

Survival of Puget Sound chinook salmon (*Oncorhynchus tshawytscha*) in response to climate-induced competition with pink salmon (*Oncorhynchus gorbuscha*)

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Abstract: We tested for competition between pink salmon (*Oncorhynchus gorbuscha*) and chinook salmon (*Oncorhynchus tshawytscha*) originating from rivers in the Puget Sound area using coded-wire-tagged subyearling hatchery chinook salmon. Following a 2-year life cycle, many juvenile pink salmon enter Puget Sound in even-numbered years, whereas few migrate during odd-numbered years. During 1984–1997, juvenile chinook salmon released during even-numbered years experienced 59% lower survival than those released during odd-numbered years, a trend consistent among 13 chinook salmon stocks. Lower even-numbered-year survival of chinook salmon was associated with reduced first-year growth and survival and delayed maturation. In contrast, chinook salmon released into coastal streams, where few pink salmon occur, did not exhibit an alternating-year pattern of survival, suggesting that the interaction occurred within Puget Sound and the lower Strait of Georgia. Unexpectedly, the survival pattern of Puget Sound chinook salmon was reversed prior to the 1982–1983 El Niño: chinook salmon survival was higher when they migrated with juvenile pink salmon during 1972–1983. We hypothesize that chinook salmon survival changed as a result of a shift from predation- to competition-based mortality in response to recent declines in predator and prey abundances and increases in pink salmon abundance. Alternating-year mortality accounted for most of the 50% decline in marine survival of chinook salmon between 1972–1983 and 1984–1997.

Résumé : Nous avons évalué la compétition entre les saumons quinnat (*Oncorhynchus tshawytscha*) et les saumons roses (*Oncorhynchus gorbuscha*) provenant des rivières de la région du Puget Sound en utilisant des saumons quinnat de pisciculture âgés de moins d'un an et marqués avec des fils de fer codés. Après 2 ans de leur cycle, de nombreux jeunes saumons roses se déplacent vers le Puget Sound les années paires, mais peu le font les années impaires. En 1984–1997, les jeunes saumons quinnat relâchés durant les années paires ont connu une survie de 59 % inférieure à ceux qui ont été relâchés les années impaires et la tendance s'est maintenue dans 13 stocks de saumons quinnat. La survie réduite les années paires est associée avec une diminution de la croissance et de la survie la première année et une maturation retardée. En revanche, les saumons quinnat relâchés dans les cours d'eau côtiers, où il y a peu de saumons roses, n'ont pas expérimenté cette alternance d'une année à l'autre dans la survie, ce qui laisse croire que l'interaction se produit dans le Puget Sound ou le détroit de Géorgie inférieur. De façon inattendue, le pattern de survie des saumons quinnat de Puget Sound a été inversé avant l'El Niño de 1982–1983, alors que leur survie était plus élevée lorsqu'ils migraient en compagnie des saumons roses en 1972–1983. Notre hypothèse veut que la survie des saumons quinnat ait changé d'un contrôle de la mortalité par la prédation à un contrôle par la compétition en réaction au déclin récent des abondances de prédateurs et de proies et l'augmentation de l'abondance des saumons roses. La mortalité à tous les deux ans explique la plus grande partie du déclin de la survie en mer des saumons quinnat entre les périodes 1972–1983 et 1984–1997.

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Introduction

Competition is recognized as an important factor affecting growth of Pacific salmon (*Oncorhynchus* spp.) in marine waters. Density-dependent growth has been observed among salmon during early marine life (Peterman 1984) and home-

ward migration (Rogers and Ruggerone 1993). Salmon originating from different regions or continents may intermingle in the North Pacific Ocean and compete for prey, leading to a reduction in growth (McKinnell 1995; Ruggerone et al. 2003). Competition for resources may also occur between species of salmon. For example, competition with pink

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salmon (*O. gorbuscha*) has led to reduced growth of sockeye salmon (*O. nerka*) (Bugaev et al. 2001; Ruggerone et al. 2003), coho salmon (*O. kisutch*) (Ogura et al. 1991), and chinook salmon (*O. tshawytscha*) (Grachev 1967), and has altered the diet (Tadokoro et al. 1996) and distribution of chum salmon (*O. keta*) on the high seas (Azumaya and Ishida 2000).

