significantly different between years (*t*-test, $P = 0.163$ for pre-March; $P = 0.869$ for post-March).

Plots of the cumulative values of the percent of individual residence times (Figure 3) indicate that 75% of fish that moved to the ecotone during fall and winter had minimum residence times ranging from 12 to 40 d between years. The other 25% resided for at least 50–84 d in the ecotone. For fish that migrated during spring, 75% resided for at least 2–10 d in the ecotone, whereas 25% resided there for at least 26–28 d.

Age-1 fish marked and recaptured in lower reach B also displayed a wide variation in residence times, with means of 19.6 ± 2.55 d for the 1998 brood and 17.0 ± 3.46 d for the 1999 brood (Figure 4), but the means were not significantly different between years (*t*-test, $P = 0.566$). The cumulative values of the individual percentages of residence times indicate that 75% of age-1 fish that migrated to reach B during spring had minimum residence times that ranged from 6 to 10 d between years, whereas 25% resided in reach B for at least 20–32 d.

The only coho salmon found in Kunz Marsh were age-1 juveniles caught during the spring emigration, March through May. Peak catches occurred in April of both 2000 and 2001, coincident with peak catches at the trap. The density of coho salmon in this habitat during peak emigration was 29.3 ± 9.09 fish/ha for the 1998 brood year and 20.9 ± 2.82 fish/ha for the 1999 brood year. A maximum of 11.2% of fish marked in Kunz Marsh

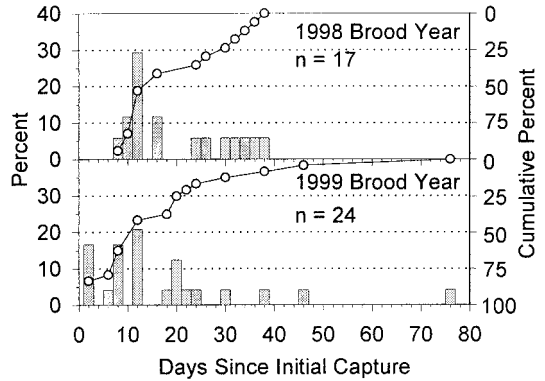


FIGURE 4.—Residence time of juvenile coho salmon that were dye-marked and recaptured in reach B (Kunz Marsh or main channel). See Figure 3 for additional details.

in any month were subsequently recaptured in this same habitat within 2 d.

Age-0 fish of the 1998 brood moved into the restored tidal channel in Dalton Marsh during April. Mean residence time was 20.4 ± 2.04 d, but 25% of the fish resided there for at least 36 d. Sampling in early June indicated 8.0% of those marked on April 19 resided in Dalton Marsh for at least 52 d, and 10.9% of those marked on April 27 lived in this habitat for at least 44 d. No age-0 fish were found in Dalton Marsh after mid-June.

In Cox Pond, fish were recaptured up to 98 d after marking, but mean residence time was 49.1 ± 2.75 d, with 75% of fish living there for at least 31 d and 25% living there for at least 58 d (Figure 5).

Lower estuary.—The migratory behavior of 8 of the 12 smolts implanted with ultrasonic transmitters was recorded. Two tagged fish were never detected, and two died in reach B (signal detection but no movement for 3 weeks). Of the eight fish that entered the lower estuary, six were detected at the middle receiver and four of the six were

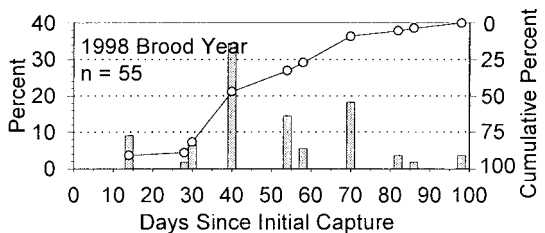


FIGURE 5.—Residence time for marked juvenile coho salmon in Cox Pond, December 17, 1999 to June 1, 2000. See Figure 3 for additional details.

