

AN ABSTRACT OF THE THESIS OF

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Title: Growth, Residence, and Movement of Juvenile Chinook Salmon within Restored and Reference Estuarine Marsh Channels in Salmon River, Oregon.

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Tidal wetland channels provide rearing habitat for juvenile Chinook salmon as they emigrate from freshwater habitat and prepare to enter the ocean. Widespread diking and drainage of estuarine marshes for agricultural and urban development may have contributed to a decline in salmon abundance in the Pacific Northwest, prompting efforts to restore estuarine salmon habitat in the region. I investigated the growth and residence patterns of age-0 Chinook salmon in two blind tidal channels in the Salmon River estuary, Oregon. One channel drained a natural high salt marsh in “reference” condition, and the other channel was in an adjacent salt marsh, restored to tidal inundation in 1996 after being diked and controlled by a tide gate for thirty five years. Recapture of individually marked fish indicated salmon growth rates were similar in the two channels, though growth rates varied more seasonally in the restored site. Average minimum residence times of individual fish were approximately ten days in each channel, and individual salmon were observed up to 79 and 117 days after initial marking in the reference and restored channels, respectively. To characterize movement of age-0 salmon within tidal channels, I tested the feasibility of stationary Passive Integrated Transponder (PIT) detection within a small

(approximately 8m wide) tidal channel within the natural marsh system. I found that a stationary PIT detector was an effective tool for monitoring tagged fish movement in a brackish water channel network. Salmon movements in the channel were asymmetrical about high slack tide, with peak movement frequency occurring late during both flood and ebb tide periods. Most movements were in the direction of tidal currents, but 20% of individuals entered the channel against the ebbing tide. Individuals occupied the intertidal channel for a median 4.9 hours and as long as 8.9 hours per tidal cycle, and few were detected moving when water depth was <0.4m. Some individuals used the channel on multiple successive tidal cycles, and others entered intermittently over periods up to 109 days. This research used individual-based fish marking methods to quantify juvenile Chinook salmon behavior and performance within tidal marsh channels, assessing functional equivalence of natural and restored sites and demonstrating the value of such habitats for conservation and restoration of salmon populations.

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Growth, Residence, and Movement of Juvenile Chinook Salmon within Restored and
Reference Estuarine Marsh Channels in Salmon River, Oregon

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

David K. Hering, Author

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project. Earl Prentice taught me to build PIT tag antennas, a tool I now use even when better tools are available, and his help was central to the success of Chapter 3.

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CONTRIBUTION OF AUTHORS

Ian A. Fleming, Daniel L. Bottom and Kim K. Jones contributed to Chapter Two, “*Abundance, growth, and residence time of age-0 Chinook salmon in two marsh channels of the Salmon River estuary, Oregon.*”

Ian A. Fleming, Daniel L. Bottom, Kim K. Jones, and Earl F. Prentice contributed to Chapter Three “*Tidal movements and residency of subyearling Chinook salmon (Oncorhynchus tshawytscha) in an Oregon salt marsh channel.*”

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CHAPTER 1: GENERAL INTRODUCTION

Estuaries provide nursery areas for many commercially and ecologically important species of marine and diadromous fish including anadromous Pacific Salmon (*Oncorhynchus* spp.) (Healey 1982; Thorpe 1994a; Beck et al. 2001). Chinook salmon (*O. tshawytscha*) that emigrate from freshwater during their first year of life, a life history strategy known as “sea-type” or “ocean-type” (Gilbert 1912; Healey 1991), are particularly adapted for estuarine rearing and often remain in estuaries for several months before moving into fully marine habitat (Healey 1982, 1991). During this period of estuarine residence, juvenile Chinook salmon forage extensively in shallow channels that intersect salt marshes and other tidal wetlands (Shreffler et al. 1992; Miller and Simenstad 1997; Gray et al. 2002). Accordingly, ocean-type Chinook salmon may be particularly vulnerable to widespread degradation of shallow estuarine habitats that has occurred through agricultural and urban development of the Pacific coast of North America over the past 150 years (Magnusson and Hillborn 2003; Bottom et al. 2005a). Understanding how juvenile salmon use estuarine habitat and the costs and benefits derived from estuarine rearing is essential to effective conservation and restoration of coastal Chinook salmon populations throughout the Pacific Northwest and is the topic of this thesis.

Estuaries and Juvenile Salmon Life Histories

Pacific salmon have evolved diverse strategies for juvenile migration and estuarine rearing (reviewed by Groot and Margolis 1991, Thorpe 1994a, Quinn 2005).

Those species and populations that migrate to saltwater as smolts aged one year or more – i.e. stream type Chinook salmon, most coho salmon (*O. kisutch*) and sockeye salmon (*O. nerka*), as well as steelhead trout (*O. mykiss*) – typically spend little time in estuaries before moving to the ocean. Pink salmon (*O. gorbuscha*) also migrate very quickly through estuaries and enter the ocean at small sizes (28-35 mm fork length, Heard 1991). Ocean-type Chinook salmon, chum salmon (*O. keta*), and some coho salmon use estuaries for longer periods. Presumably, estuarine residence confers a fitness benefit to these species, allowing estuarine rearing life histories to be maintained by natural selection. Three benefits often hypothesized to accrue from estuarine rearing include productive foraging, physiological transition to salt water, and refuge from predation (Simenstad et al. 1982).

Ocean-type Chinook salmon typically spend more time in estuaries as juveniles than any other species or life-history type of Pacific salmon (Healey 1982, 1991). Chinook juveniles can be found in some Oregon estuaries six to nine months out of the year (Reimers 1973; Myers and Horton 1982; Healey 1991), and in the Columbia River estuary year-round (McCabe et al. 1986), with peak abundance in spring and summer. Individual sub-yearling Chinook are known to remain in estuaries for as long as four months before moving into the fully marine environment (Bottom et al. 2005b). The ocean-type life history is the dominant pattern exhibited by fall-run Chinook salmon from British Columbia south to California (Healey 1991).

Within populations of ocean-type Chinook salmon, variation in timing and duration of estuarine residence is considerable. Some Chinook salmon typically

disperse to estuaries as fry immediately after emerging from spawning gravel in late winter or spring at lengths of 35-40 mm. Additional fish may rear for a short time in freshwater and then migrate to estuarine habitats as 60-80 mm long fingerlings during late spring and early summer. A typically small fraction of populations (particularly in large rivers) remain in freshwater through the first summer, behaving like stream-type fish, and migrate to estuaries as large (80-110 mm) yearling smolts (Healey 1982). To characterize this diversity of migration timing, freshwater and estuarine residence, multiple authors have described Chinook salmon populations in terms of discrete life history “types.” Three types were identified in the Skagit River in Washington (Beamer et al. 2005). In Oregon, Reimers (1973) identified five types in the Sixes River, Schluchter and Lichatowich (1977) described seven types in the Rogue River, and Bottom et al. (2005b) used mark-recapture methods to identify three or four types in the Salmon River. The patterns of migration timing and habitat use that define such types likely represent particularly successful or abundant alternatives in a continuum of life history strategies maintained by selection in variable environments (Stearns 1976; Thorpe 1994b). A recent analysis of juvenile Chinook salmon from Salmon River used otolith microchemistry to characterize a broad range of freshwater and estuarine rearing behaviors within the population rather than a series of discrete “types” (Volk et al. in press). The availability or condition of alternative rearing habitats within a watershed, for example the presence of functional estuarine wetlands, likely influences expression of the diverse rearing and migration strategies within populations (Bottom et al. 2005a, b).

Simenstad (1983) described three principal types of channel habitats found in Pacific Northwest estuaries, including main-stem, subsidiary, and blind or tidal channels. Main-stem channels are the primary paths of water transport into and out of estuaries, including the thalwegs of primary river drainages. Subsidiary channels connect main-stem channels to minor upland water sources (e.g. small streams). Blind channels drain tidally or flood-introduced water from the surface of marshes and tidal flats. Both subsidiary and blind channels may intersect estuarine marshes and provide access to wetland habitat for migrating fish, but blind channels often lack subtidal areas, dewatering completely during ebb tides. As a result, fish fauna often must vacate blind channels completely and redistribute to low tide refuges twice a day.

Despite constraints on occupancy imposed by the tides, subyearling Chinook salmon forage extensively in blind, intertidal channels that intersect salt marshes and tidal freshwater wetlands on the margins of main estuarine channels (Congleton et al. 1981; Levy and Northcote 1982; Simenstad et al. 1982). Such habitats are rich sources of invertebrate prey, including aquatic insects (e.g. diptera, trichoptera) and epibenthic crustaceans (e.g. corophiid and gammarid amphipods, mysids), as well as terrestrial arthropods that blow or are washed off the marsh surface and become available to fish (Levy and Northcote 1981; Shreffler et al. 1990; Gray et al. 2002).

The hypothesis that estuarine habitats are productive foraging areas for juvenile salmon is supported by several studies of salmon growth rate in estuarine habitat. Reported growth rates in estuaries include $0.86 \text{ mm}\cdot\text{day}^{-1}$ and $0.53 \text{ mm}\cdot\text{day}^{-1}$ in the Sacramento-San Joaquin River delta (Kjelson et al. 1982), $1.32 \text{ mm}\cdot\text{day}^{-1}$ (4-5%

body weight day⁻¹) in the Nanaimo River estuary (Healey 1980a), and 0.62 mm·day⁻¹ (3% body weight day⁻¹) in the Nitinat River estuary (Fedorenko et al. 1979). Kjelson et al. (1982) found that Chinook fry rearing in the Sacramento-San Joaquin estuary grew an average of 0.2 mm·day⁻¹ faster than conspecifics rearing in the Sacramento River. Juvenile Chinook salmon in Woodward Island marshes of the Fraser River estuary were larger than those captured concurrently 100 kilometers upstream in the Fraser River (Levy and Northcote 1982), and juveniles rearing in the Skagit River estuary also were larger on average than those rearing in the river (Congleton et al. 1981). The rapid increase in growth rate upon estuary entry is evident from increased increment widths on salmon scales (e.g. Rich 1920; Reimers 1971) and otoliths (e.g. Neilson et al. 1985, Volk et al. in press). One exception to the generally high reported rates of growth in estuaries is the San Francisco Bay, a heavily degraded estuary, where sub-yearling Chinook did not grow while migrating 65 kilometers between being marked at the head of the bay and recaptured near the mouth (MacFarlane and Norton 2002). Chinook in that study were not marked until leaving marsh areas of the Sacramento-San Joaquin delta, however, and growth in delta habitat appeared comparable to other estuarine wetlands (Kjelson et al. 1982).

Prolonged exploitation of food-rich estuarine habitats may represent an adaptive “strategy” to increase growth and subsequent marine survival of juvenile salmon (McDowall 1988; Dodson 1997). Marine mortality of salmon may be highest soon after ocean entry (Ricker 1976; Nickelson 1986; Logerwell et al. 2003) and the first winter spent in the ocean is likely a “critical period” for salmon survival (Pearcy

1992). Mortality appears to be size-dependent, declining with increasing fish size. Parker (1971) demonstrated predation on pink salmon fry was inversely related to body size. Similar results were reported for chum salmon (Healey 1980b). A strong positive relationship also existed between smolt size and survival in British Columbia steelhead (Ward et al. 1989), and faster growing (thus larger) coho salmon were more likely to survive their first marine winter in the Strait of Georgia (Beamish et al. 2004). Based on scale-analysis, Reimers (1971) concluded that in the Sixes River, surviving adult Chinook salmon were larger at ocean entry than the average from their brood year. Summarizing 17 years of data on coho salmon in British Columbia, Holtby et al. (1990) determined that smolt size was not always correlated with marine survival, but in years of poor ocean productivity, large smolts survived better. The evidence for size-dependent marine mortality points strongly to the importance of growth in estuarine rearing habitats to prepare ocean-type salmon for success in the ocean. This idea was supported by a transplant experiment in which juvenile Chinook salmon released directly to the ocean survived poorly compared with those released at riverine or estuarine locations (Levings et al. 1989).

Though the role of estuaries as foraging habitats is strongly supported by literature on growth and diet of salmon, evidence for the two other functions often hypothesized for estuarine habitats – physiological transition to seawater and predator refuge – is not as well developed (Thorpe 1994a). The ontogenetic shift from riverine to marine habitat requires that salmon dramatically transform their physiology and switch from actively retaining ions in freshwater to actively excreting them in

saltwater in order to maintain internal osmotic balance (Hoar 1976). Iwata and Komatsu (1984) demonstrated that short term acclimation in brackish water improved osmoregulation by chum salmon fry when transferred to seawater, suggesting that temporary residence in estuaries eases the transition to balancing salts in the marine environment. Though this paper is often cited to support the role of estuaries as habitats of osmoregulatory transition, improved osmoregulation in chum fry occurred after only 12 hours exposure to brackish water, suggesting that benefits of estuarine acclimation can occur over a time frame much shorter than typical estuarine residence of ocean-type Chinook salmon fry.

The capacity of fry to transition quickly to saltwater may vary within Chinook salmon populations and may be a phenotypically plastic trait influenced by individual fish condition, e.g. size or growth rate (Beckman et al. 2003). Thus some individuals may require longer residence in estuarine habitat than others before moving to full seawater. In Salmon River, surviving adult returns include a small proportion of individuals that migrate directly to fully saline water as recently emerged fry, but most fry migrants reside and grow for weeks to months in brackish areas of the estuary, including tidal wetlands (Volk et al. in press). Although estuarine residence of weeks or months may not be strictly necessary for Chinook salmon fry to transition to saltwater, reduced physiological stress likely increases the value of estuarine habitats as foraging areas. Increased understanding of salmon behavior and performance within brackish water habitats may help resolve the relative importance of estuarine habitats for physiological transition.

In some estuaries, predation on juvenile salmonids may be substantial. Based on the experimental release of coho salmon smolts at different locations, Solazzi et al. (1991) suggested mortality was high in the Columbia River estuary, perhaps due to predation by northern pike minnow (*Ptychocheilus oregonensis*). More recently, large numbers of Passive Integrated Transponder tags used to mark salmonids have been recovered on Caspian tern (*Hydroprogne caspia*) and double-crested cormorant (*Phalacrocorax auritus*) colonies in the Columbia River estuary, indicating that avian predation may also be high (Collis et al. 2001; Ryan et al. 2003). The most extreme rates of avian predation documented in the Columbia estuary have been on large, hatchery-reared or stream-type salmonids, such as steelhead and coho salmon, but birds also preyed on sub-yearling Chinook salmon, resulting in at least two to four percent mortality in 1997 and 1998 (Collis et al. 2001). Birds that nest in the lower Columbia estuary forage over a broad area, however, and it is unclear whether sub-yearling Chinook salmon are vulnerable to avian predation within shallow marsh channel habitats. Examination of cutthroat trout diets near marsh habitats in the Salmon River estuary revealed that Chinook salmon were *not* a preferred trout prey, despite seasonal abundance of Chinook in the estuary and co-occurrence of the two species at sampling sites (Jones et al. 2008).

Use of shallow tidal marsh channels may allow sub-yearling salmon to elude large predators (e.g. birds, fish, mammals) until they grow to sufficient size to move to deeper estuarine or marine habitats. Within tidal channels in a Virginia salt marsh, experimentally tethered prey species were more likely to be taken by predators in

deeper erosional areas of the channel than at shallow depositional sites (McIvor and Odum 1988). Turbidity, often higher in shallow estuarine habitats than freshwater or marine areas, may be a mechanism that allows juvenile fish to avoid visual predators. Turbidity was the most important covariate of juvenile fish density in estuarine and nearshore marine rearing habitats in Australia and South Africa (Blaber and Blaber 1980; Cyrus and Blaber 1987). Gregory and Levings (1998) provided evidence from the Fraser River system that turbidity may reduce predation on age-0 salmon by piscivorous fish. Testing the hypothesis that estuaries provide predator refuge from salmon requires further study of fish use of specific types of estuarine habitat, particularly shallow, structurally complex habitats such as sea grass beds (Hosack et al. 2006) and tidal marsh channels.

Degradation, Restoration, and Assessment of Estuarine Salmon Habitat

Because human settlement is often concentrated near the mouths of rivers and because river and estuary floodplains offer some of the only flat, agricultural land in coastal mountain ranges, habitats that support salmon in estuaries are among the most altered by anthropogenic disturbance. In Pacific Northwest estuaries, development of agricultural and port facilities resulted in the large-scale elimination of tidal wetland areas beginning in the late nineteenth century (Boulé and Bierly 1987). Among seventeen Oregon coastal estuaries reviewed by Good (2000), 68% of historic wetland area had been eliminated by 1970 including over 90% in some estuaries (Figure 1.1).

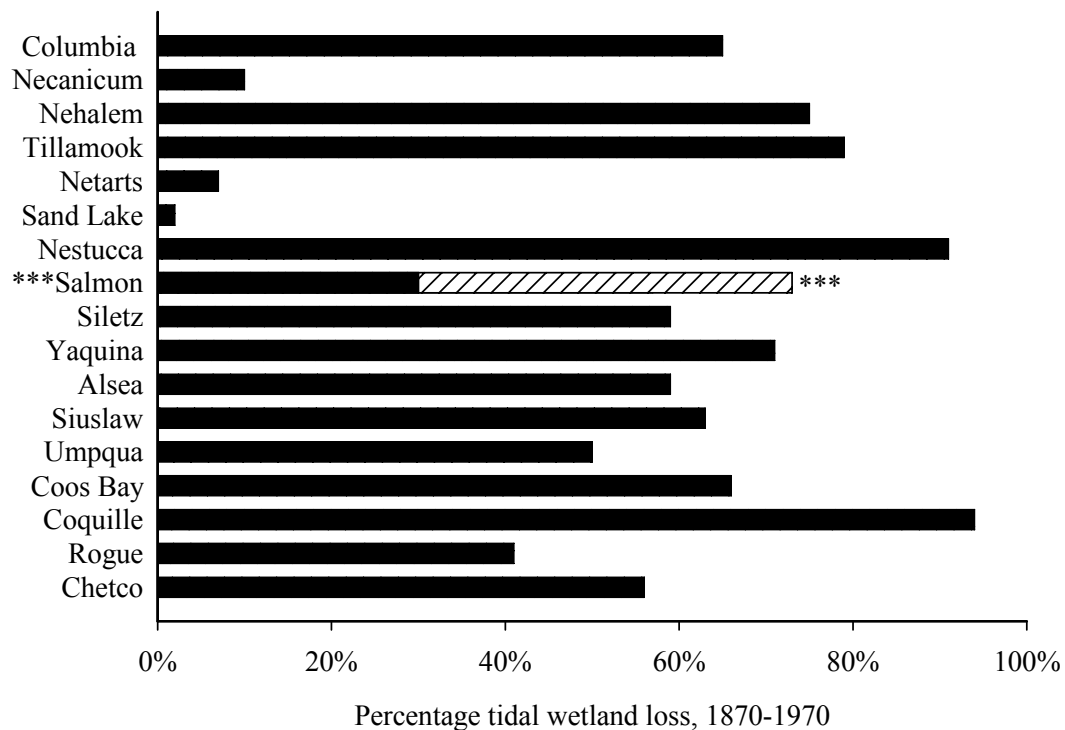


Figure 1.1. Percentage of tidal wetland area lost to diking and filling in seventeen Oregon estuaries, 1870-1970. Historic wetland loss in Salmon River estuary is indicated by hashed bar. Solid bar represents net loss after marsh restoration projects in 1978, 1987, and 1996 (data adapted from Frenkel and Morlan 1991 and Good 2000)

Similar tidal wetland losses have occurred in the Columbia River estuary (60% to 70%, Thomas 1983) and Puget Sound estuaries (71%, Thom and Hallum 1990). Historical alteration of estuarine marshes in Oregon typically has been for agricultural purposes and has involved construction of earthen dikes to prevent tidal flooding of marsh land converted to pasture. When dikes block tidal or subsidiary stream channels they often have been equipped with tidegates to allow drainage of surface water from diked areas during ebb tides but prevent intrusion of estuarine water during flood tides. Tidegates severely limit and often completely prevent juvenile salmon from accessing diked wetland channels (Giannico and Souder 2004). Even when only part of tidal marsh systems are converted by development, altered tidal hydrology due to dike construction may indirectly reduce quality and quantity of tidal channel habitat outside (i.e. seaward) of the diked areas (Hood 2004). Tidal exclusion also can result in long-lasting reduction in surface elevation (i.e. subsidence) of drained wetland areas due to changes in soil chemistry, lack of tidal sediment delivery, and soil compaction due to grazing or other land uses (Anisfeld et al. 1999; Roman et al. 1984).

Degradation of estuarine wetland areas likely has contributed to the well-documented decline in salmon abundance in the Pacific Northwest during the past century (Nehlsen et al. 1991), and may have reduced life history diversity within salmon populations that remain (Bottom et al. 2005a and b). A recent analysis of hatchery Chinook salmon returns indicated that variation in smolt to adult survival among river basins was positively correlated with the proportion of estuarine habitat remaining in natural condition (Magnusson and Hilborn 2003). In the Columbia River

estuary, ocean-type Chinook today are present in a much narrower range of times and sizes than they were when sampled in the early twentieth century, probably due in part to simplification of estuarine habitat (Burke 2004; Bottom et al. 2005a).

With the aim of restoring natural function for salmon and other species, natural resource managers have restored tidal inundation to several formerly diked salt marshes in the Pacific Northwest (Shreffler et al. 1990, 1992; Miller and Simenstad 1997; Tanner et al. 2002). Tidal wetland restoration projects often involve simply breaching dikes and/or removing tide gates to initiate passive restoration of natural function (Frenkel and Morlan 1991; Williams and Orr 2002), but restoration actions also may include actively reconstructing tidal channels in former wetland areas (e.g. Haltiner et al. 1997) or adding fill material to increase the elevation of wetland surfaces that have subsided (e.g. Cornu and Sadro 2002).

Approaches to evaluate the efficacy of marsh restoration range from simply documenting the presence or absence of fish to comprehensive studies of geomorphology, water quality, and plant and animal communities (Simenstad and Thom 1996). Due to the punctuated and transient nature of salmon residency in marsh habitats, methods used to assess habitat use by estuarine resident fish (e.g. Kneib 1997; Rozas and Minello 1997) may not be directly applicable to salmon. Moreover, simple measures of presence, absence, or abundance of salmon in restored sites may not adequately characterize recovery of restored sites. Because restoration projects are accomplished opportunistically by land managers, they rarely present the opportunity for controlled, replicated comparison of restored and reference sites.

Marsh restoration studies also seldom address population level responses in salmon production or diversity (but see Bottom et al. 2005b).

Simenstad and Cordell (2000) grouped criteria for assessing restored estuarine wetland habitat into three categories describing the (1) capacity, (2) opportunity, and (3) realized function of habitats to support rearing salmonids. Examples of capacity metrics include physical parameters (e.g. temperature and salinity) and availability and quantity of salmon prey species. Opportunity for salmon rearing can be measured by attributes that affect fish access to wetland channels such as channel connectivity and marsh elevation. Realized function metrics attempt to integrate all aspects of habitat quality by directly measuring physiological, behavioral, or fitness responses of salmon to rearing in specific habitats (e.g. growth, residence time, survival). Assessment methods based on functional performance attributes such as salmon growth and residence time in essence allow the fish themselves to diagnose ecological recovery of restored sites. The three-pronged structure articulated by Simenstad and Cordell (2000) provides the conceptual framework for a long-term research project to assess recovery of restored wetlands in the Salmon River estuary, Oregon, including the research presented in this thesis.