Few studies have demonstrated the effect of competition at sea on survival of salmon, although reduced growth is believed to lead to greater predation risk (Parker 1971) and to greater mortality during winter (Nasagawa 2000; Beamish and Mahnken 2001). Ruggerone et al. (2003) documented reduced growth and reduced smolt-to-adult survival of Bristol Bay sockeye salmon that co-inhabit offshore waters with abundant Asian pink salmon in odd-numbered years. In Puget Sound and British Columbia, competition between pink salmon and chum salmon was believed to reduce survival of chum salmon (Gallagher 1979; Beacham 1993; Fresh 1997). Furthermore, the unique abundance-at-age of adult Puget Sound chum salmon, which alternates between even- and odd-numbered years and therefore minimizes interactions with abundant juvenile pink salmon in even-numbered years, was believed to be an evolutionary response to competition during early marine life (Smoker 1984; Salo 1991). Recently, Levin et al. (2001) suggested that competition with hatchery-produced chinook salmon may lead to reduced survival of native Snake River spring/summer-run chinook salmon during years of low ocean productivity.

Pink salmon, which are the most abundant Pacific salmon and the youngest at maturation, often appear to be the dominant salmonid involved in competitive interspecies interactions. Pink salmon tend to feed at a lower trophic level than other salmonids at sea and to have the least direct diet overlap with chinook salmon, which tend to feed at a higher trophic level (Welch and Parsons 1993). Few studies have examined competition between pink salmon and chinook salmon, the largest and oldest anadromous salmonid at maturation. However, Grachev (1967) reported that scale growth of Kamchatka chinook salmon during the first 2 years at sea was inversely related to pink salmon abundance, suggesting that these two species may compete for prey, either directly or indirectly through the food web.

In Puget Sound, Washington, nearly all juvenile pink salmon migrate to sea during even-numbered years and return to spawn during the following odd-numbered year. The invariable 2-year life cycle of pink salmon and the distinct odd-year adult-return pattern provide a unique opportunity to evaluate competition by comparing release-to-recovery survival rates of subyearling chinook salmon during odd- versus even-numbered years. We hypothesized that survival of chinook salmon would be lower among fish entering Puget Sound during even-numbered years, i.e., years when juvenile pink salmon are abundant. Competition for prey might be relatively great within Puget Sound and the lower Strait of Georgia, where chinook and pink salmon densities are relatively high. We also examined potential competition effects on length at age and age composition of chinook salmon. A reduction in length or a shift to older fish at maturation during years of high pink salmon abundance would be consistent with the competition hypothesis, since reduced growth at sea tends to lead to older ages at maturation in salmon

(Helle 1979; Rogers 1987; Healey 1991). Additionally, we were interested in determining whether competitive interactions have increased in recent years in response to climatic and oceanographic changes and the apparent reduction of prey in the Strait of Georgia and the Puget Sound region (Beamish et al. 2000, 2001). It is especially important to identify and quantify factors affecting Puget Sound chinook salmon, since naturally produced chinook salmon and some hatchery stocks are listed as threatened species under the US Endangered Species Act (National Marine Fisheries Service 1999).