TABLE 2.—Migration activity of coho salmon smolts from the 1999 brood that were fitted with ultrasonic transmitters and tracked in South Slough. Holding is percent time each fish was detected in the same location for at least 1 h. The ratio of gross to net distance is the minimum distance fish traveled back and forth while moving with flood and ebb currents. Of the 12 fish implanted with transmitters, two were not detected and two died. Smolts 3, 10, 8, and 9 were only detected at the upper receiver.

Smolt number	Fork length (mm)	% time spent		Gross : net distance traveled	Mean velocity (m/s)	
		Holding	Moving		Ebb	Flood
4	149	66	34	1	0.34	
7	146	57	43	1	0.30	
1	149	52	48	7	0.30	0.65
2	146	84	16	9	0.34	1.68
3	138					
10	147					
8	131					
9	145					

detected at the downstream receivers near the mouth of South Slough (Table 2).

Tagged fish lived in reach B for a mean of 11.6 ± 3.63 d before detection at the upper receiver. This mean residence time corresponded to the calculated minimum residence time for 50% of all spring age-1 migrants, suggesting tagged fish were representative of the spring population. None of the tagged fish that were detected at the middle or lower receivers returned to the ecotone. The mean residence time in the lower estuary for the four fish that were detected at the mouth of South Slough was 5.2 ± 1.0 d.

Tagged fish traversed the 4.0-km distance between the upper and middle receivers in 2–14 h. Fish moved back and forth between the middle and lower receivers, covering as much as 22.4 km more than the 2.8-km net distance between the two

receivers prior to leaving South Slough. Fish always moved in the same direction as the tidal current and spent an average of 65% of their detected time holding their position (Table 2). There was no clear pattern in spatial distribution for the four fish that survived to the mouth of South Slough; two spent most of their detected time at the middle receiver (72% and 79%), and two spent most of their detected time at the lower receiver (57% and 99%).

The mean rate of movement was 0.30 m/s during ebb tide and 1.2 m/s during flood tide (Table 2), but for individual fish it ranged from 0.12 m/s during ebb to 2.59 m/s during flood. Peak current velocities in the main channel near the middle receiver ranged from 0.2 to 0.9 m/s (Juza 1995). Although the mean rate of movement during ebb for all fish was within the reported range of current velocities, movement during flood sometimes exceeded current velocities, suggesting fish actively swam in the direction of flood flow.

Length and condition factor.—Fish were largest in the stream–estuary ecotone and smallest in the upper watershed (Figure 6). Spring age-0 fish sampled in Dalton Marsh in 1999 had the largest change in mean length, equivalent to 0.44 mm/d, and reached a mean length of 70 mm before leaving this habitat by mid-June. Fish sampled in Cox Pond were the largest in all months, and mean length increased by an average of 0.30 mm/d between December 1999 and May 2000. The change in mean length of the dye-marked population initially sampled at the trap and recaptured in reach B and in Kunz Marsh was 0.26 mm/d between November 1999 and May 2000. Mean length of fish that reared in the upper watershed in West Fork Winchester Creek increased by an average of 0.16

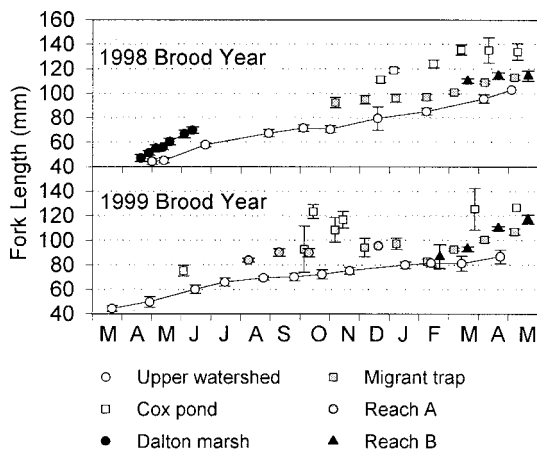


FIGURE 6.—Fork length (\pm SE) of juvenile coho salmon sampled at various sites in Winchester Creek, South Slough, Oregon.