The Salmon River Estuary

The Salmon River estuary, near the town of Otis on the central Oregon coast, is an exceptional example of estuarine marsh restoration on a landscape scale. In the early 1960's, dike construction made most of the tidal wetlands in the estuary

inaccessible to migratory fish. The United States Forest Service (USFS) took management responsibility for most of Salmon River's diked wetlands in 1973, when the estuary became part of the Cascade Head Scenic Research Area. By breaching or removing dikes in 1978, 1987, and 1996, the USFS restored tidal flooding to 145 hectares of historic marsh. An additional area of high salt marsh was never diked allowing comparison of restored sites to unmodified, reference conditions (Figure 1.2). Such a wholesale restoration of a small estuary created a unique opportunity to study the effects of marsh restoration on salmon ecology, and a collaborative project involving Oregon Department of Fish and Wildlife, NOAA National Marine Fisheries Service, University of Washington, and Oregon State University began studying the response of salmonids to marsh restoration in 1997. Both restored and reference marsh channels, including a channel restored one year prior to the start of the study, were found to support subyearling Chinook, coho, and some chum salmon, as well as non-salmonid fishes including Pacific staghorn sculpin (*Leptocottus armatus*), shiner perch (*Cymatogaster aggregata*), starry flounder (*Platichthys stellatus*), and English sole (*Pleuronectes vetulus*) (Cornwell et al. 2001). Gray et al. (2002) assessed capacity and opportunity for salmon rearing in restored and reference marshes through analysis of salmon abundance, prey availability, and diet composition. Bottom et al. (2005b) provided information about the growth and residence of Chinook salmon in the estuary as a whole and reported that the variety of salmon rearing behaviors expressed in the estuary was greater in 2000-2002 than that reported in a 1975-1977 study prior to dike removal. Most recently, Volk et al. (in press) used otolith analysis

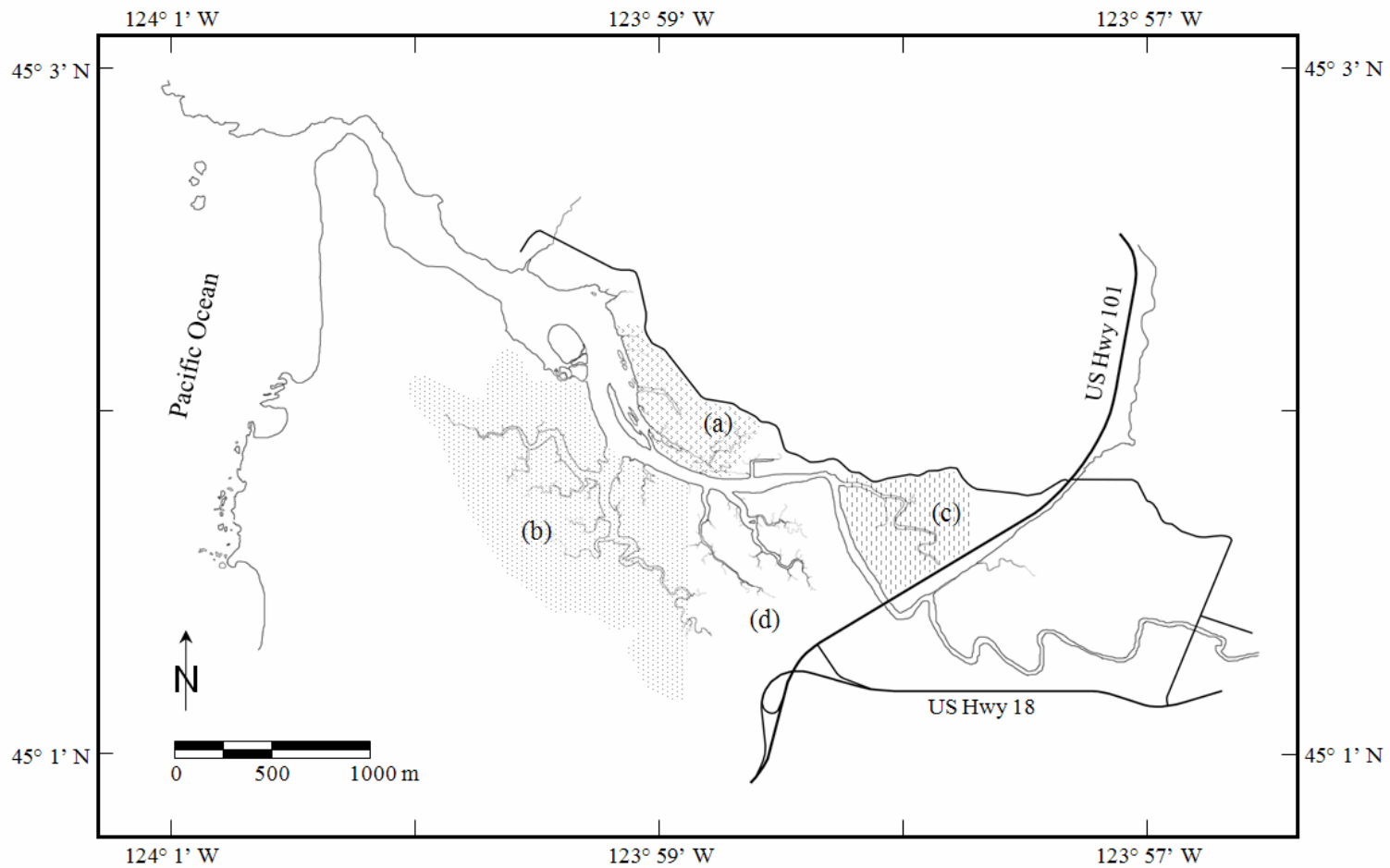


Figure 1.2. Map of Salmon River estuary depicting tidal wetland areas restored by dike removal in (a) 1978, (b) 1987, and (c) 1996. Location of an unmodified “reference” marsh area (d) is also indicated.

to infer residence patterns of juvenile Chinook salmon captured in Salmon River marshes and at the mouth of the estuary, providing further evidence for diversity of estuarine rearing behavior and estimating salmon growth rates in estuarine habitats. The restored estuary also supports diverse migratory behaviors of anadromous coastal cutthroat trout (*O. clarki clarki*; Krentz 2007; Jones et al. 2008) and juvenile coho salmon (Jones et al. 2009). These results suggest that estuarine restoration supports life history diversity and hence may have contributed to resilience of Salmon River salmonid populations (Waples et al. 2009; Healey 2009).

Though studies in Salmon River and elsewhere have supported the idea that estuarine wetland restoration benefits salmon, a more thorough understanding of the interactions between salmon and estuarine rearing habitats and the *mechanisms* through which estuarine habitats support salmon production and life history variation is necessary to guide ongoing restoration and conservation efforts. Our understanding of salmon use of specific tidal wetland channels is based on a small number of studies in only a few locations within the range of ocean-type Chinook salmon, notably marshes in the Fraser River (Levy and Northcote 1982), the Skagit River (Congleton et al. 1981), and restored wetlands in Puget Sound (Shreffler et al. 1990, 1992) and coastal Washington (Miller and Simenstad 1997). Prior to the recent work in the Salmon River, very few studies had examined salmon use of small Oregon estuaries since the work of Reimers (1971, 1973) in the Sixes River, an estuary that does not contain tidal marsh habitats, during the late 1960s. Moreover, with the exception of research by Miller and Simenstad (1997) in Gray's River Washington, no study has

specifically examined salmon behavior and growth in tidal wetland channels within small drowned-river estuaries common on the coasts of Washington, Oregon, and California.

Re-establishing tidal connections of diked marshes to support estuarine-rearing salmon implies knowledge of salmon behavioral interactions with wetland features at local and landscape scales as well as the benefits that individual salmon may derive by occupying wetland habitats. Yet, many aspects of salmon ecology and behavior in estuarine wetlands remain poorly understood – e.g. How much time do salmon spend in wetland channels? How do they move into and out of wetlands with the tides? What specific growth benefits are derived from wetland rearing? Increased understanding of these basic parameters is necessary to evaluate results of current estuarine wetland restoration projects and predict results of future habitat restoration efforts proposed to benefit salmon recovery.

Accordingly, with this thesis I seek to build on previous results of salmon research in the Salmon River estuary and increase understanding of estuarine rearing behaviors by characterizing the distribution, abundance, growth, and movement patterns of sub-yearling ocean-type Chinook salmon in marsh habitats of the Salmon River estuary. Chapter Two reports a mark-recapture experiment to quantify the growth and residence of Chinook salmon in two tidal wetland channels – one largely unmodified natural channel, and one channel recently restored following decades of tidal exclusion. Chapter Three describes in more detail the tidal movements of individual salmon into and out of a low-order natural channel. Both chapters rely on

application of a relatively new technology, Passive Integrated Transponder (PIT) tags that are small enough to uniquely mark individual salmon of the size found in tidal wetlands (Prentice et al.1990). By uniquely identifying individuals, PIT tags allow more precise measurement of individual growth and residence patterns and may provide greater insight into the *variability* of salmon responses to estuarine habitats than approaches based on average values for marked cohorts of fish. Behavioral and life history variation is of increasing interest to fisheries and natural resource managers because of its apparent link to resilience of salmon populations in dynamic environments (Waples et al. 2009; Healey 2009). I hope that the information presented herein will promote continued restoration and conservation of estuarine wetlands and the anadromous salmonids that inhabit estuaries of the Pacific Northwest.

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CHAPTER 2:

Abundance, growth, and residence time of age-0 Chinook salmon (*Oncorhynchus tshawytscha*) in two marsh channels of the Salmon River estuary, Oregon.

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ABSTRACT

We used beach seine sampling and mark-recapture techniques to monitor abundance, distribution, growth, and residence time of sub-yearling Chinook salmon (*Oncorhynchus tshawytscha*) in two intertidal marsh channels in the Salmon River estuary, Oregon. One channel drained a natural, unmodified salt marsh, and the other was a formerly diked and tide-gated channel, recently reconnected to the estuary after decades of tidal exclusion. Chinook salmon occupied both marsh channels during high tides throughout the spring and summer with peak abundance May through July. At high tide within both channels, salmon density was significantly negatively related to distance from subtidal habitat in the main-stem estuary channel. Mean growth rate of marked and recaptured individuals was similar among years in the natural marsh. During 2004, when salmon were tagged in both channels, mean growth rate was similar between channels and increased from 0.84% body weight per day in May to 2.2% per day in early July. Recaptured Chinook salmon demonstrated high fidelity to the marsh channels in which they were initially tagged. Median time-at-large of recaptured individuals was 10 days in each channel in 2004, and individuals were observed up to 79 and 117 days after initial marking in the natural and restored channels, respectively. These observations demonstrate that individual ocean-type Chinook may use tidal marsh channel habitats for prolonged periods and that such habitats may contribute significantly to salmon growth prior to ocean entry. Although the study did not include replicated restored and reference sites, results also suggest

that degraded estuarine marshes can be restored to provide salmon rearing habitat that functions similarly to natural marsh habitat.

INTRODUCTION

Estuarine wetlands provide rearing areas for many populations of Chinook salmon (*Oncorhynchus tshawytscha*), particularly those that emigrate from freshwater as sub-yearling fry or fingerlings (Healey 1982; Thorpe 1994). This life history, known as “ocean-type,” predominates in Chinook salmon populations south of 56° N latitude (Healey 1991; Quinn, 2005). Upon entering estuaries, small Chinook salmon benefit from the shallow brackish water habitat and rich terrestrial and aquatic prey resources of tidally influenced channels that intersect salt marshes and other estuarine wetlands (Healey 1982; Simenstad 1982; Thorpe 1994), and often occur in such habitats during the spring and summer prior to migrating to fully marine habitat (Congleton et al. 1981; Levy and Northcote 1982). Transplant experiments (Levings et al. 1989) and observational studies (Reimers 1971) have demonstrated that rearing in estuarine habitats may increase subsequent marine survival of sub-yearling Chinook salmon.

Shallow estuarine habitats have been modified extensively in the Pacific Northwest by agricultural and urban development (Boulé and Bierly 1987). A review of tidal wetland loss in seventeen Oregon estuaries found 68 percent of historic tidal wetland area and as much as 94 percent of wetland area per estuary was diked or filled between 1870 and 1970 (Good 2000). Loss of historic tidal wetland area has been similar in Puget Sound (71 percent, Thom and Hallum 1990). Reduction in quantity and quality of estuarine habitat available to salmon may contribute to decreased survival (Magnusson and Hilborn 2003) and reduced life-history diversity of Chinook

salmon populations (Bottom et al. 2005a and 2005b). Thus, understanding the contribution of estuarine wetlands to salmon productivity and survival is important for guiding habitat preservation and restoration efforts aimed at conservation and recovery of depressed salmon stocks. Habitat-specific growth and duration of residence by juvenile salmon are key metrics for evaluating functional condition of natural and restored estuarine salmon habitats (Simenstad and Cordell 2000).

Estuarine growth results in increased size at ocean entry and likely favors early marine survival of salmon (Parker 1971; Healey 1980b; Pearcy 1992). Beamish et al. (2004) demonstrated that faster growing (thus larger) coho salmon (*O. kisutch*) were more likely to survive a critical period of mortality during the first marine winter. In Oregon's Sixes River, Chinook salmon with prolonged estuarine residence survived better than those that moved through the estuary more quickly (Reimers 1971). Healey (1991) hypothesized that estuarine growth may be more important along the exposed coastline of California, Oregon, and Washington than in British Columbia, where sheltered nearshore marine habitat is more common and juvenile salmon tend to emigrate from estuaries at smaller average sizes.

Most studies of estuarine growth have measured the change in average size of salmon caught in estuarine habitats during spring and summer, resulting in growth rate estimates for Chinook salmon that range from $0.07 \text{ mm}\cdot\text{day}^{-1}$ to $0.9 \text{ mm}\cdot\text{day}^{-1}$. Reported growth rates of marked and recaptured Chinook salmon are often higher than those from average catch data and range up to $1.32 \text{ mm}\cdot\text{day}^{-1}$ ($\leq 5\% \text{ biomass}\cdot\text{day}^{-1}$; reviewed by Healey 1991). Rates of growth may vary seasonally within an estuary

due to changes in salmon density, prey availability, or water temperature (Reimers 1973, Healey 1982, Neilsen et al. 1985). Few studies have documented salmon growth linked to specific estuarine habitats such as tidal wetlands, and no such habitat-specific growth rates are reported for Chinook salmon in estuarine marshes south of the Salish Sea (but see Miller and Simentad 1997 for coho salmon and Volk et al. in press).

Similarly, investigations of the duration of estuarine residence by salmon often have focused on the length of time fish take to migrate through entire estuaries between first entering tidewater and entering the ocean. Examples for Chinook salmon include an average of 25 days and up to 60 days in the Nanaimo River estuary (Healey 1980, 1982), a maximum of 64 days in the Sacramento-San Joaquin estuary (Kjelson 1982), and median 35 - 42 days and up to 17 weeks in the Salmon River (Bottom et al. 2005b, Volk et al. in press). Relatively fewer studies have reported the duration over which individual Chinook salmon use specific wetland channels within estuaries. Marked Chinook salmon remained an average three to six days in a marsh channel in the Skagit River delta (Congleton et al. 1981) and up to 30 days in Fraser River marsh channels (Levy and Northcote 1982). We are unaware of documented tidal channel residence times in the southern half of the species' range.

In 1997 we began a study of salmon ecology in the Salmon River estuary in Oregon with the principal goal of evaluating salmonid use of several formerly diked tidal channels, restored to tidal inundation by the US Forest Service (USFS) between 1978 and 1996. Previously reported results demonstrated that Chinook salmon

occupied both natural and restored habitats (Cornwell et al. 2001), both natural and restored habitats had the capacity to support salmon growth (Gray et al. 2002), and the period of estuarine use by the Chinook salmon population was greater following marsh channel restoration than it was in the 1970s, prior to dike removal (Bottom et al. 2005b). Volk et al. (in press) used otolith structure and chemistry to reconstruct rearing patterns in the estuary as a whole. In 2003, we initiated studies to determine in finer detail the patterns of Chinook salmon residency within two intertidal marsh channels of the Salmon River and the benefits salmon derive specifically from marsh habitats. Our objectives were to quantify: (1) seasonal patterns of salmon abundance in marsh channels, (2) spatial distribution of salmon within channel networks during high tides, (3) growth rate of individual salmon rearing in marsh habitat, and (4) duration of marsh channel use by individual salmon (i.e. residence time). In addition, we sought to evaluate functional equivalence (Simenstad and Cordell 2000) of natural, “reference” marsh channel habitat and a formerly diked and tide-gated wetland channel, seven to nine years following dike removal, by testing the hypothesis that Chinook salmon grew similarly and remained for similar lengths of time in reference and restored sites.

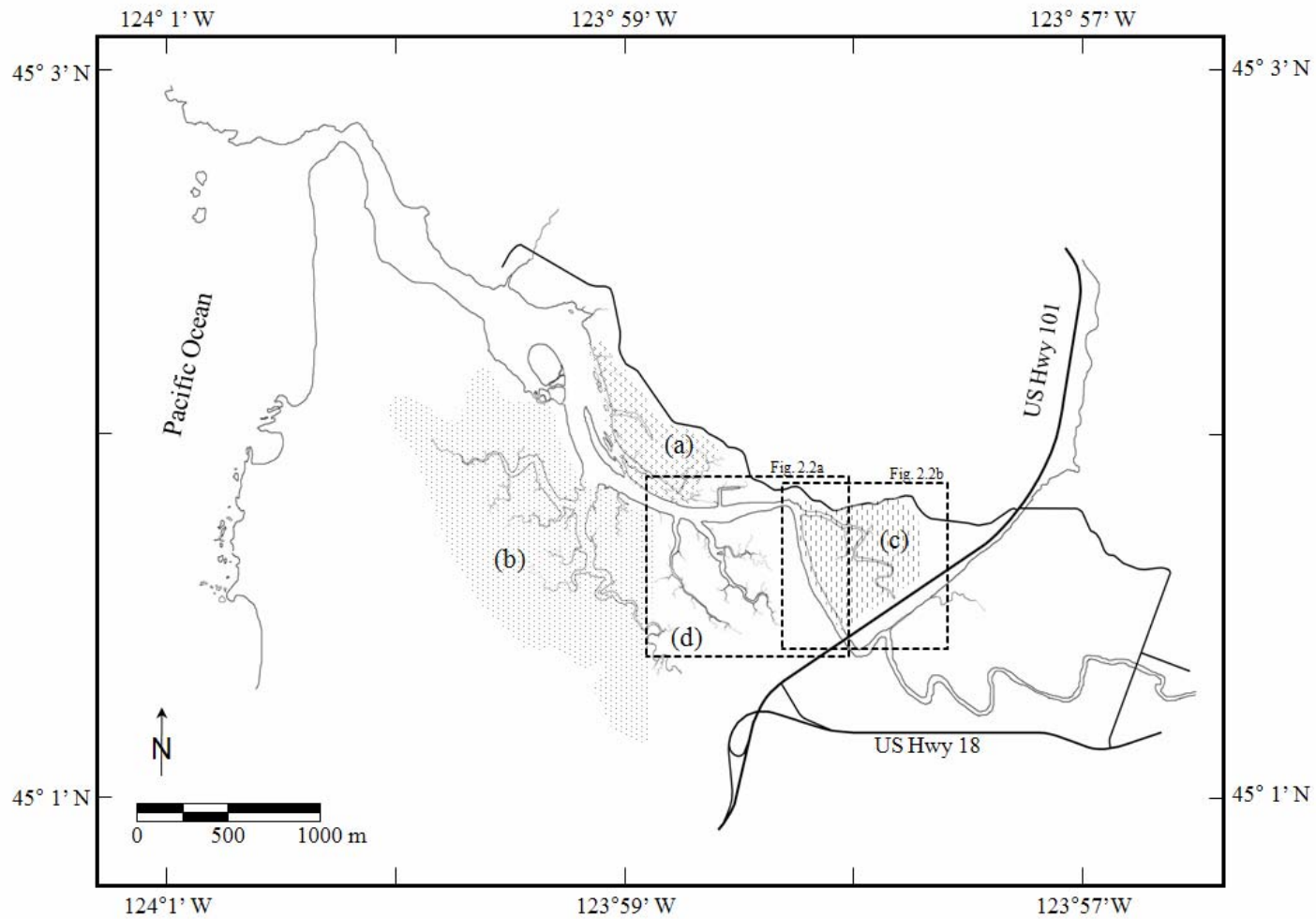


Figure 2.1. Map of Salmon River estuary indicating marsh areas restored by dike removal in (a) 1978), (b) 1987, and (c) 1996. The “reference marsh” area (d) was never diked. Dotted lines indicate areas of detail maps in figure 2.2.

METHODS

Study Area

The Salmon River drains a watershed of 194 km² and terminates in an 800 hectare estuary on the central Oregon coast (45° 01' N, 123° 58' W) (Figure 2.1). River discharge varies annually from approximately 1000 L·s⁻¹ in late summer to peak winter flows of 25,000 to 150,000 L·s⁻¹. Tidal elevation in the estuary ranges over approximately 2.3 meters.

The Salmon River salmonid community includes fall Chinook salmon, coho salmon, and a small run of chum salmon (*O. keta*), as well as steelhead (*O. mykiss*) and coastal cutthroat trout (*O. clarki clarki*). During the present study, an Oregon Department of Fish and Wildlife (ODFW) salmon hatchery at river kilometer eight released approximately 200,000 Chinook salmon and a similar number of coho salmon annually, many of which returned to spawn naturally in the watershed. Hatchery-reared Chinook salmon juveniles are generally much larger than wild Chinook salmon in the Salmon River and are identifiable by a clipped adipose fin. Although we caught a small number of hatchery-reared Chinook salmon in marsh channels during the weeks following August hatchery releases, they were excluded from our analyses. Naturally produced Chinook are the dominant salmonids in the estuary, typically occupying marsh channel habitats from March through October with peak abundance in late spring or early summer. Most Chinook in the basin exhibit an ocean-type life history and arrive in the estuary as subyearlings (age-0+).

Dikes and tide gates constructed during the early 1960's blocked tidal flow to roughly 73 percent of the 337 hectares of salt marsh present historically in the estuary (Frenkel and Morlan 1991). Diked areas were converted to pasture for livestock grazing. Since assuming management of the estuary in the 1970's, USFS has restored tidal inundation to approximately 145 hectares of the historic tidal wetland area by breaching or removing dikes on three separate marsh areas in 1978, 1987, and 1996. Our two study channels were in the most recently restored marsh – known as the 1996 marsh after the year of dike removal – and in a natural (i.e. reference) marsh that was never diked. The 1996 channel and the reference channel enter the main-stem Salmon River at rkm 3.8 and rkm 3.2, respectively (Figure 2.1).

Breaching of a dike and removal of a tide gate at the 1996 marsh restored tidal inundation to approximately 60 hectares of historic wetland and reconnected an approximately 14,057 m² tidal channel. In the seven to nine years between dike removal and the present study, the character of the marsh changed dramatically as nonnative vegetation including reed canary grass (*Phalaris arundinacea*) and blackberry (*Rubus* spp.) died and began to be replaced by a native salt marsh community. By 2004, large areas of the 1996 marsh were dominated by Lyngbye sedge (*Carex lyngbyei*). Other typical marsh plants such as Pacific silverweed (*Potentilla pacifica*), tufted hairgrass (*Deschampsia caespitosa*), salt grass (*Distichilis spicata*), and bent grass (*Agrostis* spp.) were also present (Gray 2005).

The 1996 channel is a blind tidal channel (Simenstad 1983) that follows the former path of Salmon Creek, a tributary of Salmon River that was blocked and

diverted following the construction of US Hwy 101 in the early 1960s. Today Salmon Creek enters the estuary from a small ditch constructed upstream of the highway road fill, such that any juveniles produced in the creek can only access the 1996 marsh from the main-stem estuary. Presently, the marsh channel has no overland connection to upland sources of freshwater, although it may receive some hyporheic flow from the Salmon Creek watershed. The 1996 channel contains some pools that often retain water during low tide.