Methods

The competition hypothesis was tested by comparing release-to-recovery survival rates of subyearling chinook salmon originating from 10 Puget Sound hatcheries and 3 Fraser River / lower mainland British Columbia hatcheries. During even-numbered years, chinook salmon released from these hatcheries follow numerous juvenile pink salmon of primarily natural origin into marine waters, whereas in odd-numbered years almost no juvenile pink salmon are present. Both species rear in Puget Sound and the Strait of Georgia before migrating primarily through the Strait of Juan de Fuca before entering the North Pacific Ocean. The distinct odd/even-year abundance pattern of Puget Sound and Fraser River pink salmon provided a natural experimental control to test the competition hypothesis. Furthermore, almost no pink salmon originate from coastal Washington and lower Vancouver Island, therefore chinook salmon releases from nine hatcheries in these areas were examined to evaluate whether stocks that rear largely outside Puget Sound and the Strait of Georgia were similarly influenced. If pink salmon influence the population characteristics of chinook salmon only within the confines of Puget Sound and the Strait of Georgia, we would expect to see an alternating pattern among chinook salmon from Puget Sound and the lower mainland but not among those from coastal Washington and lower Vancouver Island.

Survival of chinook salmon was estimated from the release and recovery of hatchery fish receiving implanted coded wire tags (CWTs). The CWT is a small wire (0.25 mm × 1 mm) containing a binary code that links the recovered salmon to the specific release location, release date, age at release, and other relevant information. Groups of more than 100 000 juvenile salmon can be injected with a tag containing an identifying code prior to release, but the percentage of hatchery-produced chinook salmon receiving a CWT is typically 6% or less. All fish receiving CWTs in this study were marked by removing the adipose fin so that fishery observers could readily detect CWT fish in the fisheries. Recovery of CWT fish in fisheries is achieved by initially identifying fish with a missing adipose fin, scanning the selected fish for the presence of a CWT using a magnetic field detector, then surgically removing it from the snout of the fish at the laboratory. At least 20% of the salmon catch in each commercial salmon fishery is examined for CWT fish (Johnson 1990). Sampling of sport fisheries may be somewhat less than 20% and most fish returning to the hatcheries are sampled for CWTs. Counts of CWT salmon recovered in fisheries or hatcheries are expanded by the agencies using

the percentage of total fish sampled for CWTs in each fishery and time period. The CWT data are collected and checked by state, provincial, federal, and tribal agencies before delivery to the Pacific States Marine Fisheries Commission, where the data are validated for format consistency and stored (Johnson 1990).

The CWT release and recovery data were obtained from the Regional Mark Information System database, which is maintained by the Pacific States Marine Fisheries Commission (Pacific States Marine Fisheries Commission 2003). The database was first queried for tag codes representing groups of chinook salmon released into streams feeding into the study area. These tag codes were then used to query the database for daily recoveries of each tag code in each recovery location. The period of investigation began with releases in 1972 and ended with releases in 1997, since recoveries after this period were incomplete. Survival indices were based on the release of 53.5 million CWT chinook salmon from hatcheries within the study area (Table 1).

Several restrictions were applied in selecting CWT data in order to eliminate potential bias from unusual tag groups. The analysis was limited to chinook salmon released as sub-yearlings into fresh water during April through July. The analysis excluded tag groups having body weights exceeding 2 standard deviations above or below the mean. Returning hatchery-produced salmon recovered on stream spawning grounds were excluded from the analysis because sampling of streams for CWT fish was not consistent throughout the time period.

The survival rates reported here are indices of survival based on the recovery-to-release ratio for each tag code, where recoveries occurred across multiple years and among fish ranging from age 1 to age 6:

$$(1) \quad \text{Survival index} = \sum_{\text{age } 1}^{\text{age } 6} (\text{recoveries})(\text{juvenile release})^{-1}$$

When a hatchery used more than one tag code in a release year, the survival rates were weighted by the number of fish released, then averaged. Some fish recovered in fisheries may not have been maturing in the year of capture, thus the survival rates reported here overestimate release-to-adult survival to the extent that immature fish were recovered that would have died. However, the survival indices underestimate survival of some stocks (all British Columbia stocks and Stillaguamish and Tulalip Bay stocks in Puget Sound) because hatcheries in these watersheds do not recover most returning adult salmon. Fisheries implementing catch and release may also cause underestimation of survival to recovery, since this mortality is largely unreported. The survival index largely reflects mortality in marine waters, but it also reflects some mortality in fresh water (Pacific Salmon Commission 2001).