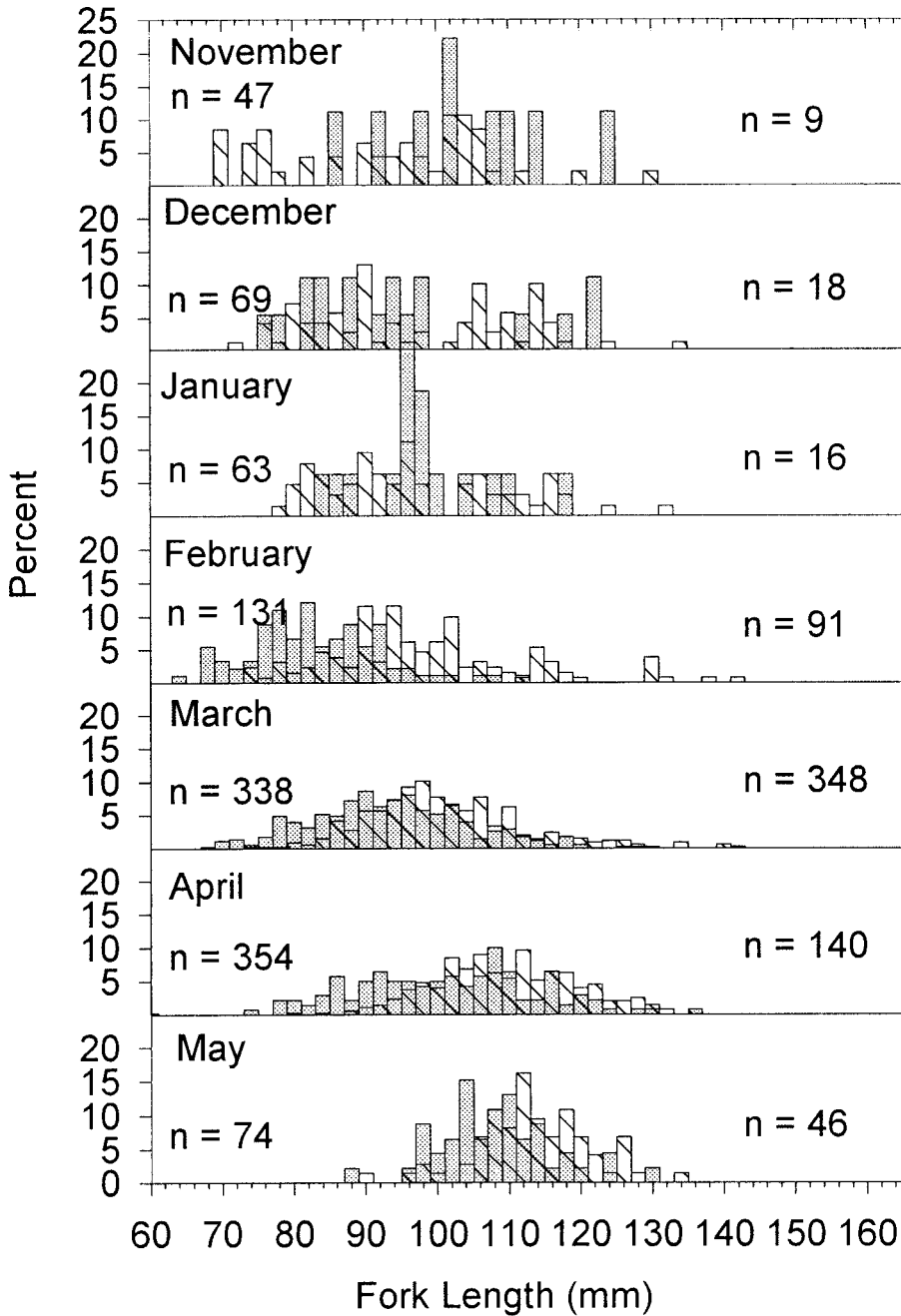


FIGURE 7.—Length frequency of 1998 (diagonally-marked bars; sample size on left) and 1999 (shaded bars; sample size on right) broods of juvenile coho salmon sampled at the rotary screw trap, Winchester Creek, South Slough, Oregon.

mm/d in winter 2000, and increased by 0.25 mm/d in spring.

Fish sampled at the trap during fall and winter displayed a nonnormal distribution in fork lengths (one-sample Kolmogorov–Smirnov [Lil-

iefors] test: $P < 0.05$ for November, $P < 0.01$ for December–February, for both brood years; Figure 7).