The reference marsh system comprises approximately 80 hectares of mature high salt marsh (Jefferson 1974). Although the marsh was never diked, it was used occasionally for light grazing and hay harvest prior to 1974. No agricultural activity has occurred in the marsh since that time, however, and the marsh provides one of the best examples of natural, reference salt marsh conditions available on the Oregon coast (Gray et al. 2002). The vegetation is typical of an undisturbed high salt marsh in Oregon and includes tufted hairgrass, Pacific silverweed, salt grass, and Baltic rush (*Juncus balticus*) (Gray 2005). Areas of low marsh dominated by Lyngbye sedge exist along tidal channels. A dendritic network of blind tidal channels drains the reference marsh. High tide surface area of the reference channel system is approximately 21,207 m². During typical summer conditions, the reference channel system de-waters completely at tidal elevations less than approximately 30cm above mean lower low water.

Typical surface water salinity at high tide is approximately 3 PSU in May in both the reference and 1996 channels, and increases to 25-30 PSU by July and August

as river discharge decreases (Cornwell et al. 2001). Because the reference marsh joins the main stem 600m nearer to the ocean, salinity in the reference channel is often 2-3 PSU greater than the 1996 channel during the period of peak salmon use in late spring.

Gray et al. (2002) and Gray (2005) identified characteristic differences between the 1996 and reference marshes in salmon prey communities and prey consumed by salmon during 1998 and 1999. Chinook diets in the 1996 site were dominated by insects (trichoptera and diptera), whereas diets in the reference marsh included relatively more crustaceans and fish larvae. The dominance of insects consumed in the 1996 marsh reflected a high proportion of dipterans in the prey community of the 1996 marsh relative to the other marshes in the estuary, a pattern that Gray et al. (2002) attributed to marsh recovery age. Due to episodic delivery of adult insects from the marsh surface, prey availability also may have been more variable in the 1996 marsh than in the reference marsh where fully aquatic prey formed a higher proportion of the diet (Gray 2005). It is likely that differences in salmon prey communities between the two marsh systems were influenced not only by restoration history but by the relative locations of the two systems on the estuarine landscape and corresponding differences in water quality and chemistry. Differences in Chinook salmon diet between the two marsh channels persisted through 2004 (Bieber 2005).

Beach Seine Sampling

This analysis draws on beach seine samples collected at high tide within the reference and 1996 marsh channels during spring and summer 2003-2005. Sampling frequency varied among years and between channels (Table 2.1). Sampling frequency was highest during 2004, when both channels were sampled approximately equally, allowing direct comparison of the two channels. Although such comparison was not possible during 2003 and 2005, we include results from those years when relevant to describe spatial and temporal patterns of salmon distribution and growth of salmon in each marsh channel during each of the three years. To evaluate longitudinal distribution of salmon within the channels, we selected nine sites within the reference channel and 10 sites within the 1996 channel. Sites extended approximately 920m up the 1996 channel and 580m up the reference channel from each channel's confluence with the main-stem Salmon River (Figure 2.2). Site selection was not randomized. Rather, we attempted to locate sites evenly through the reach of each channel that was accessible by boat during high tide.

At least one site within each marsh was sampled approximately monthly between March and October during 2003-2004. Sites within the tidal channels were visited between two hours before and two hours after the daytime high slack tide, and swept with a 38m x 2.7m beach seine (1.9cm stretch mesh wings, reduced to 0.6cm stretch mesh in center panel). During 2003, the full suite of nine reference channel sites was sampled on 16 occasions between June 10 and July 3, then approximately weekly through August 7, 2003. During 2004, as many sites as possible within both

Table 2.1. Beach seine samples collected, 2003-2005, including mean change in fork length and weight of sampled Chinook salmon.

Year	Marsh	Sample Period	Sampling Occasions	Mean Growth Rate, mm·day ⁻¹ (S.E.)
2003	Reference	Feb 6 – Nov 13	32	0.32 (0.042)
	1996	Feb 6 – Sep 22	12	0.55 (0.098)
2004	Reference	May 11 – Oct 18	41	0.37 (0.007)
	1996	Mar 1 – Oct 18	44	0.34 (0.011)
2005	Reference	Mar 9 – Aug 1	8	0.46 (0.042)
	1996	Mar 9 – Jun 1	4	0.43 (0.045)

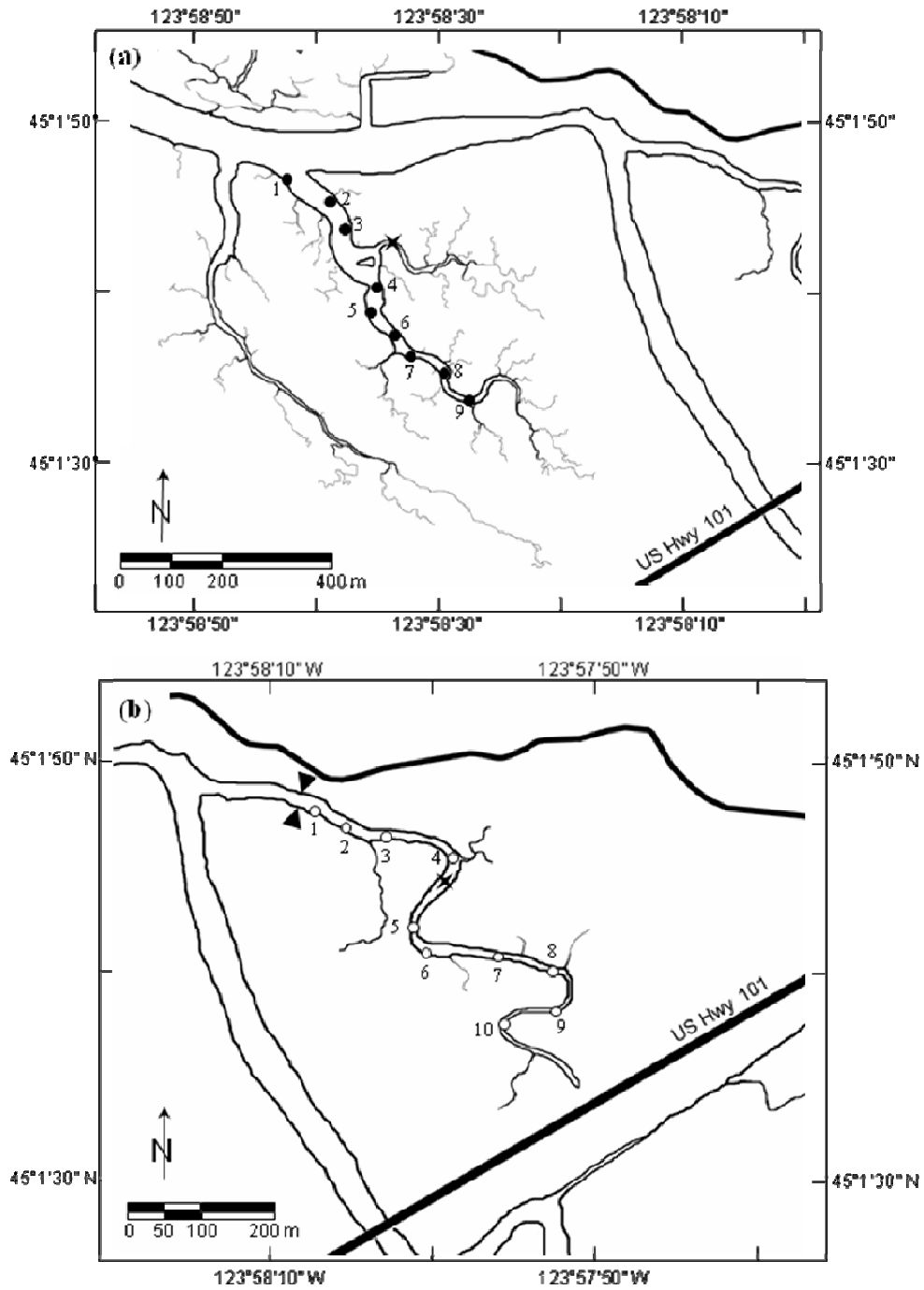


Figure 2.2. Sites sampled by beach seine in (a) the reference marsh, black circles; and (b) the 1996 marsh, open circles. Black triangles indicate location of former dike in 1996 marsh, stars indicate locations of temperature loggers, and numbers indicate site locations referred to in the text.

channels were sampled approximately every fourth high tide (i.e. every two days) between May 18 and July 13, and then at a reduced frequency (once or twice per week) through the end of September. We started the sampling regime in alternate marshes on subsequent sampling occasions during 2004 so that each channel was sampled equally on ebbing and flooding tides over the course of the season. Due to limited time for sampling on each tidal cycle, we sometimes omitted sites 7-10 in the 1996 channel later in the 2004 season since salmon were rarely caught in this area by mid- or late summer. Reference channel sites were sampled on eight occasions between June 28 and August 1, 2005, when sampling effort focused on collecting and tagging salmon for a related behavioral study within the reference channel network (Hering et al. in press).

To increase our recapture of tagged salmon for growth rate estimates, we also sampled fish during low tide within the main river channel immediately adjacent to its confluence with the reference and restored marsh channels. We swept the shallow mouth of the reference channel (< 1m deep during most low tides) with hand-held seines (1.9cm stretch mesh) and deployed our standard beach seine from a boat to sample a deep (5-7m) pool at the junction of the 1996 marsh with the main-stem estuary. Additional tagged fish were recaptured through a monthly trapping program operated by ODFW within the reference and 1996 channel networks (described by Gray et al.2002).

Fish Marking and Data Collection

Chinook salmon in all seine samples were enumerated. Between June 10 and June 13, 2003, 195 Chinook salmon ≥ 60 mm FL in the reference marsh were anesthetized (MS 222), weighed (nearest 0.1g), measured (FL, nearest mm), and tagged with Passive Integrated Transponder (PIT) tags (12.50 mm long by 2.07 mm; weight 0.102 g in air). Peritoneal injection of PIT tags has been demonstrated to have a negligible effect on survival and growth of young-of-the-year salmonids even smaller than 60mm FL (Prentice et al. 1990b; Acolas et al. 2007), but Tatara (2009) found evidence of reduced growth in some PIT tagged steelhead ≤ 74 mm FL. During 2004 all Chinook salmon were weighed and measured. Between May 18 and July 6, 2004, we PIT tagged 646 Chinook salmon in the reference marsh and 319 in the 1996 marsh. An additional 25 fish were tagged in the reference channel on August 18 and September 16, 2004. During 2005, all Chinook captured in the reference marsh were weighed and measured, and 569 were PIT tagged (Table 2.2).

Surface water temperature and salinity were recorded at all seining occasions, and water temperature was monitored continuously with a HOBO[®] temperature logger (Onset Computer Corp.) anchored in each marsh channel (Figure 2.2). During 2004, the temperature logger in the 1996 channel stopped functioning July 22 and was not replaced until June 2005.

Abundance and Distribution of Chinook in Marsh Channels

We used the number of Chinook salmon captured per standardized beach seine set (catch-per-unit-effort, CPUE) as an index of relative abundance to describe spatial and temporal distribution patterns within the marsh channels. Analysis of salmon distribution among sites within the marsh channels was limited to the two-week period during each sampling season when Chinook salmon were most widely distributed within the channels, June 16 – July 1, 2003 and June 1 – June 15, 2004.

The sample sizes of Chinook salmon and the probability of recapture of marked individuals on any given sample occasion were too low to precisely estimate abundance using open population capture-recapture models (Seber 1982). Therefore, we estimated Chinook abundance within each marsh channel on several occasions during 2004 by assuming demographic closure of the marsh populations between subsequent sampling occasions (an approach similar to Neilson et al. 1985).

Abundance estimates were calculated as the maximum likelihood Lincoln-Petersen estimator using program NOREMARK (White 1996). These estimates were likely positively biased because the populations were in fact open to the loss of tagged fish due to both emigration and mortality. Such bias should have been approximately equal between marshes, however, allowing comparison of relative abundance in the two channels.

Table 2.2. Chinook salmon mark-recapture results, 2003-2005.

Year	Marsh	Tagging Period	Tagged	Recaptured	Mean Individual Growth (S.E.)			Time-at-Large		
					mm·day ⁻¹	g·day ⁻¹	% bw ·day ⁻¹	Mean	Median	Max
2003	Reference	Jun 10 – Jun 13	195	58	0.51 (0.054)	0.13 (0.014)	1.74 (0.31)	6	3	29
	1996	--	--	--	na	na	na	na	na	na
2004	Reference	May 18 – Sep 16	671	221	0.32 (0.017)	0.070 (0.0042)	1.63 (0.087)	14	10	79
	1996	May 18 – Sep 16	319	94	0.29 (0.023)	0.047 (0.0048)	1.53 (0.13)	14	10	117
2005	Reference	Jun 28 – Aug 1	569	37	0.33 (0.049)	0.081 (0.015)	1.34 (0.23)	15	8	62
	1996	--	--	--	na	na	na	na	na	na

Size and Growth

Growth was calculated both as the change in average size of individuals in the sampled population, expressed as the slope of a linear regression of length (or weight) of captured fish on time, and as the change in size of individually marked and recaptured fish between the first and last capture occasion. An index of fish condition was also calculated from all sampled fish during each year and in each marsh channel as the slope of the linear regression of log-transformed weight on log-transformed length. For each PIT tagged and recaptured individual, we calculated absolute growth in length ($\text{mm}\cdot\text{day}^{-1}$) and biomass ($\text{g}\cdot\text{day}^{-1}$). We also determined specific growth rate (G ; $\% \text{ biomass}\cdot\text{day}^{-1}$), using the following formula (Buckley et al. 1999):

$$G = 100(e^{G_i} - 1)$$

where W_1 and W_2 were defined as the weight of a recaptured fish at the time of first capture (t_1) and second capture (t_2), respectively, and G_i is the instantaneous growth rate (Busacker et al. 1990):

$$G_i = (\ln W_2 - \ln W_1) / (t_2 - t_1).$$

Occasionally, we captured and measured individual fish twice on the same day (e.g. in both high tide and low tide samples). To eliminate faulty growth estimates caused by small errors in weight or length measurements or diel changes in stomach fullness over short recapture intervals, we excluded from growth calculations all individuals captured and recaptured over periods of 48 hours or less. Individual growth statistics were summarized by year and by marsh channel. Capture data from 2004 were also

partitioned into two-week increments to evaluate changes in growth during the course of the sampling season.

Residence Time

Because our knowledge of tagged fish presence relied on physical capture in the beach seine (i.e. we were not able to track the movement of individuals before or between capture occasions), we could not measure the *exact* duration over which any individual resided in the marsh channels. However, we could determine the *minimum* residence time of each marked and recaptured individual based on the period of time it was at large between first tagging and final recapture. The small number of fish marked and released in each channel on any one sampling occasion (maximum 63 fish) precluded more exact estimation of average residence time based on catch-per-unit-effort (e.g. Healey 1980; Pearcy et al. 1989) or estimated abundance of marked groups (e.g. Congleton et al. 1981). Thus, following the approach of Miller and Sadro (2003), we calculated the median time-at-large of all fish marked and recaptured in each marsh as an *index* of residence time for each channel. We also report the maximum time any individual fish was observed to use each channel.

RESULTS

Abundance and Distribution of Chinook in Marsh Channels

Sub-yearling Chinook salmon were present in beach seine samples collected during high tides in the reference marsh channel from late April through November 2003, mid-April through October 2004, and in all samples collected within the reference marsh between June and August 2005. Catch per-unit-effort data indicate abundance peaked in the reference channel during late June or early July 2003 and late May or early June 2004. During both 2003 and 2004, CPUE declined to a low level by mid July that persisted through the end of the sampling period (Figure 2.3).

In the 1996 channel, Chinook salmon were present in samples collected late April through mid-July 2003, but were not present in three samples collected during August and September 2003 (Figure 2.3a). During 2004, when sampling was more frequent, Chinook salmon were captured in the 1996 channel late March through mid-September, but abundance was low after mid-July (Figure 2.3b). The decline in salmon abundance in both marshes during mid-summer coincided with the period of peak annual water temperature in the estuary in both 2003 and 2004.

Within both marsh channels, CPUE was significantly and negatively related to the distance of sample locations from the confluence with the main-stem Salmon River channel during the period of maximum salmon abundance (June 16 – July 1, 2003 in the reference marsh and June 1 – June 15, 2004 in both marshes, Figure 2.4).

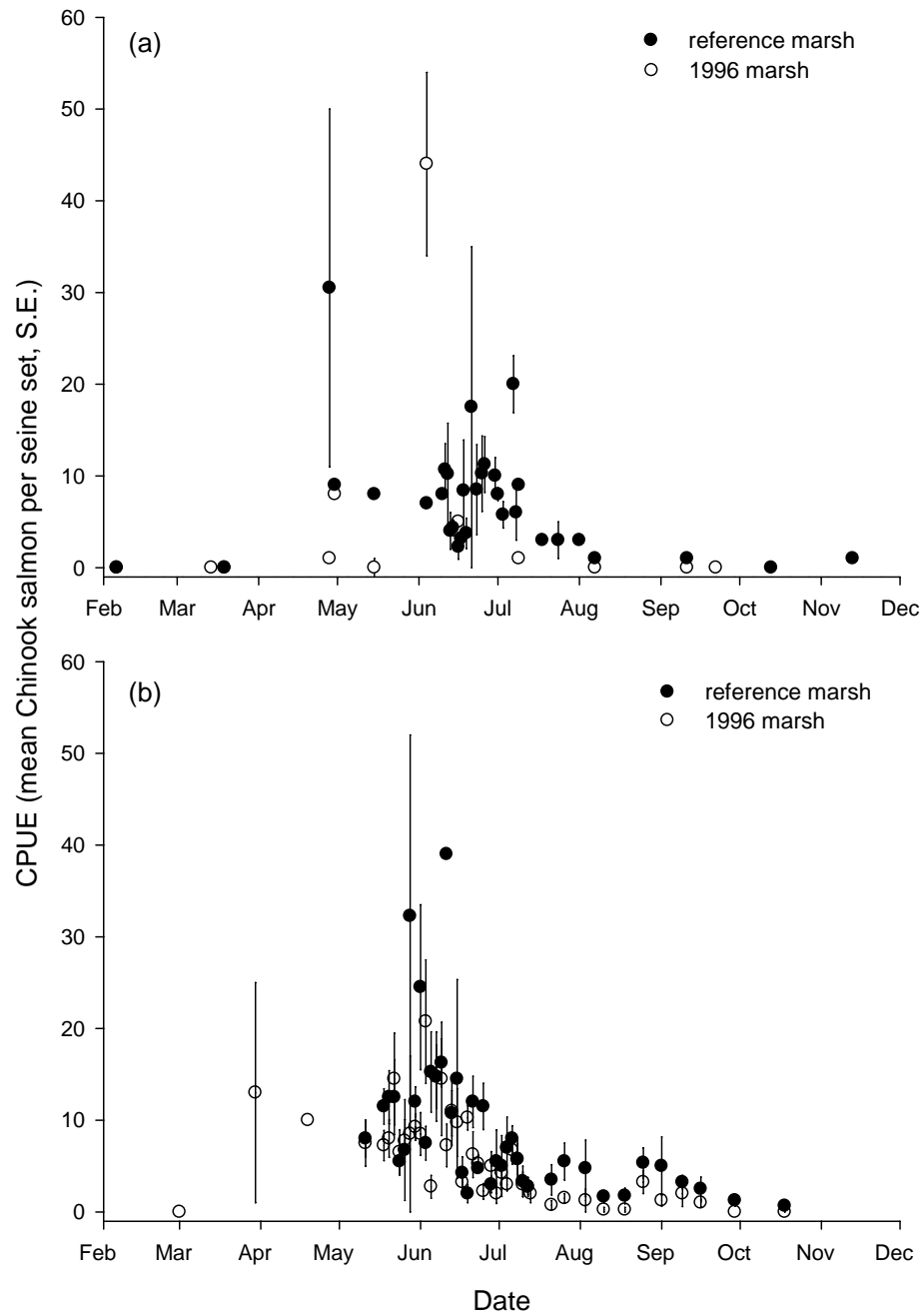


Figure 2.3. Mean catch-per-unit-effort of age-0 Chinook salmon in reference marsh (black circles) and 1996 marsh (open circles) during (a) 2003 and (b) 2004. Error bars indicate one standard error.

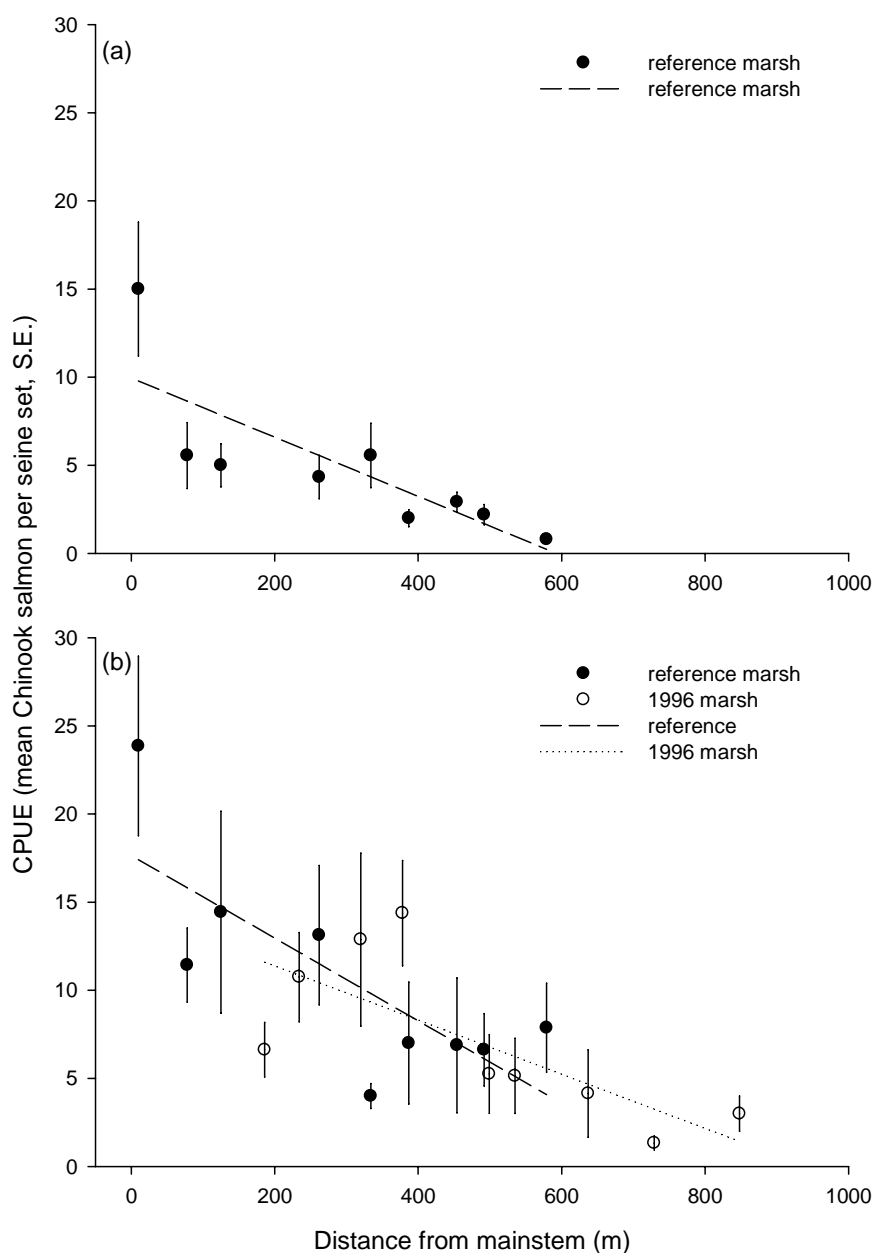


Figure 2.4. Catch-per-unit-effort of Chinook salmon (mean, \pm S.E.) at marsh seining sites during the period of peak abundance in (a) the reference marsh during 2003 and (b) both marshes during 2004. Dashed line is a linear regression of data from the reference marsh ($r^2=0.25$, $p<0.0001$ in 2003; $r^2=0.16$, $p<0.001$ in 2004) and dotted line is a linear regression of data from the 1996 marsh ($r^2=0.12$, $p=0.005$).