Age of recovered fish was based on the difference between the recovery year and the parent spawning year; thus, fish spending one winter at sea were classified as age 2. Age-specific recovery rates, or partial survival rates, were calculated from age-specific recoveries and total fish released:

$$(2) \quad \text{Age-specific recovery rate} = \sum_{\text{age } x}^{\text{age } y} (\text{recoveries})(\text{juvenile release})^{-1}$$

Age composition of returning salmon was calculated for the cohort of salmon released each year from each watershed. Since most chinook in the study area return to spawn at ages 3 and 4, the percentage of recovered fish older than 3 was used to test for a shift in age composition. Most CWT chinook salmon recovered at hatcheries are measured (fork length) by hatchery personnel. Hatchery data were used to compare age-specific lengths of fish released during odd-versus even-numbered years.

Virtual population analysis (VPA; Hilborn and Walters 1992; Coronado and Hilborn 1998) was used to reconstruct survival of odd- versus even-year-release cohorts at age 2 in an effort to identify mortality associated with delayed maturation. VPA provides an estimate of the number of chinook salmon surviving to a given age after the effects of delayed and early maturation are removed. The total number of salmon alive at age 2 (N^*), including those captured or escaped to hatcheries at ages other than 2, was calculated with the following equation:

$$(3) \quad N^* = C_1 s_1 + C_2 + C_3 / s_3 + C_4 / s_3 s_4 + C_5 / s_3 s_4 s_5 + C_6 / s_3 s_4 s_5 s_6$$

where C_t is the number of fish of a given tag group recovered at age t , and s_t is the survival rate from age $t - 1$ to age t . Age-specific natural mortality rates, which are assumed by VPA to be constant from year to year, were obtained from the Pacific Salmon Commission (2001). N^* was then substituted for recoveries in survival index (eq. 1).

The potential effect of pink salmon on chinook salmon was tested by comparing survival rates, lengths at age, and age composition depending on whether the juvenile chinook salmon were released during an odd- or even-numbered year. Survival rates and age-composition proportions were normalized using the arcsine transformation prior to statistical analysis, then retransformed when reported in the text. A two-factor Type I analysis of variance (ANOVA) was used to test for statistical differences in survival, length at age, and age composition. The two factors were year of chinook salmon release (odd- or even-numbered year) and stock. Multivariate time series analysis of these data was not possible because stock-specific data were not available for all years.

The analysis of differential survival rates of chinook salmon resulting from odd- versus even-numbered-year releases was based on the premise that pink salmon fisheries, whose season can overlap with the presence of chinook salmon, would not artificially create or mask the underlying pattern of survival. The presence of pink salmon fisheries may lead to longer fishing seasons and potentially greater harvest of CWT chinook salmon in odd-numbered years, leading to an alternating year pattern of recoveries and potential bias. To test for a potential fisheries-related bias, exploitation rates of chinook salmon released from Puget Sound hatcheries during odd- and even-numbered years were compared during recent and early time periods. During 1984–1997, chinook salmon released into the Stillaguamish

Table 1. Number of years and average annual release of coded-wire-tagged (CWT) subyearling chinook salmon (*Oncorhynchus tshawytscha*) by stock and time period.