Although fish sampled in the upper watershed from both 1998 and 1999 brood years were small-

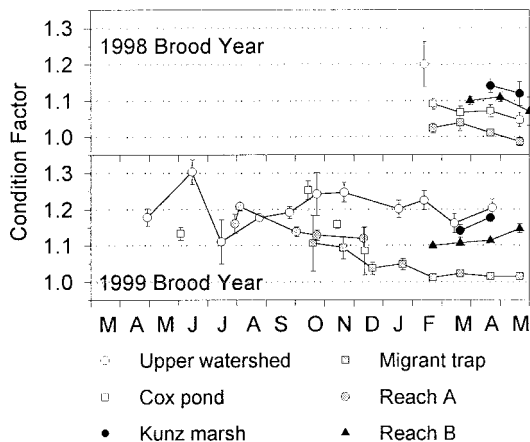


FIGURE 8.—Condition factor (\pm SE) of juvenile coho salmon sampled at various sites in Winchester Creek, South Slough, Oregon from February 2000 through May 2001.

est in length, they had highest CF during most months sampled (Figure 8). Fish sampled at the trap had the lowest CF. Mean CF of fish that moved downstream during fall was 11.6% lower than for fish in the upper watershed, whereas CF of spring migrants was 13.9% lower. Fish sampled in the main channel of reach B had intermediate CF values, reflecting the composition of this population as a mix of newly arrived migrants and fish that had lived in this habitat for some time.

Fish sampled while foraging in Kunz Marsh had the highest CF within the ecotone. Condition factor of fish caught in Kunz Marsh was significantly higher than for fish in the adjacent channel during the period of peak abundance (t -test: $P < 0.003$ for the 1998 brood year, $P < 0.001$ for the 1999 brood year; Figure 8). Mean CF of fish that foraged in Kunz Marsh decreased significantly after fish were held 24 h (1.085 ± 0.011 , a decrease of 7.8%; paired t -test: $P < 0.001$) and did not significantly differ from the mean CF of fish sampled in the tidal channel of reach B, the population from which fish in Kunz Marsh are derived (t -test: $P = 0.116$).

Discussion

Seasonal Movement and Residence Time in the Stream–Estuary Ecotone

This study provides information that links estuarine residence to seasonal movement of juvenile coho salmon and documents reach-specific residence times. These findings suggest that juvenile coho salmon that move to the estuary as presmolts

may form a significant portion of total production, and that the stream–estuary ecotone provides rearing habitat for extended periods of time.

A portion of each brood year moved to the stream–estuary ecotone of Winchester Creek during spring at age 0. Downstream movements of age-0 coho salmon have been documented in other systems in both northern and southern portions of the species' range (Mason 1975; Crone and Bond 1976; Hartman et al. 1982; Murphy et al. 1984, 1997; Solazzi et al. 2000). Tschaplinski (1988) and Murphy et al. (1997) attributed this movement to physical displacement by high streamflows resulting from either high spring runoff or freshet events during the period of fry emergence. Others (Mason 1975; Hartman et al. 1982) suggest that behavior may have a strong influence on downstream movement of age-0 coho salmon, and emigration is viewed as the consequence of over-seeding and the displacement of subordinate fish by aggressive behavior, as described by Chapman (1962). Aggressive behavior in coho salmon fry begins within the first week after emergence, and numbers displaced downstream have been found to be proportional to density of fry (Mason and Chapman 1965). We did not measure density of fry in Winchester Creek. Newly emerged fry moved at least 7 km from the spawning reach during periods when streamflows were not particularly high, thus it is not clear to what degree downstream movement was influenced by streamflow or seeding levels.

Age-0 fish of both broods were found in reach B until mid-June but then left this reach. As streamflows diminished during late spring, higher salinity and water temperature in reach B may have induced fish to leave. In 2000, we sampled upstream in reach A, where both salinity and water temperature were lower, and found juveniles in this reach all summer. This suggests that age-0 fish that use reach B through late spring likely ascend to reach A.