In the 1996 channel, few Chinook used the area above site 4, particularly late in the sampling season. Out of 19 seine sets taken above site 4 in the 1996 marsh after July 8, the median CPUE was zero.

Mark-recapture estimates of peak Chinook salmon abundance in the marsh channels during 2004 were $N = 1812$ (95% C.I. 298 to 3325) in the reference marsh and $N = 563$ (95% C.I. 159 to 967) in the 1996 channel (Figure 2.5). These abundance estimates correspond to peak densities of 0.09 (95% C.I. 0.01 – 0.16) fish·m⁻² channel area in the reference marsh and 0.04 (95% C.I. 0.01 – 0.07) fish·m⁻² channel area in the 1996 marsh. The low precision of abundance estimates was due to the small number of salmon marked and recaptured on any two subsequent sampling occasions. Despite this imprecision and the probable bias of estimates described above, the results demonstrated a pattern that mirrored changes in abundance indicated by CPUE over the course of the summer. Abundance estimators were significantly and positively correlated to CPUE in both the reference marsh (Pearson's $r = 0.62$, $p < 0.05$) and 1996 marsh (Pearson's $r = 0.79$, $p < 0.01$) (Figure 2.6).

Temperature and Salinity

During the 2004 sampling season, surface water temperature in the reference channel ranged from 10.5°C to 23°C at all sites sampled, and high tide temperatures at the bottom of the channel ranged from 9.2 to 18.9 (Figure 2.7a). Chinook salmon were present through the full range of temperatures measured. In the 1996 marsh, surface temperature ranged from 9.5°C to 23°C and from 10°C to 22°C at sites where

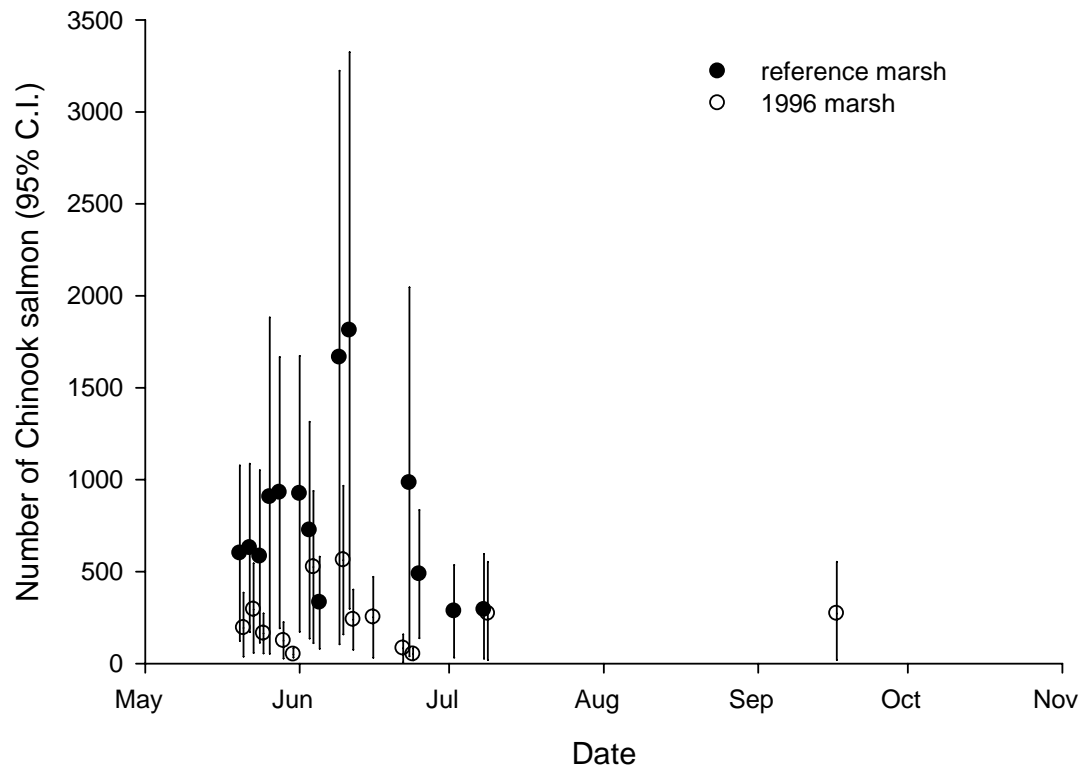


Figure 2.5. Lincoln-Petersen estimate of Chinook salmon abundance in reference marsh (solid circles) and 1996 marsh (open circles) during 2004. Error bars indicate 95% confidence interval of estimates.

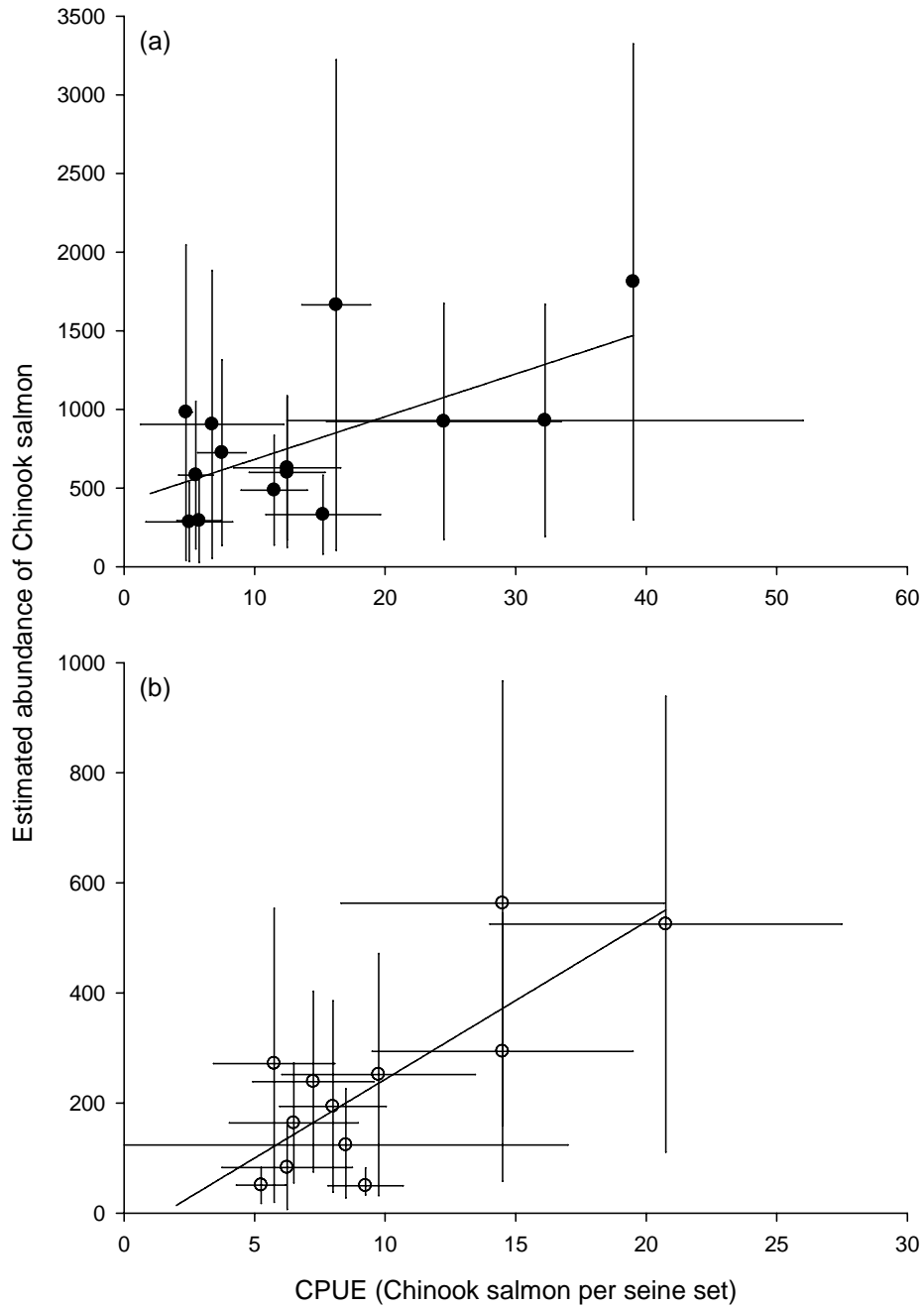


Figure 2.6. Relationship of Lincoln-Petersen abundance estimates and mean catch-per-unit-effort (CPUE) in (a) reference marsh and (b) 1996 marsh during 2004. Error bars indicate 95% confidence interval of abundance estimator and one standard error of mean CPUE.

Chinook were captured (Figure 2.7b). Temperature on the bottom of the 1996 channel at high tide ranged from 10.8°C to 21.1°C. The difference between surface and bottom temperature was often greater in the reference channel than the 1996 channel suggesting greater vertical stratification by temperature in the reference site.

Surface water salinity varied with tides and weather conditions, but generally increased through the sampling period in all years (Figure 2.8). In 2004, surface salinity ranged from 2 PSU to 35 PSU in the reference channel and from 2 PSU to 33 PSU in the 1996 channel. Surface salinity was often 2 PSU or 3 PSU lower in the 1996 marsh than the reference marsh, but sometimes salinity in the 1996 channel was similar or greater than the reference channel. Salinity was low (2 PSU to 6 PSU) during the period of peak Chinook salmon abundance, and was not consistently greater than 10 PSU until early July.

Recapture of Tagged Chinook

We recaptured 30% of all PIT tagged individuals released in the reference channel during 2003, 33% in the reference marsh during 2004, and 29% in the 1996 marsh during 2004 (Table 2.2). During 2005, when we sampled much less frequently over a shorter period of time, we recaptured 6.5% of tagged fish. Most individuals were captured only twice, but many individuals were captured on multiple (≤ 9) occasions. Tag loss appeared negligible; out of 523 occasions in 2004 when captured fish exhibited tagging scars, only three fish ($<0.01\%$) did not contain readable tags.

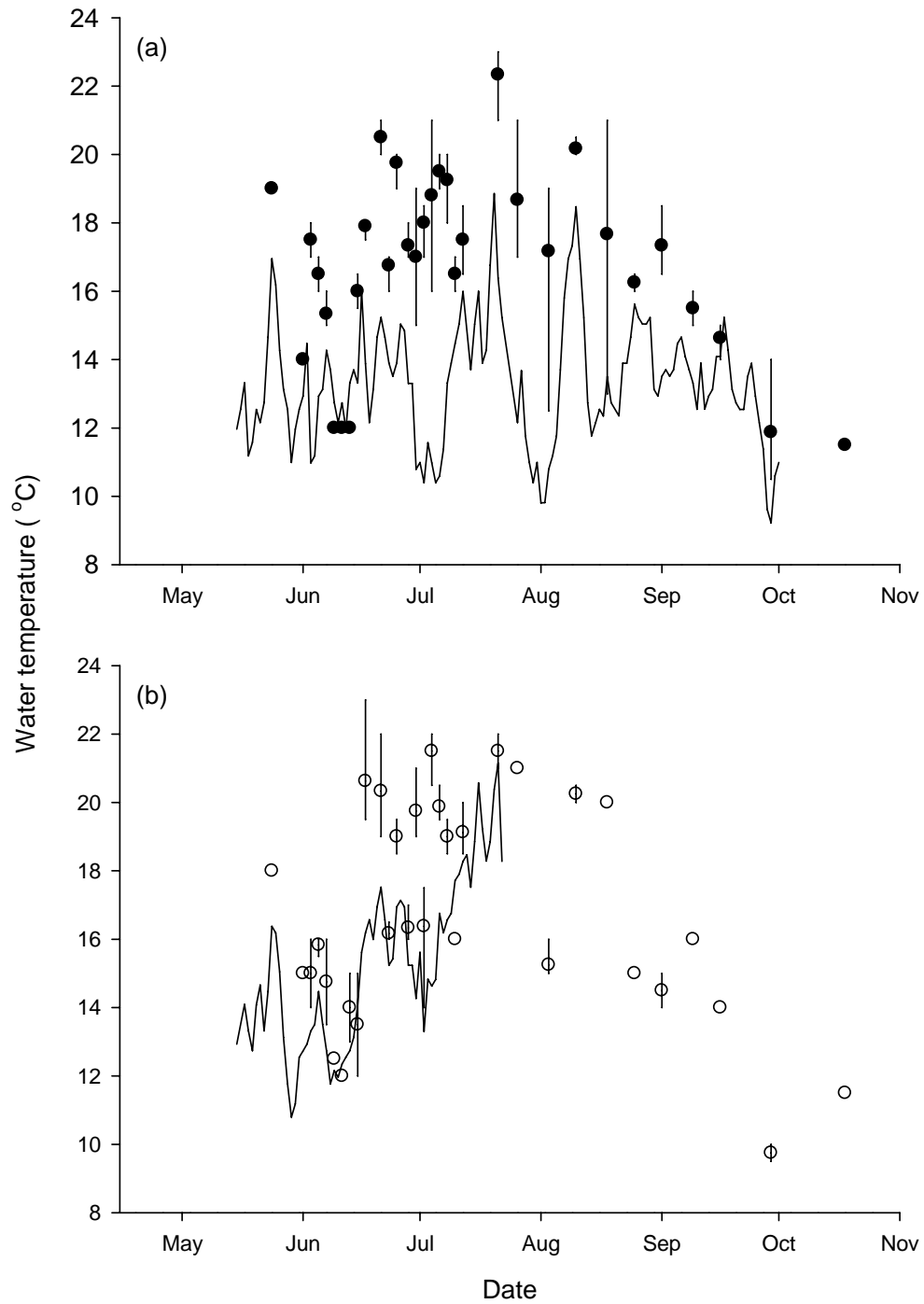


Figure 2.7. Mean (circles) and range (error bars) of surface water temperature and mean daily high tide temperature measured on bottom of channel (lines) in (a) reference channel and (b) 1996 channel during 2004.

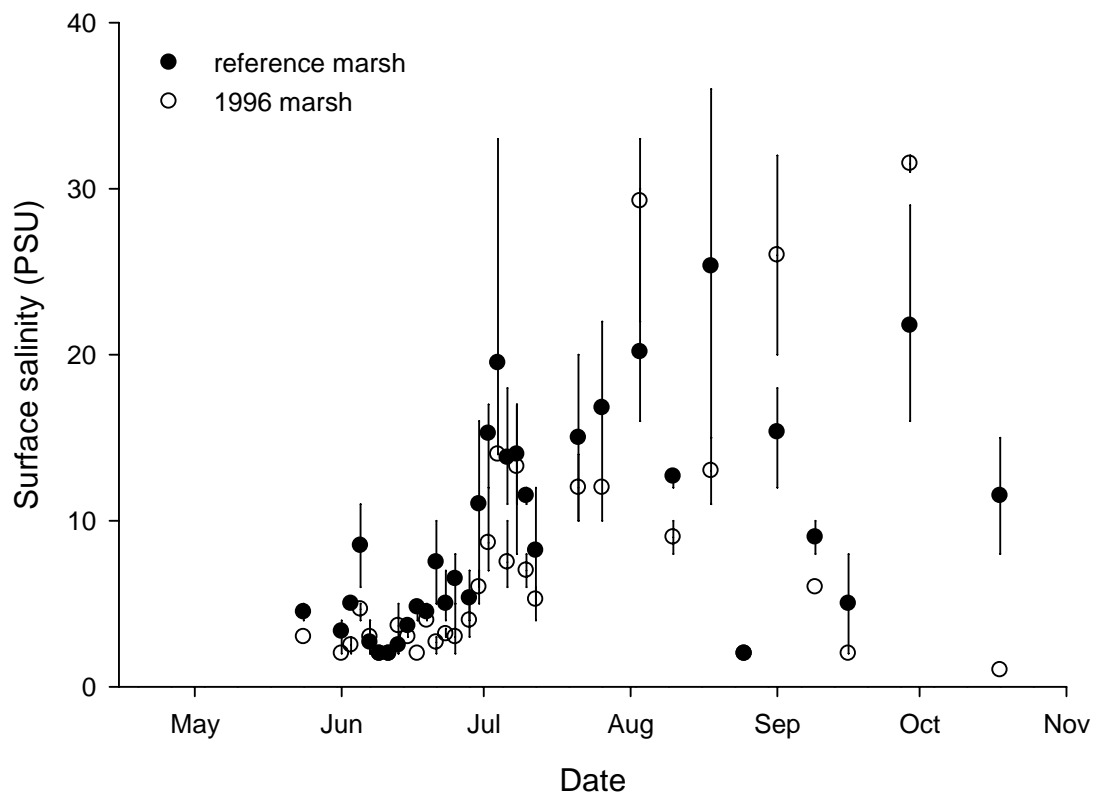


Figure 2.8 Mean and range of surface water salinity measured at reference marsh (black circles) and 1996 marsh (open circles) sample sites during high tides in 2004. Error bars indicate range of temperatures recorded.

Recaptured Chinook salmon demonstrated high fidelity to the marsh channels in which they were initially tagged. Only three of 315 individuals recaptured during 2004 were observed in both channels. One was caught first in the reference marsh and then in the 1996 marsh, a second exhibited the opposite pattern (moved from 1996 to reference), and a third fish was captured four times, alternating between the 1996 and reference channels. Although fish may have left the marsh channels and spent time in other, un-sampled areas of the estuary, so few tagged individuals were observed in both channels that we consider the two marsh channels to have contained essentially independent groups. Accordingly, we attribute growth of individual salmon between capture occasions to the marsh channel complex in which they were captured.

Size and Growth

Chinook salmon captured within the marsh channels appeared to be almost entirely age-0 individuals and ranged in size from 42 mm to 159 mm FL and 1.9 grams to 47.3 grams. Average fork lengths of Chinook salmon sampled in marsh channels increased between $0.32 \text{ mm}\cdot\text{day}^{-1}$ and $0.55 \text{ mm}\cdot\text{day}^{-1}$ (Table 2.1, Figure 2.9). During 2004, when both channels were sampled during a similar time period, the rate of increase in fork length was similar between channels, but fish captured in the 1996 channel were 6.5mm shorter on average than fish in the reference channel (multiple linear regression of fork length on time and location; $r^2=0.60$, $p<0.001$; Figure 2.9b). Salmon condition was similar between channels during all years (year and site factors were not significant in linear regression of log transformed weight on fork length).

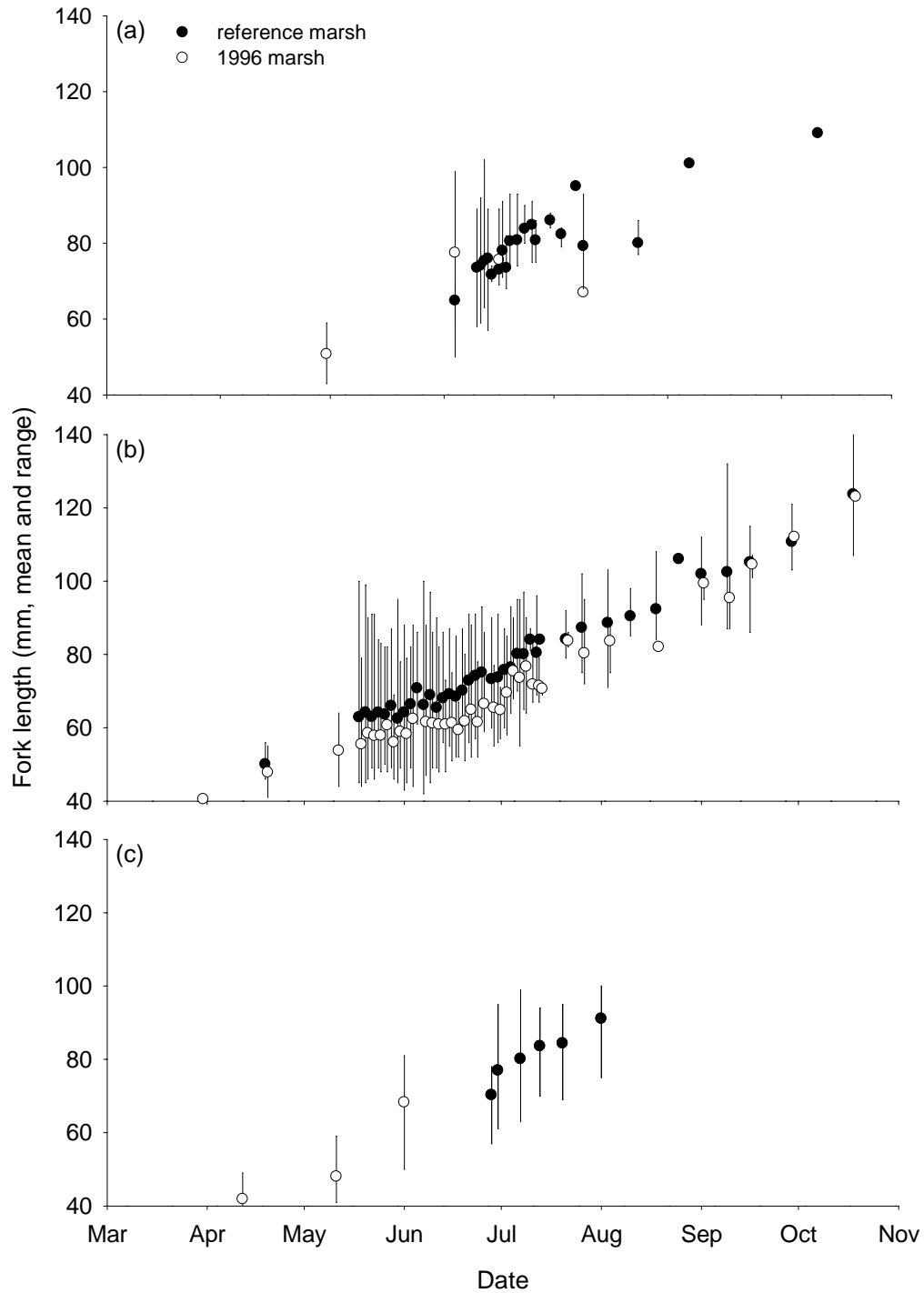


Figure 2.9. Mean fork length of Chinook salmon sampled in reference marsh (black circles) and 1996 marsh (open circles) during (a) 2003, (b) 2004, and (c) 2005. Error bars indicate the range of lengths observed.