| Stock | Subarea | 1972–1983 | | | 1984–1997 | | |
|-------------------------------|-----------------|--------------|--------------------------|--------------------|--------------|--------------------------|--------------------|
| | | No. of years | No. of CWT fish per year | Average weight (g) | No. of years | No. of CWT fish per year | Average weight (g) |
| Puget Sound | | | | | | | |
| Duwamish | Mid-Sound | 10 | 170 029 | 4.2 | 12 | 246 780 | 5.9 |
| Grover | Mid-Sound | 0 | 0 | | 13 | 171 134 | 7.7 |
| Lake Washington | Mid-Sound | 5 | 192 375 | 5.6 | 3 | 196 029 | 4.8 |
| Minter | South Sound | 0 | 0 | | 10 | 206 778 | 8.3 |
| Nisqually | South Sound | 4 | 42 500 | 5.2 | 14 | 209 292 | 8.5 |
| Nooksack | North Sound | 9 | 77 120 | 5.2 | 9 | 288 285 | 5.6 |
| Sammish | North Sound | 4 | 173 139 | 4.1 | 12 | 202 742 | 5.0 |
| Skagit | North Sound | 2 | 105 342 | 3.4 | 6 | 197 942 | 6.4 |
| Stillaguamish | Mid-Sound | 0 | 0 | | 10 | 112 653 | 5.6 |
| Tulalip | Mid-Sound | 0 | 0 | | 5 | 180 524 | 5.0 |
| Coastal Washington | | | | | | | |
| Quinalt | Middle | 8 | 87 612 | 11.4 | 11 | 182 865 | 10.5 |
| Humtulpis | Middle | 0 | 0 | | 6 | 190 255 | 6.4 |
| Queets | Middle | 6 | 64 269 | 10.7 | 13 | 148 892 | 12.0 |
| Sooes | North | 0 | 0 | | 10 | 183 579 | 6.1 |
| Willapa | South | 3 | 211 337 | 5.5 | 6 | 321 508 | 5.7 |
| Lower British Columbia | | | | | | | |
| Chehalis | Lower Fraser R. | 0 | 0 | | 14 | 143 362 | 2.5 |
| Chilliwack | Lower Fraser R. | 2 | 104 877 | 6.1 | 14 | 124 233 | 6.4 |
| Capilano | Lower Mainland | 10 | 179 042 | 5.7 | 14 | 116 928 | 6.7 |
| Chemainus | SE Vancouver I. | 4 | 87 833 | 7.3 | 11 | 74 775 | 8.8 |
| Cowichan | SE Vancouver I. | 2 | 38 109 | 2.7 | 10 | 105 266 | 5.3 |
| Qualicum | SE Vancouver I. | 12 | 123 762 | 6.4 | 14 | 218 842 | 6.5 |
| Robertson | SW Vancouver I. | 10 | 162 722 | 5.0 | 14 | 261 806 | 5.9 |

River and Tulalip Bay were excluded from this analysis because the hatcheries did not attempt to recover fish. Exploitation rates for each stock were calculated as follows:

$$(4) \quad \text{Exploitation rate} = \sum_{\text{age}1}^{\text{age}6} (\text{fisheries recoveries}) (\text{total recoveries})^{-1}$$

Trends in pink salmon abundance since the early 1970s were examined in relation to chinook salmon survival and abundance. Pink salmon harvest and spawning escapement data for Puget Sound, Fraser River, and southern Vancouver Island were obtained from the Washington Department of Fish and Wildlife (J. Packer, 600 Capitol Way North, Olympia, WA 98502, USA, personal communication), Fisheries and Oceans Canada (L. Hop Wo, 3225 Stephenson Point Road, Nanaimo, BC V9T 1K3, personal communication), and the Pacific Salmon Commission (B. White, 600 – 1155 Robson Street, Vancouver, BC V6E 1B5, personal communication).