Recapture of age-0 fish within the ecotone indicated residence times of up to 159 d. Because we were unable to dye-mark very small fish as they first entered the ecotone, the measured residence times did not include time spent in the estuary for fish that moved downstream soon after emergence, causing an underestimation of minimum residence times. Age-0 fish that move to the ecotone during spring may live within this reach for up to 8 months (March to October), during which time they establish temporary territories. This is consistent with the lack of movement of

juvenile coho salmon that lived in the stream–estuary ecotone of Porcupine Creek, Alaska, during summer (Murphy et al. 1984), and with the summer residence of age-0 coho salmon in the tidal reach of Carnation Creek, British Columbia (Tschaplinski 1982, 1988).

The abundance of juveniles in reach A declined during fall, and by December fish were mostly gone from this habitat. Subsequent recovery of marked fish at the trap indicated the majority of those fish marked in reach A during summer (62.6%) ascended Winchester Creek to overwinter and did not re-enter the estuary until spring as age-1 migrants. This same behavior was observed in Alaska (Murphy et al. 1984), and analogous behavior was observed in Wilson River, Oregon, where fish that utilized the main stem for rearing during summer ascended into tributaries to overwinter (Skeesick 1970). The change in flow regime in reach A during fall may be a factor causing fish to leave this reach. The channel is narrow and deeply incised, and higher streamflows that are enhanced by ebb tidal flows may create water velocities that reduce fish residence.

Between one-quarter and one-third of each brood entered the ecotone during fall and winter. Downstream movement of age-0 coho salmon during fall and winter has also been recorded in other systems (Knight 1980; Hartman et al. 1982; Rodgers et al. 1987). These movements corresponded with freshet events, but the underlying cause was attributed to overseeding and displacement of subordinate fish. Rodgers et al. (1987) concluded that coho salmon moving downstream during fall in Knowles Creek, Oregon, were seeking overwinter habitat because fish did not show physiological signs of smoltification and had low CF values. In Winchester Creek, fish of the 1998 brood year displayed a peak in downstream movement during fall that corresponded with the first freshet event. The following year, streamflows were moderate during fall, with no significant freshet events, and there were no apparent peaks in downstream movement of fish. This suggests higher streamflows provide a cue for dispersal. Higher flows may also be necessary for downstream passage in reaches where fish may be entrained behind beaver dams, as noted by Rodgers et al. (1987).

Fish that moved downstream during fall and winter used the main channel, adjacent marshes, and tributary channels in reach B. This behavior is different from that described for fish residing in reach A during summer, most of which ascended above the tidal reach to overwinter and then mi-

grated downstream during spring. Whereas these subpopulations overwintered in different reaches, the common behavior was that both components of the population moved, either upstream or downstream, to seek overwinter habitat. This behavior highlights the variable benefits to juvenile production provided by the ecotone, with the uppermost tidal reach providing summer habitat and the lower reach providing habitat during winter.

Because most age-0 fish that reared in the ecotone during summer appeared to ascend Winchester Creek to overwinter and some age-1 fish made short-term movements upstream within the ecotone, some fish were subsequently resampled at the trap. This indicates that the estimates of spring migrants for each brood year are slightly inflated.

Juvenile coho salmon moved into Cox Pond principally during fall and winter, when temperatures in the pond decreased and when the beaver dam was less likely to be a barrier. The population that moved into this habitat during fall was composed primarily of migrants from above the ecotone but may have included some juveniles that reared in reach A during summer. During fall and winter, fish remained in Cox Pond longer than in any other habitat within the ecotone. The regular immigration of fish dye-marked at the trap during spring indicated age-1 migrants also used this habitat for short periods. This habitat was once a common feature of bottomlands in Oregon (Sedell and Luchessa 1982). Numerous studies have shown that juvenile coho salmon use beaver ponds during winter (Bustard and Narver 1975; Tschaplinski and Hartman 1983; Hartman and Brown 1987) and Nickleson et al. (1992) have concluded that with adequate spawning escapement, production of coho salmon in most Oregon coastal streams may be limited by availability of such habitat.