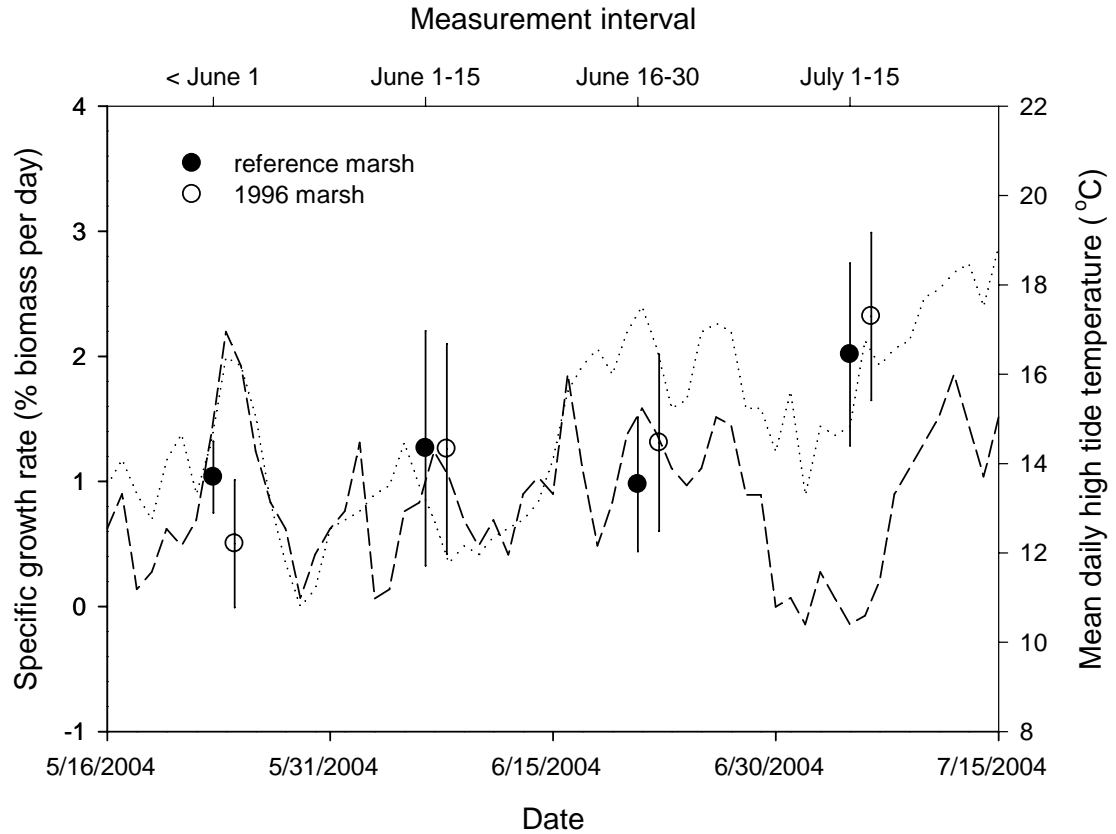


Figure 2.10. Mean specific growth rate of individual Chinook salmon captured and recaptured within 15 day periods in the reference marsh (black circles) and 1996 marsh (open circles) during 2004. Error bars indicate 95% confidence interval of mean. Mean daily high tide temperature is plotted for reference marsh (dashed line) and 1996 marsh (dotted line).

Observed growth rates of recaptured individuals ranged from $-1.31 \text{ mm}\cdot\text{day}^{-1}$ to $2.10 \text{ mm}\cdot\text{day}^{-1}$. Observed specific growth in biomass ranged from $-2.0\%\cdot\text{day}^{-1}$ in each marsh to a maximum of $4.2\%\cdot\text{day}^{-1}$ in the 1996 marsh and $11.0\%\cdot\text{day}^{-1}$ in the reference marsh, with the most extreme values calculated over short time intervals. Annual mean growth in length of recaptured fish ranged from $0.29 \text{ mm}\cdot\text{day}^{-1}$ to $0.51 \text{ mm}\cdot\text{day}^{-1}$ and mean specific growth ranged from $1.34\%\cdot\text{day}^{-1}$ to $1.74\%\cdot\text{day}^{-1}$ (Table 2.2). Growth did not differ significantly among years or between marsh channels. Specific growth rates calculated over two week increments during the 2004 season also were similar between marshes and generally increased from May through early July in both marshes (Figure 2.10). The 1996 channel had the lowest ($0.50\%\cdot\text{day}^{-1}$) and the highest ($2.32\%\cdot\text{day}^{-1}$) mean growth rates calculated during any of the two-week periods examined.

Residence Time

Of all recaptured individuals, the median time-at-large between release date and last capture was approximately 3 days in the natural marsh during 2003, 10 days in both the restored and the natural marsh during 2004, and 8 days in the natural marsh during 2005. Differences in sampling schedule among years preclude comparison of times-at-large among years. Maximum observed residence times of individual tagged Chinook were 117 days in the 1996 channel and 79 days in the reference channel, both during 2004 (Table 2.2).

DISCUSSION

Previous work in the Salmon River estuary demonstrated that subyearling Chinook salmon may be found in intertidal marsh channel habitat nearly year-round and that juvenile salmon can occupy formerly diked marsh areas immediately after tidal inundation is restored (Cornwell et al. 2001; Gray et al. 2002). The present study examined in more detail the distribution and abundance of Chinook salmon within channel networks and the growth benefits salmon derive from marsh residence during late spring and summer. By sampling during high tides at several sites distributed within each marsh channel and by uniquely marking and recapturing individual fish, we demonstrated that: (1) Chinook salmon density in intertidal channels decreased with distance from subtidal refuge habitats; (2) individual salmon returned to intertidal channels for a median three to ten days and up to several months and demonstrated high fidelity to the channel in which they were marked; (3) salmon gained a mean 1.34% to 1.74% biomass per day while using intertidal marsh habitat; and (4) salmon growth and residence time were generally similar between a natural, reference channel and a restored channel, though overall Chinook salmon abundance was lower and growth appeared more variable in the restored site.

Prior to recent work in Salmon River (Gray et al. 2002; Bottom et al. 2005b; Hering et al. in press; Volk et al. in press), few studies have investigated juvenile salmon use of intertidal wetland habitats outside the Salish Sea. The present results provide the first empirical estimates of residence time and growth of individually

marked and recaptured Chinook salmon in an Oregon tidal wetland and validate independent estuarine growth and residency estimates inferred from otolith analyses (Neilson et al. 1985; Volk et al. in press) and bioenergetic modeling (Gray 2005, Bieber 2005). The similarity of individual salmon growth and residence patterns in the restored and reference wetlands indicates that restored habitat can function equivalently to a natural site for rearing salmon, while differences in salmon abundance suggest lower overall capacity of the restored site. It is unclear, however, whether capacity differences are due only to land-use history or other intrinsic physical differences between the sites (e.g. channel size or landscape location).

Temporal Patterns of Abundance

Occurrence of Chinook salmon in intertidal channels followed a seasonal pattern similar to that described previously in the Salmon River and other estuaries (e.g. Healey 1982, Gray 2002). Salmon were present in spring, abundance peaked during early summer, and most salmon vacated marsh habitats by mid-July. Beach seine samples collected for this study were too infrequent to adequately describe salmon abundance in the marshes during early spring, but our results are consistent with the conclusion of Volk et al. (in press) that most salmon arrive in the marsh areas of the upper Salmon River estuary between March and July.

The mid-summer decline in abundance within the marsh channels coincided with peak annual water temperatures in the estuary. Previous studies have suggested that juvenile salmon may vacate shallow estuarine habitats due to high temperatures

during the summer (Healey 1980; Roegner et al. 2008), though the effect of temperature is hard to separate from the coincident ontogenetic motivation for salmon to move toward the ocean. High tide temperatures in the marsh channels approached 22°C in July, exceeding the levels at which Chinook salmon feeding and growth were shown to decrease in experimental studies (Brett 1952). Healey (1980) reported that Chinook fry moved away from sampling stations in the Nanaimo River estuary when temperature exceeded 21-22°C. Though few salmon were captured in the marsh channels during late July and August, abundance increased slightly in September, and some Chinook salmon were captured in the reference marsh during limited sampling in November 2003. An increase in salmon use of intertidal habitat during late summer and autumn may have been associated with an influx of late migrants that enter Salmon River estuary from upriver rearing habitats (Volk et al. in press) or may have represented movement back into marsh habitats from the main-stem channel in response to seasonally cooling water temperatures.

The number of salmon that occupied each channel may reflect a difference in the capacity of the two systems to support salmon due to physical characteristics of each site (e.g. channel area, elevation, complexity). Abundance estimates based on the recapture of marked fish during 2004 suggest an order of magnitude difference in the peak number of Chinook salmon supported by the two sampled channels, but the difference was not statistically significant due to low precision of the estimates. CPUE at the lowermost sites in the 1996 channel was generally similar to reference channel sites, however, and the highest single day CPUE of all sites was recorded in

the 1996 marsh, indicating that despite differences in overall abundance, salmon occurred at similar densities within the occupied portions of each marsh (especially during periods of peak seasonal abundance). When salmon density was computed from abundance estimates and the wetted area of each channel at high tide, the peak density in the much larger reference channel network ($0.09 \text{ fish}\cdot\text{m}^{-2}$) was somewhat higher but of the same order of magnitude as that of 1996 channel ($0.04 \text{ fish}\cdot\text{m}^{-2}$). These density estimates are comparable to the range of values for Chinook salmon in tidal channels reported from trap net sampling in other studies (e.g. $0.01 - 0.04 \text{ fish}\cdot\text{m}^{-2}$ in Salmon River tidal channels [Gray et al. 2002]; mean $0.18 \text{ fish}\cdot\text{m}^{-2}$ in three Fraser River tidal channels [Levy and Northcote 1982]). Although they were not the focus of this study, coho salmon also were observed rearing in the Salmon River tidal channels and were much more abundant in the 1996 channel than in the reference channel. Therefore, although Chinook salmon density appeared slightly lower on average in the restored site, total salmon rearing density was likely more similar than estimates of only Chinook salmon suggest.

Spatial Patterns of Abundance

The expanded suite of beach seine sites sampled in 2003 and 2004 allowed us to discern structure in the distribution of salmon within the marsh channels at high tide that was not evident from previous efforts that employed limited beach seine sites or trap nets to sample the whole channel population from one point (e.g. Gray 2002). Within both intertidal channels examined, we found a strong negative relationship

between Chinook salmon density and the distance of wetland sample sites from sub-tidal habitats within the main-stem Salmon River. This relationship was particularly strong in the reference marsh where channels drain completely during nearly all summertime low tides. Although the relationship held generally in the 1996 marsh, the highest relative abundance of salmon in the 1996 channel consistently occurred at site number four, approximately 378 meters from the Salmon River main stem. Site four was located at a relatively deep pool in the restoring channel that often retained water during low tides and may have provided a refuge for salmon to remain in the 1996 channel throughout the tidal cycle. Thus, our findings are consistent with the idea that salmon density at high tide decreases with distance from sub-tidal habitats.

Because Chinook salmon were not evenly distributed within the tidal channels, actual rearing densities in the lower portions of the channels were greater than the average calculated using the entire channel area. This was particularly the case in the 1996 channel, where Chinook distribution was generally limited to the lower half of the sampled area of channel – 94% of total catch in the 1996 marsh during 2004 occurred at sites 1-6. The lack of Chinook salmon at sites far into the 1996 channel likely reflects the distance fish must travel to reach these sites from subtidal main-stem habitat. Sample sites in the 1996 channel sites extended 340 meters farther from the main stem than those in the reference marsh.

The spatial distribution of Chinook salmon in Salmon River marshes differed from that reported for Fraser River marsh channels by Levy et al. (1979) and Levy and Northcote (1981). Similar to the present results, salmon were abundant near the

mouth of one Fraser marsh channel, but another channel appeared to have low densities of salmon near the mouth, a result the authors speculated could have been due to poor sampling efficiency. Within the Fraser channels, however, density often increased with greater penetration into the marsh – a pattern opposite of that we observed with the Salmon River channels. Few other studies have investigated distribution of salmon specifically within intertidal channels, but similar to our findings for Chinook salmon, the density and diversity of estuarine fish generally were greater in higher order (thus lower elevation) channels within tidal networks in a San Francisco Bay salt marsh (Visintainer et al. 2006).

Growth

Growth rates based on changes in mean body size of estuarine populations are often considered minimal estimates due to the transient residence and size-dependent emigration of salmon in estuaries (Healey 1991). Similar to results from the Sixes River (Reimers 1973), however, we did not observe a substantial difference between the change in average size of the marsh channel populations over the course of a sampling season and the growth rates estimated from marked and recaptured individuals. During 2004 and 2005 mean growth rate of marked individuals was actually slightly slower than the rate of increase of the overall population. Observed growth rates also were somewhat slower than those reported for marked Chinook fry in other estuaries, including $0.86\text{mm}\cdot\text{day}^{-1}$ and $0.53\text{mm}\cdot\text{day}^{-1}$ in the Sacramento-San Joaquin delta (Kjelson 1982), $1.32\text{mm}\cdot\text{day}^{-1}$ ($4\text{-}5\%$ body weight $\cdot\text{day}^{-1}$) in the

Nanaimo River estuary (Healey 1980), and $0.62 \text{ mm}\cdot\text{day}^{-1}$ (3% body weight $\cdot\text{day}^{-1}$) in the Nitinat River estuary (Fedorenko 1979).

One difference between the present study and those reporting faster estuarine growth may be that we limited sampling to specific intertidal marsh channels, whereas other studies sampled a broader range of sites within estuaries. Slower growing individuals may have been more likely to remain in the marsh channels and were thus more susceptible to recapture than faster growing individuals that left marsh habitats for deeper areas of the estuary or the ocean. It is also possible that handling stress from PIT tagging temporarily reduced the growth rate of marked individuals over the typically short recapture intervals in the marsh channels. Implantation of PIT tags can cause minor, often statistically insignificant depressions in short term growth rate in the days immediately following tagging (Sigourney et al. 2005; Acolas et al. 2007; Tatara 2009), though this may be compensated by subsequent growth increases (Prentice 1990a, b; Bateman and Gresswell 2006). Stress from PIT tagging, however, should be no greater than that of other techniques for marking salmon in estuaries, such as spray marking with fluorescent grit (Healey 1980; Levy and Northcote 1982) or freeze branding (Neilson et al. 1985). Moreover, our growth measurements were consistent with those of Volk et al. (in press), who used otolith microstructure to back-calculate daily growth of Chinook captured in Salmon River marshes in 2001 and 2002. They found mean growth rates ranging between $0.19 \text{ mm}\cdot\text{day}^{-1}$ and $0.65 \text{ mm}\cdot\text{day}^{-1}$ and like the present results, no significant difference among marsh sites.

Our measurements were generally incongruent with both the range of growth rates and the seasonal trend in growth predicted for Chinook salmon in Salmon River marshes using bioenergetic models that incorporated empirical information on salmon diet, water temperature, caloric value of prey items, and other variables for each marsh (Bieber 2005; Gray 2005). During 2004, the only year in which growth was both modeled and measured, growth rates of fish recaptured in the reference marsh during May were less than half of model predictions ($1.0\% \cdot \text{day}^{-1}$ versus $5.8\% \cdot \text{day}^{-1}$) and while measurements in July were more similar, they remained lower than model estimates ($1.2\% \cdot \text{day}^{-1}$ versus $1.8\% \cdot \text{day}^{-1}$). Not only did fish tagged in 2003 and 2004 not grow as fast as model predictions, but the change in growth rates we observed during the 2004 season was opposite the seasonal pattern predicted in each of the four years examined by Gray (2005); rather than decreasing as predicted, growth rates measured in 2004 increased from May to July. Although our measurements corroborate the finding that growth potential was more variable in the restored site than the reference site, the variability we observed followed a markedly different pattern than that predicted by bioenergetic models. This may be in part because the model predicts growth *potential* in the marsh channels, rather than realized growth. As such, while the bioenergetic approach provides a useful heuristic tool for comparing estuarine rearing sites, it may not accurately predict fish performance.

Empirical growth data imply that adequate prey resources were available to support salmon metabolism and growth even as marsh temperatures warmed during the early summer. When the 2004 recapture data were partitioned into two-week

intervals it was evident that growth rate in both channels was higher in early July than in May or June. Brett (1952) found that the optimum temperature for growth of juvenile Chinook salmon fed a maximum daily ration was approximately 19°C, whereas feeding and growth decreased above 22°C. Thus, provided abundant prey exists in the tidal channels, salmon may face a tradeoff between growth opportunity and thermal stress by occupying marsh habitats during mid- to late summer. High growth rates recorded in July also were coincident with the seasonal reduction in salmon abundance in the marsh channel. Therefore, increased growth may have been a density-dependent response to reduced competition for resources within the marshes. A similar increase in salmon growth was observed as Chinook salmon abundance declined seasonally in the Sixes River estuary, leading Reimers (1971) to hypothesize that salmon density limited salmon growth during periods of peak salmon abundance.

Greater variability in water temperature and/or intermittent availability of high energy prey items in the 1996 marsh (e.g. adult and larval diptera and trichoptera; Gray et al. 2002; Gray 2005) may have created more variable growth conditions in the restored channel than in the reference site. Seasonal changes in salmon growth may explain the difference in average growth of recaptured fish in the reference marsh between 2003 and 2004. During 2003, we did not begin tagging until mid-June, so recaptured fish may have experienced a warmer thermal environment on average than those recaptured earlier in the season during 2004.

Residence Time

Differences in median observed residence time among sampling years were as likely due to changes in sampling duration and frequency as actual differences in fish behavior. During 2003, we sampled daily immediately following initial tagging efforts and then greatly reduced sampling frequency later in the summer. As a result most recaptures occurred over short time periods early in the sampling period and the median time-at-large was three days. During 2004 and 2005, greater sampling effort later in the season and more equally distributed sampling effort over time increased the probability of recapturing tagged fish later in the summer and produced longer median recapture intervals (ten and eight days, respectively). These recapture intervals were similar to median Chinook salmon residence times in the reference channel documented with a continuously monitoring PIT detector during 2004 and 2005 (16 days and 9.5 days; Hering et al. in press). Sampling protocols in the two study channels were comparable and mean and median recapture intervals were identical during 2004, suggesting that individual fish occupied each channel on average for a similar length of time. Because we continued sampling during 2004 until the catch of marked Chinook in the marshes was essentially zero, we suspect the decay of recaptures over time approximated the loss rate of individuals from the general population and the distribution of observed times-at-large accurately reflected time spent in the marshes by individual salmon.

Our mark-recapture approach revealed a greater duration of estuarine wetland use by individual Chinook salmon than has been reported previously. Approximately

twenty percent of recaptured individuals remained in marsh habitats ≥ 20 days, including one tagged individual that used the restored tidal channel over a period ≥ 117 days. Average times-at-large were on the order of one or two weeks, similar or slightly longer than residence times reported for natural marshes in the Skagit River (Congelton et al. 1981) and Fraser River (Levy and Northcote 1982) estuaries and in a restored tidal wetland in the Puyallup River estuary (Shreffler et al. 1990). Bottom et al. (2005b) reported median travel time for Chinook salmon from the head of tide in Salmon River to the lower estuary was approximately 35 days. Accordingly, our results suggest an average individual Chinook salmon in the Salmon River spends about one quarter of its estuarine residence rearing in one of the tidal wetland complexes.

Salmon River Chinook salmon may exhibit unusually long marsh residence, but it is also likely that we simply sampled more frequently and over a longer period than previous marsh channel studies. Moreover, unlike other marking methods (e.g. fin clips, acrylic paint; Bottom et al. 2005b), the ability to detect PIT tags did not diminish with time, so we may have been more likely to correctly identify fish several months after initial capture. If Chinook salmon do remain longer in wetland habitats at Salmon River than other estuaries in Puget Sound and British Columbia, the behavior could be an adaptation to local marine habitat. Fish entering a much less protected open ocean, such as those in the current study, may benefit from an additional growth period in the shelter of estuarine wetlands (Healey 1991).

Factors underlying within population variability in marsh channel residence call for further examination. The pattern of salmon abundance in the marsh channels indicates that many fish left the channels by late June, and relatively few remained using the marshes through late summer. Some tagged salmon captured in tidal channels in August or September had resided in the marsh systems since early summer, reaching sizes similar to fish that had already entered the ocean. Our study did not illuminate proximate or ultimate cues that cause some individuals to remain in marsh habitats while others continue moving through the estuary.

Fidelity

An unexpected result was the high degree of fidelity of individually tagged Chinook salmon to the marsh channel in which they were initially captured. Despite extensive sampling in 2004, less than one percent of individuals tagged in the 1996 marsh were later observed in the reference marsh. The limited movement between channels was particularly remarkable because the 1996 channel and reference channel join the main-stem Salmon River only 600 meters apart, and all the salmon using the channels during high tide must retreat to sub-tidal habitats in the main stem during most low tides. Also, we expected to recapture individuals in the reference channel as they moved downriver toward the ocean after being marked in the 1996 channel. Minimal use of both marshes by individual salmon is consistent with the results of continuous PIT tag monitoring in the reference channel network during 2004 (Hering et al. in press). Even using a continuously operated, *in situ* tag detector in the

reference channel, we detected a nine-fold smaller proportion of fish tagged in the 1996 marsh than those tagged in the reference system (D. Hering unpublished). Our recapture results suggest that Chinook salmon in Salmon River may establish residence in a particular wetland system and remain there before moving relatively quickly to the lower estuary and ocean, rather than occupying multiple marsh channel networks in sequence as they move seaward (Simenstad et al. 2000). The apparent high fidelity of marked fish to particular marsh channel networks gives us confidence that growth measured in recaptured individuals was attributable to rearing conditions in the marsh system where each individual was captured. Furthermore, this rearing behavior suggests that restoration of additional marsh area in estuaries may increase salmon rearing capacity in a largely additive way by providing habitat for additional, independent cohorts of juvenile salmon.

Efficacy of Restoration

Many investigators have demonstrated that juvenile salmon may inhabit restored tidal wetlands soon after dike removal (e.g. Shreffler et al. 1990; Miller and Simenstad 1997; Tanner et al. 2002). In the Salmon River, juvenile Chinook salmon and coho salmon were observed in the 1996 marsh channel less than one year after restoration of tidal inundation (Cornwell 2001). Presence of fish in a restored marsh channel is a suitable measure of the *opportunity* for fish to access restored habitat, but it does not adequately indicate the *realized function* of restored habitat to support fish production (Simenstad and Cordell 2002). We sought to assess function directly by

measuring the growth and behavioral responses of juvenile salmon rearing in restored and reference channels – allowing the fish to serve as integrative indicators of the costs and benefits of rearing in the restored and natural sites.

Although the present study lacked replication and thus did not formally test the efficacy of recreating marsh channel habitat through dike removal, our results suggest that, at least in the Salmon River, restored marsh channel habitat can function similarly to natural habitat for rearing salmon. Individually tagged and recaptured Chinook salmon grew similarly in the reference and the 1996 marsh channels and remained associated with each channel for similar lengths of time. When considered together with comparisons of fish performance in similarly un-replicated restored and reference sites in Puget Sound (Miller and Simenstad 1997) and on the east coast of the United States (Tupper and Able 2000; Miller and Able 2002; Teo and Able 2003a, b), the present study adds to a growing body of evidence that restoration of degraded marsh habitats can increase rearing capacity for estuarine-dependent fish.

Both the restored and reference site provided suitable rearing habitat for salmon, but some differences between marshes were apparent, including more variable growing conditions for salmon in the restored site and possible differences in salmon capacity of the two systems. Gray et al. (2002) concluded that differences in salmon rearing potential among Salmon River marshes likely were due to both landscape position of the sites and restoration history, and the lack of replication of natural and restored sites in the present study makes it difficult to separate these confounding influences. Our observations of spatial distribution of salmon within marsh channels

suggest that physical characteristics such as proximity to adequate subtidal habitat may influence salmon use of intertidal sites. Continued monitoring of the 1996 marsh and other restored sites over time will be necessary to evaluate whether further development of physical attributes such as channel complexity will increase restored marsh capacity and lead to full recovery of habitat function for juvenile salmon.

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CHAPTER 3:

Tidal movements and residency of subyearling Chinook salmon (*Oncorhynchus tshawytscha*) in an Oregon salt marsh channel.

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ABSTRACT

A novel application of full-duplex passive integrated transponder (PIT tag) technology was used to investigate movements of individual subyearling Chinook salmon ($FL \geq 60\text{mm}$) into and out of tidally flooded salt marsh habitat in the Salmon River estuary, Oregon. PIT interrogation was effective, with mean tag detection $\geq 92\%$. Salmon movement peaked late during both flood and ebb tide periods, indicating salmon did not drift passively. Most movements were in the direction of tidal currents, but 20% of individuals entered the channel against the ebbing tide. Individuals occupied the intertidal channel for a median 4.9 hours and as long as 8.9 hours per tidal cycle, and few were detected moving when water depth was $< 0.4\text{m}$. Some individuals used the channel on multiple successive tidal cycles, and others entered intermittently over periods up to 109 days. Using an individual-based approach, we characterized diversity of juvenile Chinook salmon behavior within a marsh channel, providing insight into the value of such habitats for conservation and restoration of salmon populations.