Results

Time-trend analysis

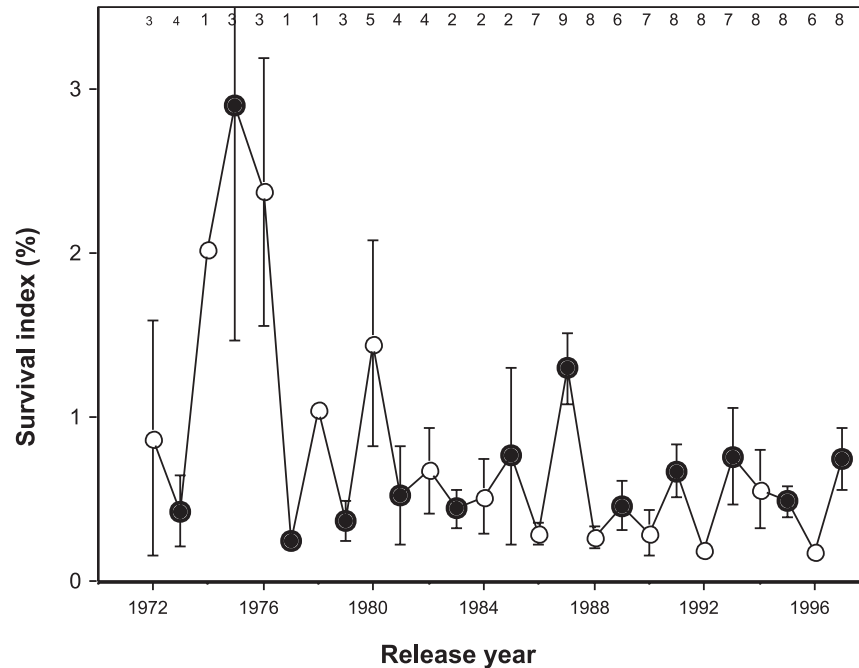
Analysis of release-to-recovery survival estimates during 1972–1997 revealed that the pattern of survival from odd- and even-numbered-year releases of subyearling Puget Sound

chinook salmon switched in the early 1980s, corresponding to the 1982–1983 El Niño event. During release years 1984–1997, survival of even-numbered-year releases of chinook salmon was consistently lower than that of odd-numbered-year releases, whereas during 1972–1983, survival of even-numbered-year releases tended to be relatively high (Fig. 1). Survival during 1984–1997 tended to be lower than during 1972–1983, a pattern that was opposite to that of adult pink salmon abundance (see below). Within the early period, salmon survival was exceptionally high during 1974–1976, years that immediately preceded the shift in the Pacific Interdecadal Oscillation Index (Mantua et al. 1997). More years of CWT data and numbers of tagged fish released per year were available during 1984–1997 than during the earlier period (Table 1), therefore the statistical power of tests was greater for the recent period. Thus, subsequent analyses of survival, size at age, and age composition were analyzed by period of release: 1972–1983 and 1984–1997.

Fishery exploitation rates

Rates of exploitation of chinook salmon were examined to test for potential bias influenced by pink salmon fisheries, which occur in odd-numbered years. During release years 1984–1997 (two-factor ANOVA, $F_{[1,64]} = 0.879$, $P = 0.352$) and 1972–1983 ($F_{[1,533]} = 0.533$, $P = 0.475$), exploitation rates of chinook salmon did not differ by odd and even year of release, indicating that survival estimates were not biased

Fig. 1. Survival index for subyearling chinook salmon (*Oncorhynchus tshawytscha*) released into Puget Sound streams during 1972–1997. Survival values during even- (○) and odd-numbered (●) years are shown. Values are unweighted means (± 1 standard error) of one or more stocks. The number of contributing stocks each year is shown at the top.



by the fisheries. This observation is further supported by the age-specific recovery-rate estimates described below. Exploitation rates were not influenced by potential interaction between odd/even year and stock during either period ($P > 0.50$).