The residence time of spring age-1 migrants in the ecotone was consistent with the estimated residence time for coho salmon from other systems. Myers and Horton (1982) documented an approximately 2-week delay in peak abundance of wild coho salmon migrants between the upper and lower Yaquina, Oregon, estuary during spring. In the Taku River and estuary in Alaska, Murphy et al. (1997) found a 1-week delay between peak smolt abundance in the river (late May) and estuary (early June).

Residence Time in the Lower Estuary

Compared with the time spent in the upper estuary, the residence of spring age-1 migrants in the lower estuary was brief. Moser et al. (1991)

tracked juvenile coho salmon in Gray's Harbor, Washington, and although they did not determine when individuals left the estuary, their data indicate that juveniles were present for an average of 3 d in 1988 and 1 d in 1989, comparable to our findings.

Although fish displayed migration rates that would allow them to move through the lower estuary in less than 24 h, the combined behaviors of holding and occasionally ascending with flooding currents had the net effect of prolonging their residence in the lower estuary. This behavior may allow for final physiological adaptation to marine waters prior to ocean entrance.

Fork Length and Condition Factor

Fish sampled in habitats within the ecotone displayed the largest increases in mean length compared with fish sampled in the upper watershed. These changes may not accurately reflect growth, because we do not know whether larger or smaller fish may have differentially moved into or out of the sample reaches. The bimodal distribution of lengths observed in fish sampled at the trap during winter 2000–2001 suggests that these migrants originate from different subpopulations, but sample sizes collected from above the trap were inadequate to allow us to discern whether the population upstream was also bimodal or whether differences in fish lengths existed between reaches in the upper watershed.

The value of many habitats within the ecotone varies seasonally, but the value of specific habitats also varies on smaller temporal scales. Mixed semidiurnal tides limit access to salt marshes, but the high level of productivity in these habitats contributes to abundant and diverse invertebrate prey resources available to foraging juvenile fish (Simenstad et al. 2000). During spring of both study years, the surface of Kunz Marsh was accessible to coho salmon only 10.6–12.9% of each month. After a short period of foraging in the marsh during high tide, fish experienced an average increase in CF of 5.8% over those fish caught in the adjacent main channel. Because this increase was lost following evacuation of gut contents, the short-term change in CF can be considered a measure of foraging success (stomach fullness). A number of studies (reviewed by Craig and Crowder 2000) have found that fish caught during ebb tides have fuller stomachs than fish caught during flood tides, suggesting better forage opportunity in those habitats that fish select at high tide.

Management Implications

There is considerable regional variation in the structure and function of estuaries in the north-eastern Pacific as well as among subbasins within individual estuaries. In addition, there are profound regional differences in nearshore oceanographic conditions that juveniles must experience upon ocean entrance. It is reasonable to expect that coho salmon populations are locally adapted to this variation at all scales. Despite the variation in physical environment, similarities in juvenile life history of coho salmon can be found in both northern (Murphy et al. 1984; Tschaplinski 1988) and southern (this study) portions of the species' range. These similarities include downstream movement to the stream–estuary ecotone at age 0 during both spring and fall, use of this reach for months, and upstream movements during fall to overwinter in habitats above the ecotone.

In the Pacific Northwest, more than 75% of wetlands have been lost due to agricultural and industrial development, pollution, and other human activities (Simenstad et al. 1982; Boule and Bierly 1986). Much of this loss has occurred in the upper reaches that form the stream–estuary ecotone. Our research documents the disproportionate use of upper reaches of the estuary compared with lower reaches, and highlights the importance of the stream/estuary ecotone as rearing habitat. We suggest that protection and restoration of tidal freshwater marshes, reestablishment of lowland beaver ponds, restoration of upper estuarine salt marshes, and enhancement of corridors linking these habitats are all vital to increasing the productivity of estuaries for juvenile coho salmon.

Acknowledgments

Funding to the South Slough National Estuarine Research Reserve for this study was made possible through grants from the Oregon Watershed Enhancement Board and the U.S. Fish and Wildlife Service, Oregon Fish and Wildlife Office, Jobs In The Woods Program. This manuscript was improved through the comments of C. Cornu, J. Hodder, J. Miller, and J. Rodgers. Valuable comments were also provided by J. Thedinga and an anonymous reviewer.

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