INTRODUCTION

During their juvenile migration from freshwater to marine habitat, ocean-type Chinook salmon (*Oncorhynchus tshawytscha*) may rear for prolonged periods in subsidiary and blind channel networks that connect main-stem estuarine channels with peripheral tidal wetlands (Congleton et al. 1981; Simenstad 1983; Healey 1991). Such

channel networks are often intertidal, necessitating twice daily evacuation of wetland areas and redistribution of nekton communities across hundreds of meters of habitat as channels flood and drain with the tide (Rozas 1995; Gibson 2003). Despite obligatory tidal emigrations, mark-recapture experiments indicate that individual Chinook may return to particular wetland channels for days to months, moving into flooded channel networks during high tides and retreating to subtidal habitats during low tides (Congleton et al. 1981; Levy and Northcote 1982; Shreffler et al. 1990).

The use of tidal channels as salmon rearing habitats has been the subject of multiple studies over the past several decades. Research has emphasized seasonal patterns of salmon abundance (Congleton et al. 1981; Levy and Northcote 1982), salmon feeding habits and prey resources (Shreffler et al. 1992; Gray et al. 2002), and restoration and recovery of habitat function in formerly degraded wetlands (Shreffler et al. 1990; Miller and Simenstad 1997; Gray et al. 2002). Recent work suggests that the presence or condition of estuarine marsh habitat may be linked to life-history diversity and hence resilience of salmon populations (Bottom et al. 2005a and 2005b). Understanding the behavior of individual salmon within estuarine wetlands is necessary to evaluate habitat–life history associations and to predict changes to salmon populations that might result from wetland degradation or recovery (Simenstad and Cordell 2000). Yet patterns of salmon movement within and among tidal channels – including the timing and duration of tidal excursions into marsh habitats – remain poorly understood, particularly at fine temporal and spatial scales.

One impediment to studying salmon behavior in tidal marshes has been difficulty tracking individuals with ocean-type life histories that are most likely to reside in marsh habitat. Because such fish (typically 40-100 mm fork length) are too small to monitor using active radio or acoustic telemetry, active telemetry studies of salmon in estuaries have used larger yearling migrants (e.g. Moser et al. 1991; Miller and Sadro 2003; Schreck et al. 2006) and/or hatchery-reared fish (Semmens 2008.) The few studies that have described movement of small salmon in intertidal marsh channels have relied on physical recapture of marked fish using seines or traps (Levy and Northcote 1982; Shreffler et al. 1990). Repeated capture and handling may alter fish behavior, however, and such conventional methods are poorly suited to resolving movements that occur over the short time scale of tidal cycles.

We sought to address this problem by using full-duplex (FDX) passive integrated transponder (PIT) tag technology (Prentice et al. 1990a). PIT tags are common tools in freshwater fish research, where detection systems incorporating stationary, in situ PIT antennas have allowed passive monitoring of fish movements at multiple scales in natural and simulated stream habitats (reviewed by Zydlewski et al. 2006). High-salinity water has limited application of PIT detection technology in marine and estuarine habitats by reducing the distance over which PIT tags can be detected (e.g. McCormick and Smith 2004). Adams et al. (2006) and Meynecke et al. (2008), however, both reported using half-duplex (HDX) PIT tag detection systems for monitoring the movement of fish in salinities ranging from 2 to 28 PSU. Both investigators used 23.1-mm long by 3.4-mm diameter HDX PIT tags weighing 0.6 g in

air. Such tags (the smallest HDX tags commercially available) are too large and heavy for use with subyearling salmon, but at the time of our study, FDX tags measuring 12.5mm long by 2.07mm diameter and weighing 0.102g in air were available. Improvements in the read range of FDX tags and improved performance and capability of the transceiver system (e.g. electromagnetic interference filtering, operation of multiple antennas from a single transceiver, and antenna design) recently have increased the feasibility of using FDX PIT tag technology with small fish in brackish water habitats.

We operated a stationary FDX PIT tag detector within a blind, tidal salt marsh channel of the Salmon River estuary, Oregon, for several months during the summers of 2004 and 2005, coincident with a conventional mark-recapture experiment in the estuary using FDX PIT tags (Chapter Two). Our objectives were to assess the utility of this approach for monitoring movement of small salmon in shallow estuarine habitats, investigate the timing and duration of intertidal channel use by individual age-0 Chinook salmon, identify environmental limits (e.g. temperature, depth) on channel occupancy, and test whether patterns of tidal movement varied among individuals of different sizes or tagging location.

METHODS

Study Area

The Salmon River drains a catchment of 194 km² in the Oregon coastal mountains and flows into the Pacific Ocean at Cascade Head (45° 01' N, 123° 58' W;

Figure 3.1). The lowest 6.5 river kilometers (rkm) form a tidally influenced estuary, and the area of the estuary between rkm 2.0 and rkm 4.5 includes over 200 hectares of salt marsh intersected by tidal marsh channels. Sub-yearling Chinook salmon are the dominant salmonids in the estuary, typically occurring in marsh channel habitats from March through October with peak abundance in late spring or early summer. The estuary is the site of a long-term study of salmon rearing in tidal marsh channels (Gray et al. 2002; Bottom et al. 2005b).

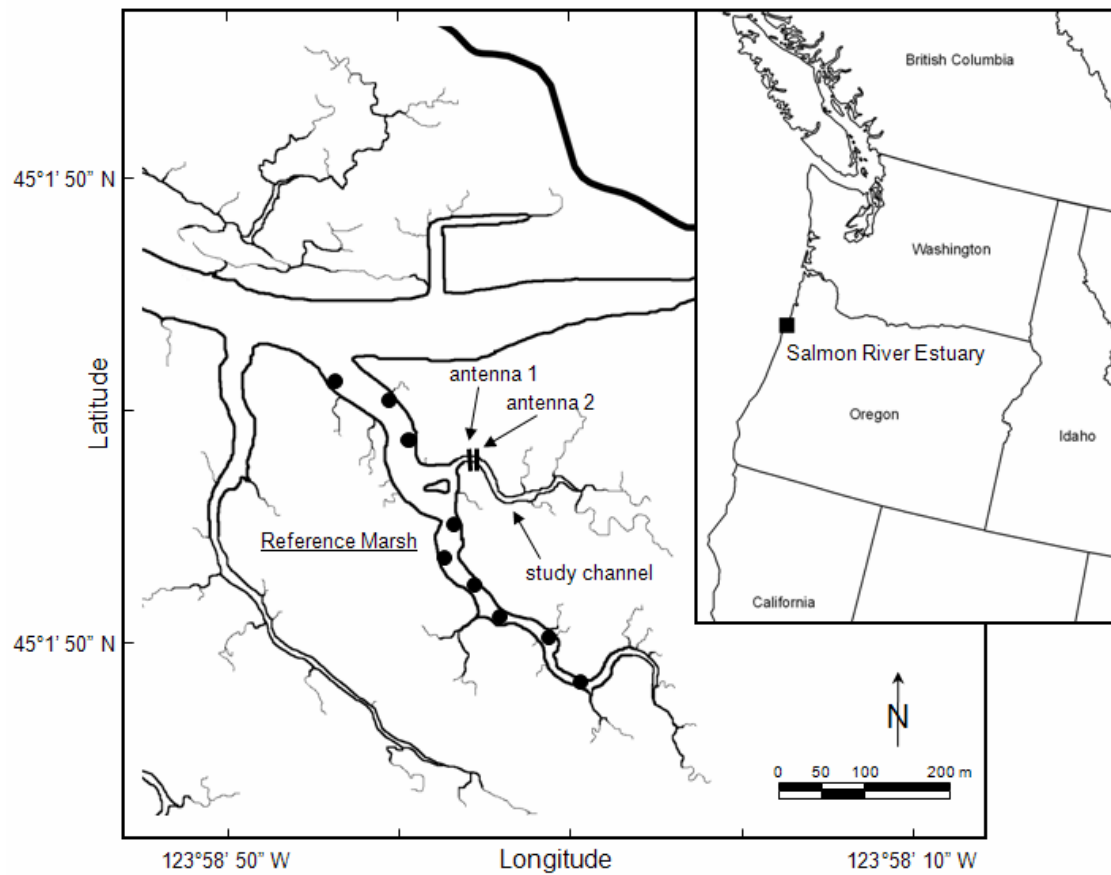


Figure 3.1. Map of study site in Salmon River estuary showing location of stationary PIT antennas. Closed circles indicate locations where Chinook salmon were PIT tagged in the Reference Marsh in 2004 and 2005.

Our study channel was a blind, secondary channel within a dendritic network of intertidal channels that joins the main-stem Salmon River at rkm 3.2 (Figure 3.1). This larger channel network intersects an 80 hectare, mature high salt marsh (Jefferson 1974) previously described as the Salmon River “reference marsh” or “control marsh” (Gray et al. 2002). Surface area of the study channel was approximately 2005 m², comprising 9.5% of the entire reference channel network. Width of the study channel at the detector site was 8 meters, and water depth varied from approximately 1.5m at high tide to <0.1m on most summertime low tides. During both 2004 and 2005, high tide surface water salinity in the study channel varied from less than 5 PSU in June to 28-30 PSU in August and September. The water column was often stratified by salinity in late summer.

Fish Tagging

During high tides between May 18 and July 6, 2004, juvenile Chinook salmon were captured by beach seining, PIT tagged, and released at nine sites within the primary channel of the reference marsh (N=671) (Figure 1). Tagging followed the techniques of Prentice et al. (1990a) using 12.50 mm long by 2.07 mm FDX PIT tags (model TX1411ST Digital Angel Corp., weight 0.102 g in air). Prior to tagging fish were anesthetized in a bath of ambient water from the marsh channel containing ≤ 50 mg·L⁻¹ tricainemethanesulfonate (MS 222). Tags were inserted into the body cavity using a 12-gauge syringe, and tagged fish were allowed to recover from anesthesia in an aerated water bath before their release near the site of capture. Using the same

methods, an additional 572 Chinook were tagged and released at the same reference marsh sites between June 28 and August 1, 2005. Water temperature and salinity during tagging ranged from 9 °C to 19 °C and 3 PSU to 18 PSU respectively.

All tagged Chinook were naturally produced (i.e. not spawned in a hatchery) and ranged from 60 mm to 116 mm fork length at the time of tagging. Previous studies have shown that PIT tagging has a minimal effect on survival, growth, and performance of salmonids this size and larger (Prentice et al. 1990b; Ombredane et al. 1998; Newby et al. 2007). Tag weight ranged from 0.8% to 5.4% of body weight (median 3%). Brown et al. (2007) detected no effect on growth or swimming speed of juvenile Chinook salmon implanted with transmitters between 3.1 and 10.7% body weight.

Detection Equipment and Data Collection

In 2004, the PIT tag detection system consisted of a single 24 volt FS-1001A transceiver (Digital Angel Corp.) powered by four 12V batteries, and connected to one antenna anchored in the tidal channel. A Palm[®] M130 handheld computer connected to the transceiver's serial port recorded time, date, and tag code information for each tag detection, and periodically logged the transceiver's current, phase, and noise level using the program FS1001 v1.1 (Oregon RFID, Portland OR).

In 2005, we replaced the FS-1001A transceiver with a newer model FS-1001M transceiver (Digital Angel Corp.). The FS-1001M was capable of multiplexing – operating up to six antennas by sequentially switching power to each antenna several times a second. To the new multiplexing transceiver we attached the same antenna

used in 2004 (antenna 1), and an additional antenna (antenna 2) anchored approximately 20m farther into the study channel (Figure 3.1). The two antennas enabled direction of fish movement to be determined via the time and date stamped tag detection data. The FS-1001M transceiver was capable of tuning the antenna fields dynamically (automatic tuning) to maximize tag read distance. This feature improved tag detection efficiency across tidally and seasonally variable water depth and salinity. During 2005, tag detection and transceiver diagnostic data were logged with a Dell™ Axim™ handheld computer using the program MiniMon v1.4 (Pacific States Marine Fisheries Commission).

During both years, the transceiver, batteries, and data logger were contained within a 1m x 1m x 0.5m stainless steel box anchored on the marsh surface above maximum high tide elevation. Batteries were exchanged weekly and recharged onshore.

Both antennas originally were designed and constructed by Digital Angel Corp., to detect PIT tagged adult fish passage at McNary Dam on the Columbia River (Muir et al. 2001). Each antenna consisted of a continuous length of 14 AWG Teflon coated wire wrapped 13 times into a 170cm x 64cm rectangular coil. A “shield” of 24 cm wide, 6mm thick sheet aluminum channel surrounded the exterior of the wire coil with approximately 10cm of open space between the shield and the coil on all sides. Both the antenna coil and aluminum shield were housed within an air-filled watertight housing of 18cm x 27cm fiberglass (antenna 1) or welded plastic (antenna 2) box channel. The inside dimension of these rectangular housings (i.e. the area fish passed

through to be detected) measured 50 cm x 157 cm (0.78 square meters) on each antenna. Laboratory testing using FS-1001 transceivers under RF noise conditions similar to the Salmon River study site indicated that these antennas detected model TX1411ST PIT tags when the transceiver current was as low as 1.9 amps.

We attached each antenna to two wooden posts driven into the marsh channel substrate, with the long axes of the antennas oriented vertically and located so that the antenna openings were centered on the thalweg of the tidal channel. Nets (0.5cm mesh) extended from the wooden posts to the shoreline both above and below the antennas to direct fish through the antenna openings (Figure 3.2).

In 2004, we operated the detector system from June 15 to July 10, and August 18 to October 21. We removed the nets in mid July to avoid interfering with an ongoing long-term fish trapping study in the study channel. In 2005, the detector operated continuously June 28 through September 12, except for five days when the transceiver shut down due to low battery power.

During 2004, we monitored water temperature at the detector site with a HOBO temperature logger (model H8, Onset Computer Corp.). In 2005, we monitored both water temperature and depth with a data logger positioned on the channel bottom between the two antennas (HOBO model U-20-001-01, Onset Computer Corp.). Salinity at the water surface and within the water column was recorded at least twice a week during both years using a handheld refractometer or electronic salinity meter (YSI, Inc.).



Figure 3.2. Antenna 1 installed in study channel at a moderately low tide.

Detection Efficiency

Periodically during high tides, we verified the ability of the detection system to recognize PIT tags by passing test tags taped to a stick through the center of each antenna. Twice in 2004 and five times in 2005, we also released groups of tagged salmon into the study channel above the detector system during high tides to test the efficiency with which the nets and antennas combined to detect tagged fish moving out of the study channel. Twenty-seven such “efficiency fish” were released in 2004 and 76 were released in 2005.

Efficiency testing was based on the assumption that all fish released above the antennas would leave the channel as it de-watered on the ebbing tide. Accordingly, we defined detection efficiency as the percentage of each group of efficiency fish detected on the first ebbing tide after release. Because efficiency fish released in 2005 must have passed antenna 2 to reach antenna 1, the efficiency with which antenna 2 detected fish *exiting* the study channel was defined as the percentage of efficiency fish detected on antenna 1 that were also detected on antenna 2. Similarly, fish that were tagged and released outside of the study channel (i.e. in the adjacent, higher-order reference channel, Figure 3.1), subsequently moved into the channel volitionally, and were detected on antenna 2 provided a means to evaluate the efficiency with which antenna 1 detected fish *entering* the study channel. We could not independently assess the efficiency with which antenna 2 detected incoming fish, but we have no reason to believe it would differ substantially from the outgoing efficiency.

RESULTS

Performance of Detection Equipment

Brackish water flooding increased the electrical load on antennas and caused transceiver current to vary tidally, decreasing as the amount of water in the channel increased (Figure 3.3). Transceiver current ranged from 2.4 amps to 6.2 amps but never dropped below the 1.9 amps threshold of tag detection, even when salinity was highest during late summer. Water depth accounted for a large proportion of the observed variation in current for each antenna (linear regression of transceiver current on water depth in 2005, $r^2=0.93$ for antenna 1, $r^2=0.70$ for antenna 2; $p<0.0001$). Test tags passed manually through the center of the antenna fields during high tides confirmed that both antennas maintained sufficient electromagnetic field strength to detect tags throughout the tidal cycle at surface water salinity as high as 29 PSU.

Detection rate of tagged “efficiency fish” exiting the channel ranged from 69% to 100% (mean 92%, Table 3.1). During the two tests with efficiencies lower than 90%, efficiency fish had been distributed particularly high in the study channel system, which may have reduced the likelihood of exiting the channel on the ebbing tide. Also, the large number of efficiency fish released on 30 June, 2005 may have resulted in “tag collision” a condition when two or more tags are in the detector field at the same time (Connolly et al. 2008), reducing detection efficiency. Antenna 1 also detected 89 of 92 individuals (97%) that were released outside of the study channel, subsequently entered the channel, and were detected on antenna 2. Following

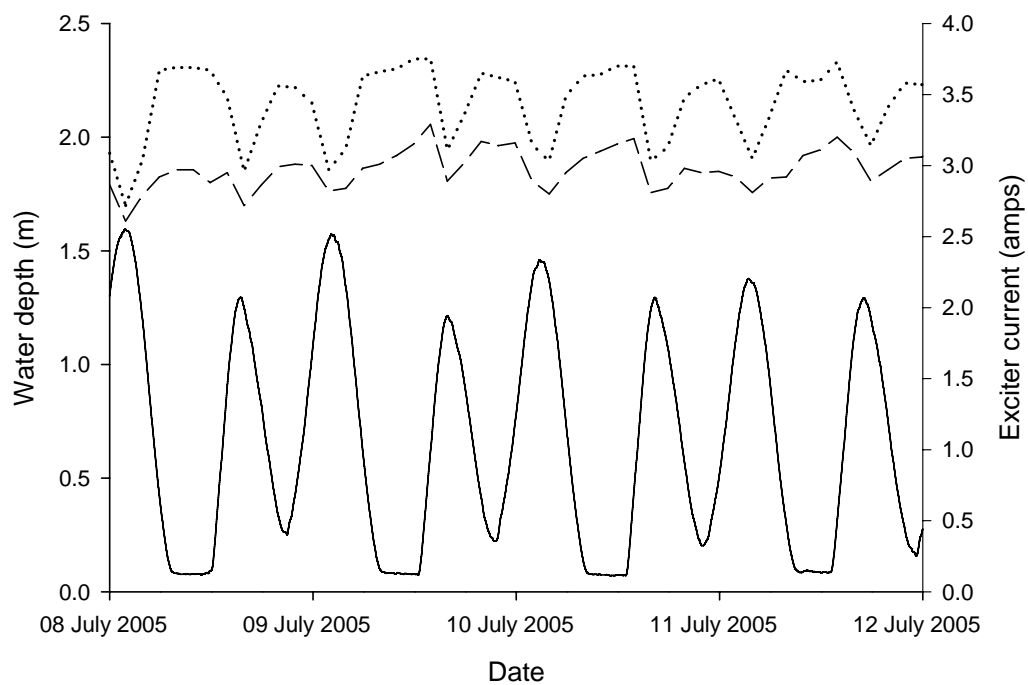


Figure 3.3. Exciter current of antenna 1 (dotted) and antenna 2 (dashed) during a typical series of tides indicated by water depth (black) during July 2005.

Table 3.1. Detection efficiency of tagged salmon released into study channel at high tide (i.e. efficiency fish).

Date	Number Released	Number Detected			Not Detected	Antenna 1	Antenna 2	Overall Efficiency
		Both Antennas	Ant 1 Only	Ant 2 Only				
18 Aug. 2004	13	na	9	na	4	69%	na	69%
16 Sep. 2004	14	na	14	na		100%	na	100%
30 Jun. 2005	31	13	8	5	5	68%	62%	84%
7 Jul. 2005	10	10				100%	100%	100%
13 Jul. 2005	12	11	1			100%	92%	100%
20 Jul. 2005	13	12			1	92%	100%	92%
1 Aug. 2005	10	9	1			100%	90%	100%
					mean	90%	89%	92%

efficiency tests, most efficiency fish (90%) returned to the study channel on subsequent tides (up to 32 days following release), and the system recorded a total of 91 and 224 detections of these fish in 2004 and 2005, respectively. Detections of efficiency fish were not used for other analyses of salmon movements or residence times

Detection of Tagged Salmon

In 2004 the PIT detector recorded 493 detections of 123 unique individual tagged salmon that moved into the study channel volitionally after being released elsewhere in the estuary. These individuals included 18% of Chinook salmon tagged and released in the reference marsh (Table 3.2). In 2005, the system recorded 369 detections of 75 unique fish, 15% of Chinook tagged in the reference marsh but outside the study channel.

During both years, the body size of salmon detected in the study channel was representative of the tagged population. Likelihood of detection and duration over which individuals used the study channel did not appear related to body size when tagged. Likelihood of detection in the study channel was greater for fish captured and tagged at sites above the confluence with the study channel than for those tagged and released below the confluence (Figure 3.4; G-test with Williams correction to compare fish tagged above and below the channel, $p=0.0014$ in 2004 and $p=0.0025$ in 2005).

Tagged fish were detected between five hours before and six hours after high slack tides. Frequency distributions of all detections for both years indicate that peak movement of tagged salmon through the antennas occurred roughly one to two hours

Table 3.2. Summary of Chinook salmon tagged and released in Salmon River estuary outside of the study channel and subsequently detected by PIT antenna during 2004 and 2005.

Year	Tagging Dates	Individuals Tagged	Total Detections	Individuals Detected	Percentage Detected	Time-At-Large	
						Median (days)	Maximum (days)
2004	18 May – 6 Jul.	697	493	123	18	16	128
2005	28 Jun. – 1 Aug.	572	369	75	15	9.5	48

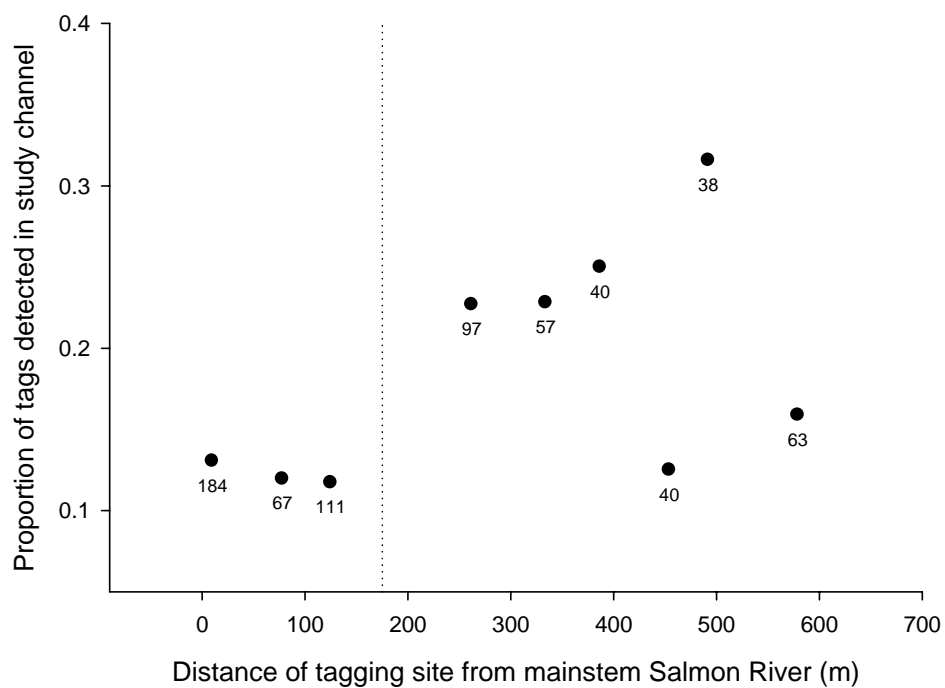


Figure 3.4. Proportion of individuals detected in the study channel after initial capture and release within the reference channel. Data are grouped by tagging site and arranged by distance of tagging site from the main-stem Salmon River (see Figure 1). Sample sizes of fish tagged are indicated for each site.

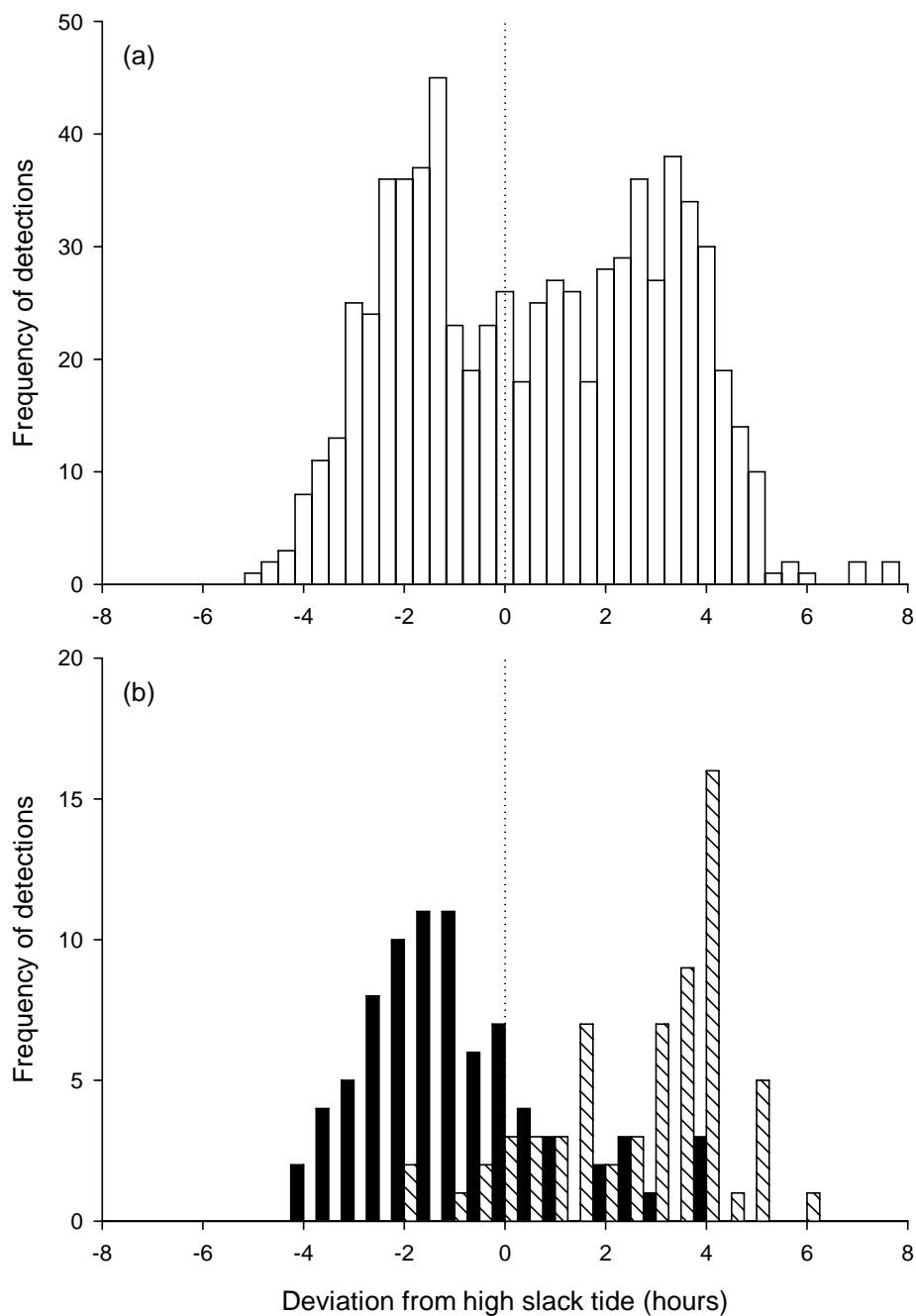


Figure 3.5. Frequency of all PIT tag detections at antenna 1 (a), and frequency of fish movements into (black bars) and out of (hashed bars) the study channel in 2005 (b), relative to the tidal cycle. Dotted lines indicate timing of high slack tide.

before and three to four hours after high slack tide (Figure 3.5a). Tagged salmon were detected during both daytime and nighttime tides. Of 862 total detections during both years, roughly half (449 or 52%) occurred between one hour before sunset and one hour after sunrise.

Among all detections at both antennas during 2005, median water depth was significantly shallower when fish were detected during ebb tides than during flood tides (median depth 0.75m vs. 0.95m, Wilcoxon rank sum test $p=0.0012$). Results from 2004, when we did not measure water depth directly, were qualitatively similar. Only 21 (6%) of the total detections in 2005 occurred when water depth was 0.4m or less, despite the fact that shallow depths made up the greatest proportion of depths recorded at the antenna site (Figure 3.6). Of these 21 detections, 17 (81%) occurred during low light conditions between one hour before sunset and one hour after sunrise.

Median water temperature at the bottom of the channel when fish were detected was 14.9°C (inter-quartile range 13.7 to 16.0°C) in 2004 and 16.4°C in 2005 (inter-quartile range 15.0 to 17.4°C) (Figure 3.7).

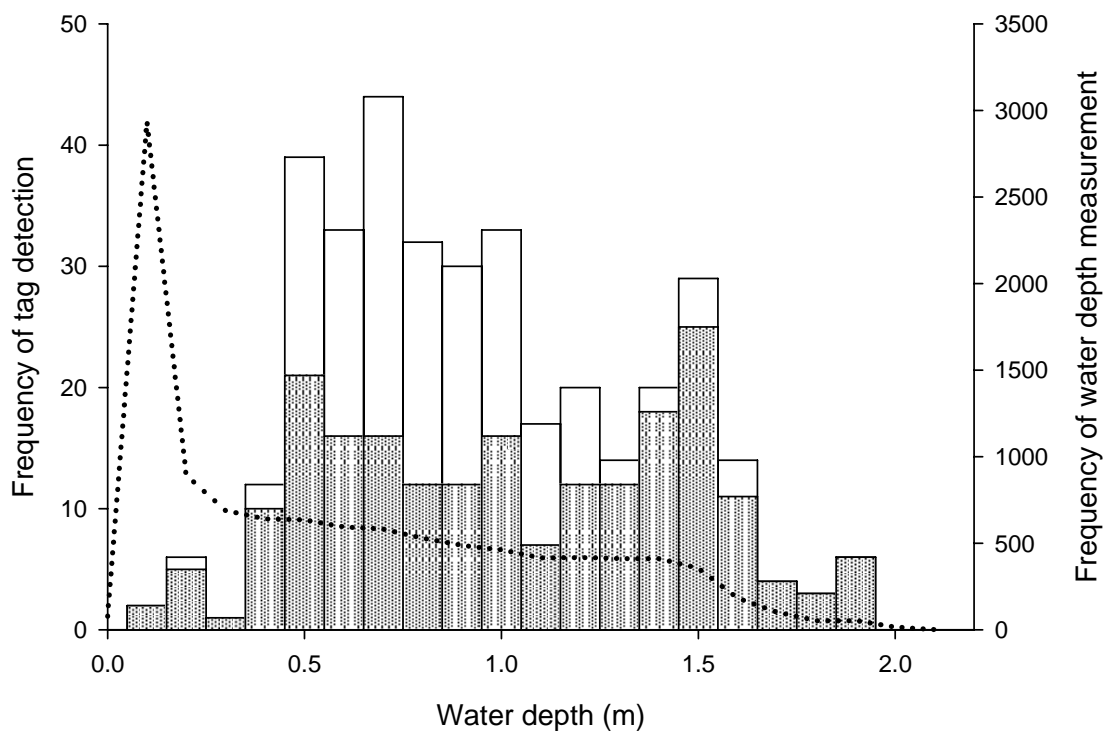


Figure 3.6. Frequency of PIT tag detections by water depth at the detector site in 2005. Shaded portion of bars represents detections that occurred during low light conditions. Dotted line indicates frequency of depth records during the period of time fish were detected (June 29 – September 13).

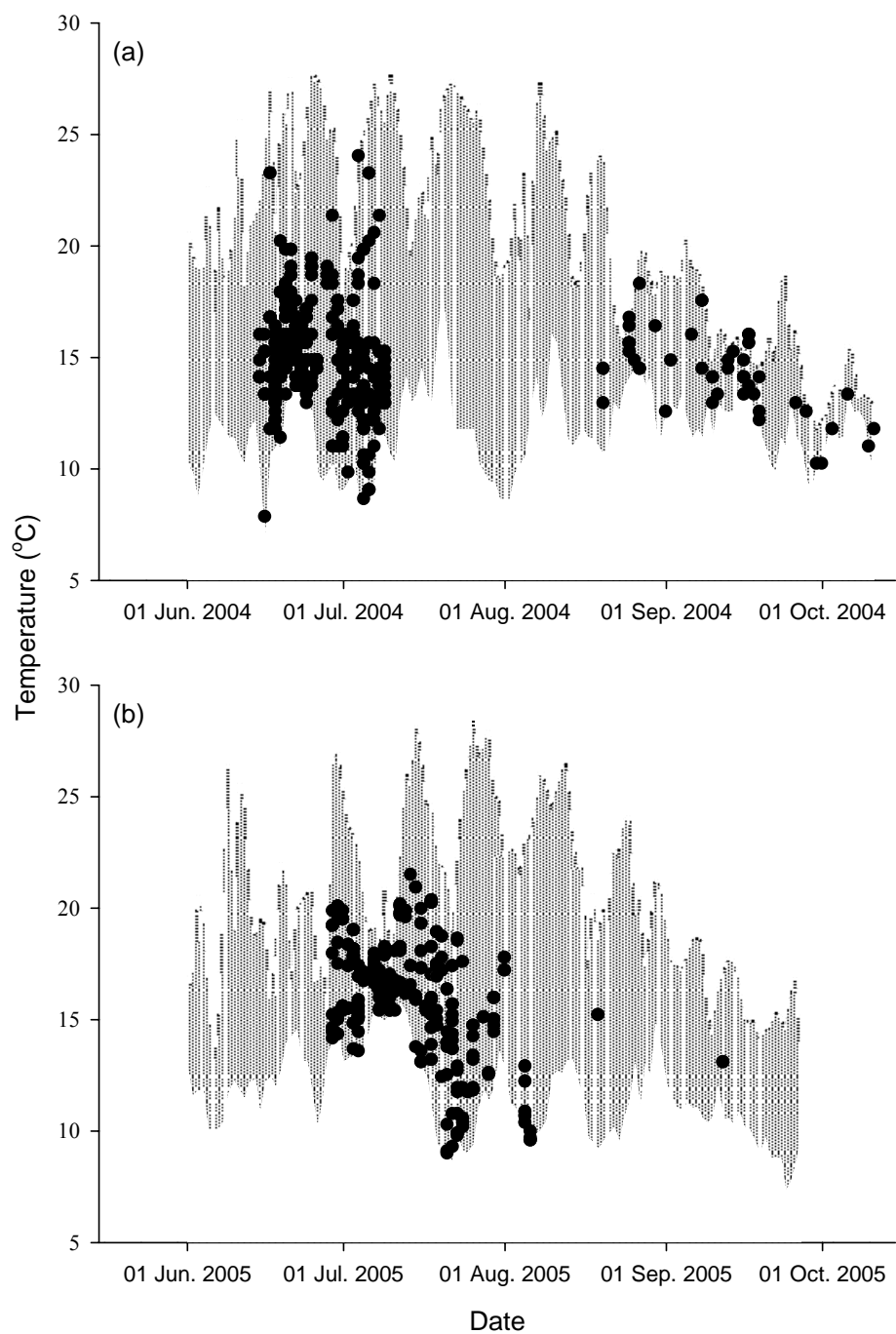


Figure 3.7. Water temperature at the bottom of the study channel when tagged fish were detected (black dots) and the range of water temperatures recorded over time.

Patterns of Movement and Residence Time of Individual Salmon

Most individuals recorded by the PIT tag detector were detected on few occasions – a median of two detections per fish – but several individuals were detected on multiple occasions, including single individuals that were detected up to 44 times in 2004 and 33 times in 2005. Most fish (~65% of those detected) occurred in the study channel during one or two tidal cycles within a few days of tagging and then did not enter the channel again (Figure 3.8a). Of the remaining fish, some individuals demonstrated fidelity to the study channel, entering and leaving the channel over multiple successive tidal cycles (as often as 22 tide cycles in 24 day period) (Figure 3.8b). Others were detected on two or more tide cycles separated by several days or weeks without detection, indicating they used the study channel only sporadically during a prolonged period of estuarine residence (Figure 3.8c).

The maximum time-at-large between initial tagging in the reference marsh and final detection in the study channel was 128 days in 2004 and 48 days in 2005. Median times-at-large were 16 and 9.5 days after tagging in 2004 and 2005 (Table 3.2).

Figure 3.8. (next page) Complete detection histories of three individual salmon demonstrate diverse patterns of marsh residence: Panel (a) shows a typical fish that used the channel on only one tidal cycle after being tagged on 6/28/05 (85mm, 7.3g when tagged). The individual in panel (b) was also tagged 6/28/05 (86mm, 7.3g) but showed fidelity to the study channel over several tidal cycles. Panel (c) demonstrates occasional use of the channel by one individual over several months during 2004 (tagged 6/7/2004 at 72mm, 4.3g). 'X' indicates detection on antenna 1 and 'O' indicates detection on antenna 2 (no antenna 2 in 2004). Solid line represents the tidal cycle as water depth at the study site (2005) or predicted tidal stage (2004). (Shaded area in panels (a) and (b) indicates a period 7/5/05 – 7/7/05 when the PIT detector was not operating.)

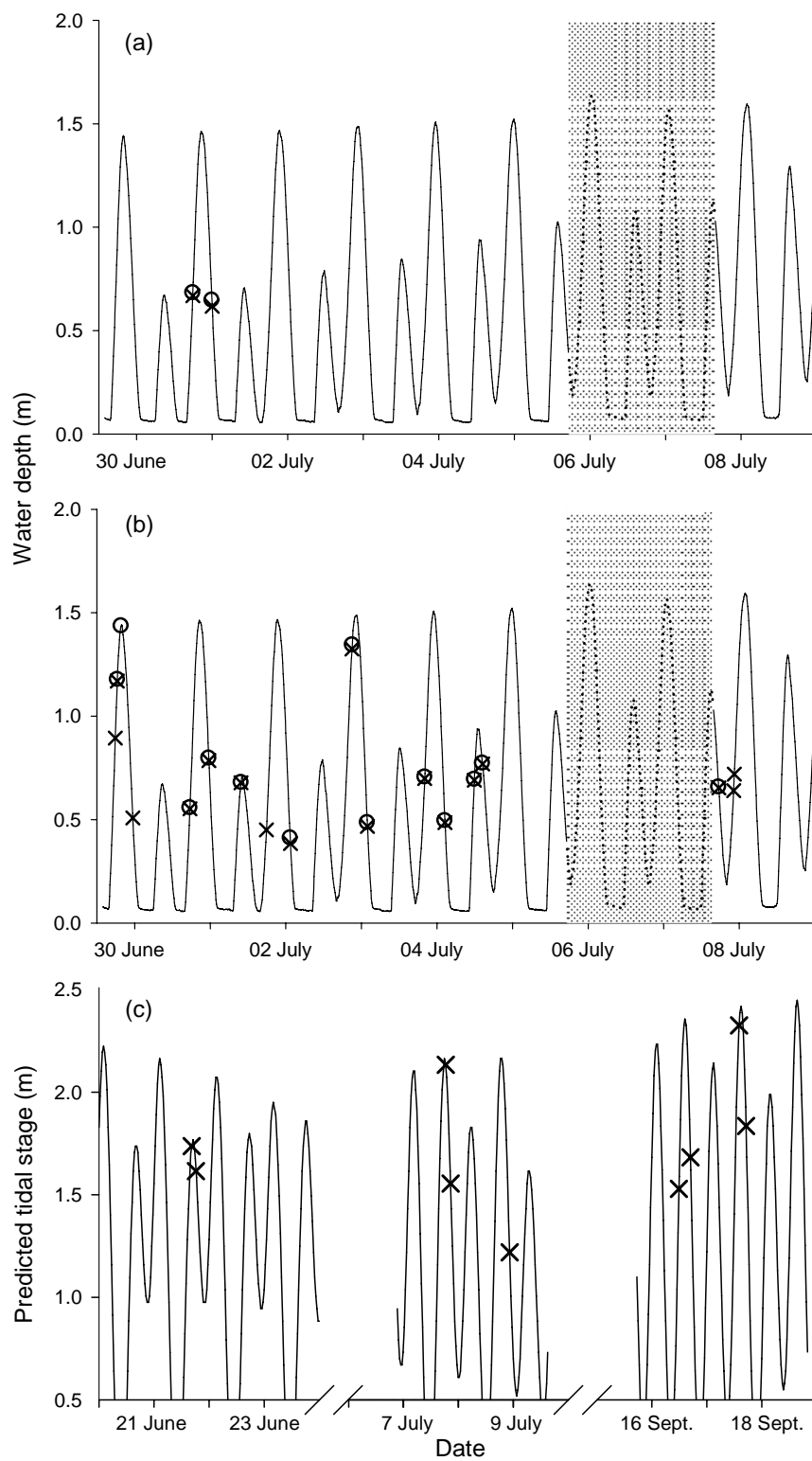


Figure 3.8.

Using individual detection data from both antennas in 2005, we defined 80 clear entrance movements (individuals detected successively on antenna 1 then antenna 2) and 65 clear exit movements (detected on antenna 2 then antenna 1; Figure 5b). Most fish moved in the direction of tidal currents: 80% entered during flooding tides and 92% exited on the ebb, 20% entered on the ebb, and 8% exited on the flood. The timing of entrance and exit movements was consistent with periods of peak tag detection before and after high slack tide. Several individuals did enter the channel against the ebbing tide, however, accounting for 20% of all entrance movements. Eight percent of exit movements occurred during flood tides.

On 57 occasions, individual fish exhibited clear entrance and exit movements during single tidal cycles. Based on these 57 observations (from 36 unique individual fish), the median individual residence time within the channel per tidal cycle was 4.9 hours (range 0.37 hours to 8.9 hours). Residence time showed a weak but significant positive association with tidal magnitude (linear regression of residence time on depth in the channel measured at high slack tide, $r^2 = 0.16$, $p = 0.002$). The longest observed residence times were associated with particularly high tides that occurred at night. On a given tidal cycle, individual fish tended to exit the channel when the water depth was equivalent to or shallower than the depth when they entered. The mean difference in depth between entrance and exit was 20cm (S.E. 5cm), and water depth at exit was significantly shallower than depth at entrance (t-test, one-sided $p = 0.0004$, $n = 57$).

DISCUSSION

Development of FDX PIT tag technology for the first time has allowed quantification of the fine-scale movements of small, individual fish within intertidal salt marsh habitat. By monitoring movements of PIT tagged subyearling Chinook salmon into and out of a tidal wetland channel, we determined that: (1) occupancy of marsh channel habitat was governed by active rather than passive movement behavior; (2) salmon used marsh channel habitat over a broad range of tidal conditions when water depth was greater than 0.4 meters; (3) individuals remained in the intertidal channel for an average of 4.9 hours and as long as 8.9 hours per tidal cycle; (4) salmon exhibited some fidelity to rearing sites within the estuarine marsh landscape, but also moved between marsh channel networks in the estuary; and (5) individuals within the population exhibited diverse patterns of residence in the study channel, ranging over periods of hours to months.

Juvenile salmon usually entered and departed the marsh channel in the direction of tidal currents, but peak movement occurred during mid- to late-flood tides (i.e. 1-2 h before high slack tide) and late during ebb tides (i.e. 3-4 h after high slack tide; Figures 6 and 11). Furthermore, 20% of individuals entered the channel against the ebbing tide, 8% exited against the flooding tide, and fish exited the channel at water depths that were on average 20 cm shallower than when they entered. We rarely detected fish movement when water was shallower than 0.4m. The asymmetry in movement about high slack water suggests that Chinook do not drift passively, but rather enter and remain in intertidal habitat until late in the tidal cycle.

Presumably, salmon behavior in tidal habitats is adapted to maximize foraging success while minimizing risk of predation and physiological stress (Craig and Crowder 2000; Rountree and Able 2007). Patterns of salmon residence in the study channel supported this hypothesis. Tagged fish avoided shallow water where avian predation, potential for stranding, and elevated water temperatures may pose increased risks of mortality during receding tides. Occasions when fish were detected in shallow water were usually periods of low light (Figure 7). Chinook are known to feed actively in Salmon River marsh channels on invertebrate taxa produced within the marsh (Gray et al. 2002). By remaining within the channel as the tide ebbs, individuals may maximize encounters with drifting invertebrate prey exported from the marsh channel network and concentrated during receding tides.

Few studies have examined the fine-scale timing of fish movement into and out of tidal marsh channels. Using trap nets set across marsh channels at high tides, Levy and Northcote (1982) found that Chinook salmon remained in marsh channels of the Fraser River estuary for several hours after high slack tide and exited channels later than other salmon species. “Transient” estuarine nekton (e.g. juvenile diadromous fish) entered an intertidal creek in South Carolina later than “resident” nekton species that complete their entire life cycles within estuaries (Bretsch and Allen 2006). Because Chinook salmon were the only species monitored with PIT tags in the present study, we cannot compare their movements with other members of the salt marsh fish community. Nonetheless, to the extent that PIT tagged Chinook salmon entered our study channel late during flood tides and remained for several hours after

high slack water, their behavior appeared consistent with results of the few previous investigations (Levy and Northcote 1982; Bretsch and Allen 2006).

Catch data from beach seine and purse seine sampling in the Columbia River estuary suggested that large subyearling Chinook salmon occupied deeper estuarine habitats than smaller individuals (McCabe et al. 1986), and beach seine sampling within the Salmon River reference marsh detected a slight, but statistically significant decrease in salmon body size with increased penetration into the channel network (D. Hering unpublished). Bretsch and Allen (2006) observed a positive relationship between body size and the water depth at which juvenile nekton entered intertidal marsh habitat. We did not detect a relationship between the body size of tagged Chinook salmon and the water depths when individuals entered the study channel, but the size range of tagged salmon may have been too small to detect such a pattern. Also, probability of detection in the study channel did not appear to be related to body size, although individuals >90mm fork length when tagged were rarely detected (Figure 2). Because fish were captured and tagged within the intertidal area of the estuary, our study population may have excluded larger salmon rearing in deeper estuarine habitats outside the marsh channel network.

Although Chinook that rear in the 1996 marsh must travel past the reference marsh network as they move downstream to the ocean, individuals tagged in the 1996 channel were detected in the study channel in a much lower proportion than those tagged in the reference marsh network (Table 2). This result implies that most fish tagged in the 1996 marsh did not spend time in the reference channel network or did

not penetrate far enough into the network to be detected in the study channel. The finding is consistent with conventional mark-recapture studies in Salmon River marshes that demonstrated fidelity of Chinook salmon to the channel network in which they were marked (Hering, in prep). It also suggests that subyearling Chinook salmon exhibit diverse scales of wetland use – some individuals used multiple wetland sites across the estuarine landscape and others demonstrated fidelity to local sites.

Individual salmon also may exhibit fidelity to rearing sites on a finer scale within intertidal channel networks. For example, some individuals used the study channel repeatedly on successive tides (Figure 10). Moreover, fish tagged in the reference marsh network above the confluence with the study channel were more likely to be detected than those tagged below the confluence (Figure 5). Presumably this was because fish in the upper portion of the marsh system again penetrated high into the channel network on subsequent tides. Although many individuals that were detected multiple times occurred in the study channel sporadically, it is unclear whether such fish were faithfully using another, unmonitored area within the reference network. Because the entire population of the intertidal channel network is concentrated within a limited number of subtidal refuge habitats in the main-stem estuary during low tide, some redistribution of individuals within the network likely occurs with each tidal cycle. Consequently, site fidelity may be weaker at fine spatial scales within the channel network than at the coarser scale between networks.

We are aware of no previous studies that have used *in situ* detection of PIT tags to monitor juvenile salmon in an estuarine salt marsh. The continuous, 24-hour-

per-day sampling frequency revealed potential limitations of conventional survey methods. For example, typical studies designed to quantify juvenile salmon abundance in marsh habitats have employed fixed trap nets set periodically across tidal channels at high slack tide and fished passively only during the tidal ebb (e.g. Levy and Northcote 1982; Shreffler et al. 1990; Miller and Simenstad 1997; Cornwell et al. 2001). The small but noteworthy proportion of tagged Chinook salmon we observed to enter the study channel during ebbing tides (Figure 11) would be excluded from a channel – and thus not included in abundance estimates – by the conventional trapping approach.

Most studies of marsh habitat use by estuarine nekton have sampled during daylight hours, which may greatly underestimate marsh channel use by animals that are more active or abundant at night (Rountree and Able 2007). Although we did not observe a substantial difference in the number of tagged salmon detected between night and day, the longest tidal residence times of individuals within the marsh occurred during nighttime tides (Figure 12). Passive, *in situ* tag monitoring did not require additional labor or expense to sample daytime and nighttime tides equally.

Most importantly, conventional survey methods that use fixed nets to sample periodically (e.g. daily, weekly, or monthly) may greatly underestimate wetland residency by individuals that occupy study sites infrequently over long time periods. Through continuous monitoring, our PIT tag methodology indicated for the first time that individuals may revisit the same small wetland channel intermittently over periods of weeks or months. Our approach was limited somewhat by the dimensions of the

PIT tag antennas available for this research, which required that we artificially narrow the study channel with nets. Improved, unshielded FDX PIT tag antennas measuring approximately 3m x 0.5m – about twice the detection area of the antenna used in the present study – since have been tested successfully in salinities up to 28 PSU (E. Prentice, unpublished). Moreover, the small shielded antennas that we used likely could detect smaller, 8mm-long FDX PIT tags that are now commercially available, potentially allowing monitoring of even smaller fish. These improvements and the ability to link multiple antennas to a single multiplexing transceiver offer considerable flexibility to span larger channels and to continually monitor the residency and movements of small fish in estuarine habitats.

Human development of coastal areas has altered dramatically many estuaries used by salmon (Boulé and Bierly 1987), and in some Oregon estuaries, as much as 80% of former tidal wetland area has become inaccessible to migratory fish due to diking, filling, and the installation of tide gates (Good 2000). Wetland restoration projects often attempt to recreate habitats that function equivalently to natural reference sites, and fish behaviors, including residence times and movement patterns, have been proposed as important measures of restoration success (Simenstad and Cordell 2000). The fact that tagged salmon occupied our intertidal study channel only when water reached a minimal depth affirms that restored channels intended as salmon rearing habitat must be designed to maintain sufficient depth during high tides for salmon access (perhaps greater than 0.4m). Although higher elevation tidal channels may support and export salmon prey to other areas of the estuary, they likely will not

be used by salmon directly. Based on the timing of movement we observed, tide-gates also are likely to inhibit salmon movement if they remain closed or alter tidal flow at any time during the period beginning roughly four hours before and ending roughly six hours after high tide. Thus, although many recent restoration efforts have modified tide-gates to improve passage of adult and juvenile fish (Giannico and Souder 2004), it is likely that any gate that functions to limit tidal flooding (the fundamental purpose of tide-gates) will negatively affect access to habitat by juvenile salmon. The small proportion of tagged fish that entered our channel during the ebbing tide, however, suggests that salmon may opportunistically access habitats above tide-gates if gates open early enough and remain open for a sufficient period during ebb tides.

Bottom et al. (2005b) provided evidence that restoration of marsh habitat in the Salmon River estuary has expanded expression of estuarine-rearing life histories within the contemporary Chinook salmon population. Juvenile Chinook now enter the ocean at a broader range of sizes and times compared with a period prior to marsh restoration. Such behavioral diversity may spread the risks posed by variable oceanic or climatic conditions and increase resilience of the salmon population. The individual-based approach in this study reveals on a fine scale the ways in which juvenile Chinook interact with and exploit intertidal wetland habitat and affirms a diversity of marsh rearing patterns are present in the estuary. The behavior of individuals on this finer scale is the mechanism that leads to the population-scale responses to restored habitat structure observed by Bottom et al. (2005b).

Preserving connectivity of intertidal marsh habitats with the estuary is critical to maintaining expression of behavioral diversity in estuarine rearing salmon. Future marsh rearing studies should incorporate multiple PIT detection sites to examine the patterns of habitat use by individuals across the estuarine landscape and the connections among habitats that support diverse salmon rearing and migration behaviors.

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CHAPTER 4: GENERAL CONCLUSION

During their anadromous life history, individual salmon may travel hundreds or thousands of kilometers through rivers, estuaries, and marine areas, and the physical habitats encountered form a template that has shaped the evolution of salmon life histories. The condition and connectivity of those habitats affect expression of alternative salmon life history strategies and the capacity of ecosystems to support salmon populations. Many populations of anadromous Pacific salmon have declined in abundance or have been extirpated during the past century, largely as a result of habitat degradation associated with human development of the landscape (Nehlsen et al. 1991). Accordingly, understanding the relationships between salmon and the full variety of specific habitats they occupy is essential to effective management, conservation, and recovery of remaining populations.

Because salmon use estuaries at a critical point in their life history – a period of transition between dramatically different freshwater and marine rearing environments and a time when juveniles must feed and grow to escape new sources of potentially size-dependent mortality in the ocean – the importance of estuarine habitats to salmon productivity and resilience may be disproportionately high relative to the small fraction of total life history spent in estuaries. Yet to date, our understanding of Pacific salmon ecology in estuaries is based on relatively few studies conducted in a small portion of the genus' range. Moreover, although biologists generally agree that estuarine wetlands are important habitats and that diversity is a key feature of salmon

populations, past studies rarely have linked growth or behavior of salmon to specific tidal wetland channels and even more rarely have quantified variation in these attributes among individual fish.

This thesis contributed to our understanding of estuarine rearing Chinook salmon by providing new information about the relationships of subyearling salmon and tidal wetlands, a habitat type that has suffered significant degradation from human land management practices over the past century. By coupling traditional capture methods (e.g. beach seining) with novel individual-based methods of marking and detecting fish (e.g. PIT tags and an *in situ* tag detector), I attempted to link the behavior and performance of fish to particular wetland habitats more specifically than had been done in past studies. Additionally, I sought to evaluate the effects of wetland restoration directly by comparing attributes of salmon living in a natural and a restored salt marsh.

The research presented in Chapter Two supports the idea that tidal wetlands are places where subyearling Chinook salmon reside and grow prior to entering the ocean, presumably increasing their probability of survival to adulthood. To my knowledge, the duration of marsh channel use by individual salmon documented here, up to 117 days, is the longest known residence time for Chinook salmon in a specific tidal marsh channel. Because individual salmon appeared to remain associated with either the reference marsh or the 1996 marsh between capture events, Chapter Two also provides direct measures of salmon growth that can be attributed to specific

wetland channels, thus quantifying the benefit that fish gained from these specific local habitats.

In addition to contributing descriptive information about wetland habitat use, Chapter Two presents a rare empirical test of the efficacy of marsh channel restoration and suggests that formerly diked wetlands can provide benefits for salmon that are approximately equivalent to natural sites. Many dike removal or other habitat restoration projects are undertaken without adequate time or funding to monitor the results of restoration actions for the species intended to benefit. The attributes I measured, growth and duration of channel residence, were intended to integrate the physiological and behavioral responses of fish to restored and natural marsh habitats. Based on these metrics alone, habitat quality appeared very similar in the two channels.

With the benefit of hindsight, it is apparent that additional metrics would help to fully evaluate equivalence of restored and reference marsh sites. For example, fewer fish appeared to use the 1996 marsh than the reference site, and this was probably related to physical characteristics of the marsh systems that limited their capacity to support salmon. Detailed physical measurements of the marsh channel networks have been prepared by colleagues from the University of Washington using a high resolution Global Positioning System but the analyses were not yet available to incorporate in this thesis. A comparison of channel metrics for the two marsh systems (e.g., sinuosity, amount of vegetative edge, width to depth ratio, etc.) could shed additional light on the factors affecting their relative salmon-rearing capacities. In

addition, I did not directly evaluate mortality of salmon in the two sites (though presumably higher mortality would be reflected by shorter average residence time). Although growth should be correlated with future survival and fecundity, I could not directly link use of the restored or natural channel with ultimate survival and fitness of individuals. The methods employed here can serve as a model for empirically evaluating function of other similar restored and natural wetlands, but by incorporating additional physical and biological parameters, future evaluations may better address the overall function of rearing habitats and the fitness benefits realized by juvenile salmon that use them.

Chapter Three demonstrated that *in situ* detection of full duplex PIT tags is feasible, at least on a small scale, in brackish estuarine channels. This methodological result alone is useful and should lead to increased understanding of estuarine fish behavior, but the paper also suggests some interesting biological conclusions. Importantly, salmon did not always move with tidal currents, indicating that occupying marsh channel habitat is an affirmative behavioral “choice.” The fact that salmon elected to spend energy by swimming against the current to remain in intertidal habitat implies an energetic benefit of marsh channel residence. Chapter Three also demonstrated that estuarine rearing behavior varies considerably among individuals within the population. Although I classified tidal movement patterns as exemplifying certain types, it is safe to say that no two tagged salmon moved through the PIT antenna in exactly the same way. Documenting this variety of rearing patterns

was a principal benefit of using PIT technology, as the effort required to collect similar information would have been prohibitive using conventional surveys.

Although I have emphasized the benefits of PIT tag technology in this thesis, there also were drawbacks to the method, including reduced sample sizes due to the time and expense of marking and a possibility that the marking method artificially depressed salmon growth rate over short recapture intervals. In part because I was interested in documenting variation, unique identification of individuals was important to me. If my goal had been only to quantify residence time or estimate abundance, however, a batch marking approach may have been preferable. I encourage investigators planning future salmon studies in estuaries to consider the costs and benefits of alternative marking techniques and choose a method suited to their objectives (Pine et al. 2003).

A particularly interesting result of both chapters was that individual salmon appeared to have high fidelity to intertidal channel networks and were very rarely detected in beach seine or PIT antenna “samples” outside the marsh where they were marked. I hesitate to make too much of this finding, as some tagged fish *were* detected in the reference channel after being first captured in the 1996 marsh upstream, but the low number of such fish in the sample suggests that this behavior may be rare. Because this pattern, if it exists, contradicts the intuitive assumption that salmon use available marsh habitats sequentially as they move seaward across the landscape, the topic begs further study. Landscape-scale patterns of habitat use could be documented further using methods similar to those described here but with a larger sample of fish

tagged at upriver sites. Or, future work might include experimental transplant of fish from one channel habitat to another to test strength of site fidelity.

Other topics for future study include identifying the cues that underlie variation in marsh residence time among individual salmon and the sources and rates of salmon mortality in marsh channel habitat. Do fish emigrate from marsh habitats only after reaching some threshold size, or is residence time affected by growth rate while rearing in the marsh (i.e. faster or slower growing individuals remain longer than others)? PIT technology may provide a tool to test for correlates of residence time among individual fish. Marsh residence time is defined by the sum effect of both emigration and mortality, but I did not attempt to partition these two processes. A better understanding of mortality within tidal wetlands would not only increase understanding of residence time but would shed light on the largely untested assumption that shallow estuarine habitats shelter juvenile salmon from predation.

Although these and many other questions about the ecology of salmon in estuaries remain to be addressed, I hope that this thesis has resolved some uncertainty and improved our ability to manage estuarine habitats for preservation of salmon. This work indicated that tidal wetland channels such as those in the Salmon River are productive rearing habitats for Chinook salmon and that some salmon spend considerable time in wetland habitats prior to entering the ocean. Not all salmon within Salmon River population used tidal wetlands in exactly the same way, and preserving such behavioral diversity should be a conservation goal. Lastly, restoring tidal inundation to previously diked wetlands appears to recreate functional rearing

habitat and add to the overall salmon rearing capacity of an estuary. Accordingly, restoration of estuarine marsh channels should be a high priority for conservation and recovery of ocean-type Chinook salmon.

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APPENDIX:

Duration of Estuarine Residence and Growth of Chinook Salmon Tagged in the Upper Estuary and Recaptured Near the Mouth of Salmon River

INTRODUCTION

Together with colleagues from the Oregon Department of Fish and Wildlife, I sampled with the beach seine at several sites in the lower Salmon River estuary during 2003, 2004, and 2005 as part of the ongoing Salmon River Estuary Study (Cornwell et al. 2001; Bottom et al. 2005b, Volk et al. in press). These surveys occasionally recaptured juvenile Chinook salmon tagged in marsh channel habitats upriver (Chapters Two and Three), providing additional information about their rates and sizes while migrating through the Salmon River estuary to the ocean (Bottom et al. 2005b, Volk et al. in press). This appendix summarizes all PIT tag recaptures in the lower estuary during 2003-05.

METHODS

Fish tagging techniques and locations are detailed in Chapters Two and Three. In total, we PIT tagged and released 198 Chinook in the reference marsh and 15 Chinook in the 1996 marsh during 2003, 697 Chinook in the reference marsh and 319 in the 1996 marsh channel during 2004, and 572 Chinook in or near the reference marsh during 2005.

We completed a total of 216 sample sets at six sites in the lower estuary below river kilometer (rkm) 2 during 2003-2005 (Table A1.1). We used the same beach seine (38m, 1.9cm stretch mesh in wings, 0.6cm stretch in center panel) and, in most cases, the same sampling protocol as described for the marsh studies in Chapter Two. The

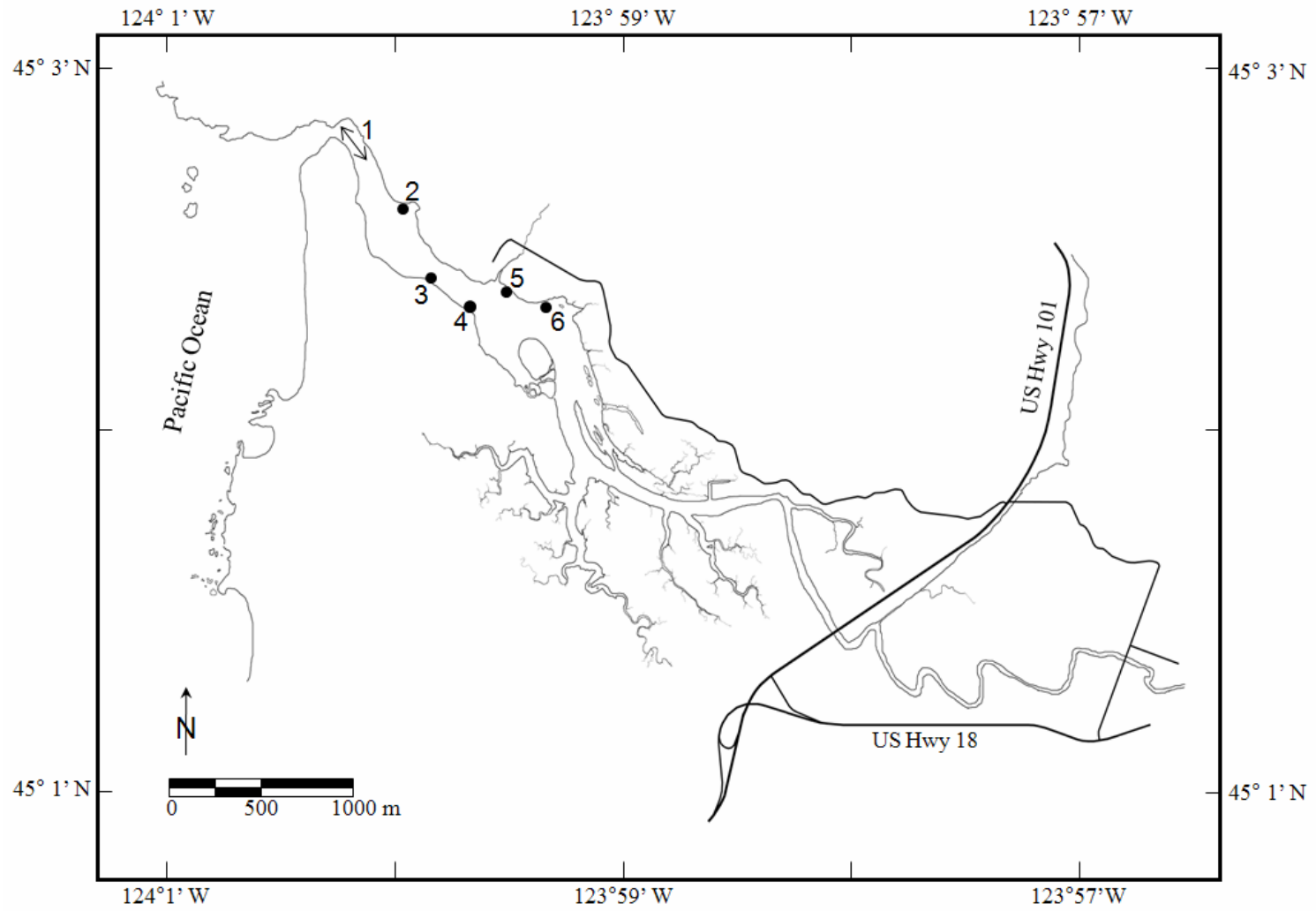


Figure A.1. Map of Salmon River estuary indicating location of beach seine sites in lower estuary, 2003-2005.

Table A.1. Beach seine samples collected in lower Salmon River estuary, 2003-2005. Site numbers refer to locations indicated in Figure A1.1. Exact location of site 1 varied among three sample sites (indicated as 1a, 1b, and 1c) based on weather and tide conditions.

Year	Site Number	Site Name	Dates	Number of Seine Sets	Total Chinook salmon
2003	1	Estuary Mouth	4/30 – 10/30	21	704
	2	Sitka Cove	1/23, 12/9	2	2
	3	Powerlines	2/6 – 11/13	14	169
	4	YWCA	1/23 – 10/23	4	45
	5	Crowley Creek	1/9 – 11/13	23	267
	6	Lighthouse Corner	1/9 – 12/1	55	1086
2004	1	Estuary Mouth	4/19 – 10/28	19	493
	2	Sitka Cove	4/19 – 10/28	3	3
	3	Powerlines	5/18 – 8/18	3	52
	4	YWCA	4/19 – 10/28	5	6
	5	Crowley Creek	1/13 – 4/19	6	34
	6	Lighthouse Corner	1/27 – 8/18	8	80
2005	1	Estuary Mouth	4/12 – 10/12	31	796
	2	Sitka Cove	10/12	2	2
	3	Powerlines	4/12 – 6/1	3	20
	4	YWCA	3/9 – 10/12	8	55
	5	Crowley Creek	8/23 – 10-12	4	55
	6	Lighthouse Corner	3/9 – 10/12	5	37

seine was deployed from a boat and pulled to shore by at least two people standing approximately 12m apart. However, at times tidal currents distorted the shape of the seine, or we dragged the seine along shore for up to one hundred meters to increase the sample area and total catch.

All Chinook salmon captured were counted and scanned for PIT tags using a handheld PIT tag reader. Tagged fish were measured, weighed, and sacrificed for otolith analysis.

RESULTS AND DISCUSSION

A total of 2273, 668, and 965 Chinook salmon were collected in 2003, 2004, and 2005, respectively (although some of these fish were captured before tagging began in the marsh channels each year, Table A1.1). This catch included 12 tagged salmon – two in 2003, five in 2004, and five in 2005. All lower estuary recaptures in 2003 and 2004 were collected at the “Lighthouse Corner” site (rkm 2), approximately 1.5 kilometers below the reference marsh channel. In 2005 we recaptured three tagged fish at the “Estuary Mouth” site (rkm 0.1) and two tagged fish at the site called “Crowley Creek” (rkm 1.6). In all three years, all tagged fish recaptured in the lower estuary were initially tagged and released in or near the reference marsh channel. None of the 334 salmon tagged in the 1996 marsh were recaptured in the lower estuary, but due to the low numbers of fish tagged and recaptured, the difference in

recapture proportion between the reference and 1996 marsh tagging sites was not statistically significantly (two tailed Z-test, $p=0.30$).

Among the seven fish captured at lighthouse in 2003 and 2004, median observed travel time between the reference marsh and lighthouse was 29 days (range 2 days to 41 days). In 2005 two fish were captured at Crowley Creek 15 and 49 days after tagging (mean 32 days), and three fish were captured at the estuary mouth 32, 56, and 62 days (mean 50 days) after tagging. Growth rate of the eleven fish recaptured more than 2 days after release ranged from 0.88% to 2.37% body weight·day⁻¹ with mean 1.73% and median 1.69 % body weight·day⁻¹ (Table A1.2).

Previous measurements of whole estuary residence time for Chinook salmon in Salmon River were calculated from cohorts of fish marked weekly with different colors of paint at a migrant trap near the head of tide (Bottom et al. 2005b) or back-calculated to the point of brackish water entry using otolith microchemistry (Volk et al. in press). The median estuarine residence time of fish marked and recaptured by Bottom et al. (2005b) was 35 days reported, but 20% of recaptured fish were in the estuary 63 days or more. Median estuarine residence based on otolith increments was 41.5 days (Volk et al. in press). The present results from recaptured PIT tagged salmon (median 33 days, range 2 to 62 days) correspond well with previously reported residence measurements, especially considering PIT tagged fish were marked in the reference marsh after they had already entered the estuary. The reference marsh is approximately four kilometers downstream of the marking location at head of tide used in previous studies (Bottom et al. 2005b) and presumably also some distance

closer to the ocean than the head of the saline estuary indicated by otolith microchemistry.

Table A.2. Partial capture history of individual Chinook salmon tagged in marsh channels and recaptured in lower estuary, 2003-2005. (Recapture events within upper estuary marsh habitats are not included.)

Year	Tag#	Date	Tagging/Capture Site	Length (mm)	Weight (g)	Absolute Growth (mm·day ⁻¹)	Time-at-Large (days)	Specific Growth (%·day ⁻¹)
2003	7882233	6/11/2003	Reference Marsh	74	4.6	0.54	28	2.13
		7/9/2003	Lighthouse	89	8.3			
	6555529	6/10/2003	Reference Marsh	77	4.9	0.41	29	1.48
		7/9/2003	Lighthouse	89	7.5			
2004	24351557	5/20/2004	Reference Marsh	68	3.4	0.32	41	1.48
		6/30/2004	Lighthouse	81	6.2			
	24408276	5/22/2004	Reference Marsh	61	2.2	0.41	39	2.02
		6/30/2004	Lighthouse	77	4.8			
	24414878	7/6/2004	Reference Marsh	76	4.7	0.35	20	1.48
		7/26/2004	Lighthouse	83	6.3			
	24439116	6/1/2004	Reference Marsh	72	3.8	0.42	33	1.87
		7/4/2004	Lighthouse	86	7			
	*24440509	7/2/2004	Reference Marsh	84	6.3	*-1	*2	*-0.80
		7/4/2004	Lighthouse	82	6.2			
2005	27992361	6/28/2005	Reference Marsh	74	5.9	0.61	49	1.64
		8/16/2005	Crowley Creek	104	13.1			
	28262616	6/28/2005	Reference Marsh	74	4.5	0.64	56	2.11
		8/23/2005	Estuary Mouth	110	14.5			
	27808911	6/30/2005	Reference Marsh	73	4.2	0.38	32	1.62
		8/1/2005	Estuary Mouth	85	6.9			
	28260458	8/1/2005	Reference Marsh	97	9.3	0.27	15	0.88
		8/16/2005	Crowley Creek	101	10.6			
	27985763	6/30/2005	Reference Marsh	72	4.1	0.69	62	2.37
		8/31/2005	Estuary Mouth	115	17.5			
Mean						0.46	34	1.73
Median						0.41	33	1.69

*Tag # 24440509 was excluded from growth analysis due to short recapture interval.