Pink salmon abundance

Juvenile Puget Sound pink salmon migrate to sea during even-numbered years and return to spawn during odd-numbered years. Exceptionally few adult pink salmon return during even-numbered years, averaging less than 1% of odd-year abundances. Odd-numbered-year returns of adult pink salmon corresponding to juvenile migration years 1984–1996 averaged 1.34 million fish (± 0.22 million fish (standard error, SE)) and were approximately 80% greater than returns corresponding to 1972–1982 juvenile migration (Fig. 2). Most pink salmon return to northern Puget Sound rivers such as the Skagit and Snohomish. Both run size ($F_{[1,11]} = 5.232$, $P = 0.043$) and spawning escapement ($F_{[1,11]} = 9.094$, $P = 0.012$) were significantly greater during 1984–1997 than in the earlier period. The corresponding production of pink salmon fry entering the relatively confined waters of Puget Sound was approximately 43 million per even-numbered year during 1984–1997 and 24 million during 1972–1983, assuming 3.1% survival at sea (International Pacific Salmon Fisheries Commission 1986; Heard 1991).

The Fraser River is a major producer of pink salmon and, like Puget Sound, primarily produces juvenile pink salmon that migrate to sea during even-numbered years and return to spawn during odd-numbered years. During smolt years 1984–1997, odd-numbered-year returns of Fraser River pink salmon averaged 14.7 million (± 2.1 million (SE)) and were approximately 29% greater than returns during 1972–1983

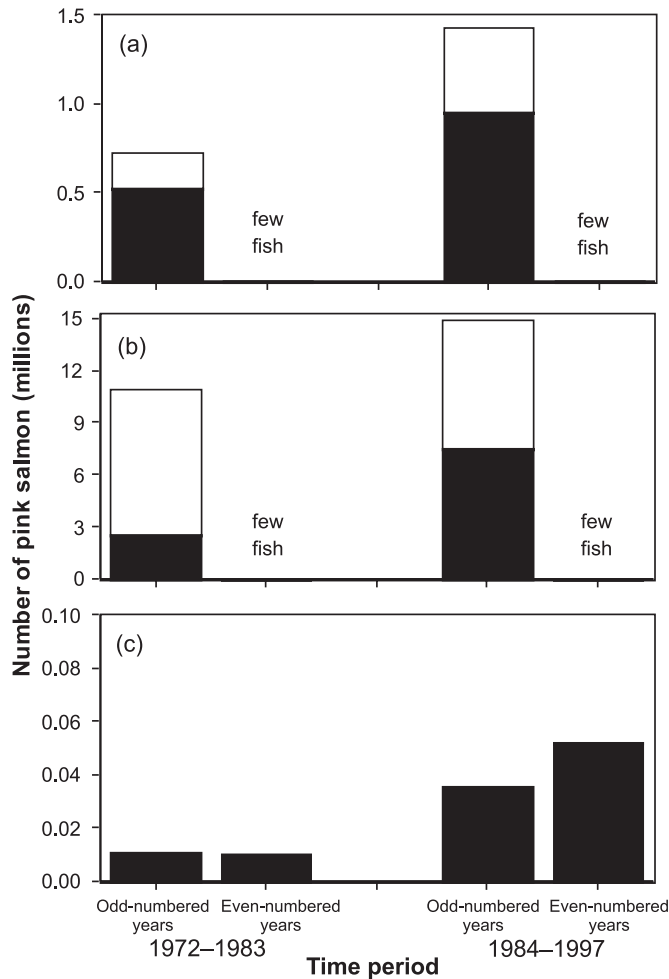
(Fig. 2). Pink salmon spawning escapements averaged 192% more spawners during 1984–1997 than during the 1972–1983 smolt period ($F_{[1,11]} = 11.393$, $P = 0.006$), indicating significantly greater numbers of juvenile pink salmon during 1984–1997. Thus, approximately 470 million pink salmon fry per even-numbered year entered the lower Strait of Georgia during 1984–1997 compared with 367 million pink salmon fry per even-numbered year in 1972–1983, assuming 3.1% survival at sea.

In contrast to Puget Sound and the Fraser River, exceptionally few pink salmon return to streams along the Washington coast (Phinney and Bucknell 1975) and along the west coast of Vancouver Island (L. Hop Wo, Fisheries and Oceans Canada, 3225 Stephenson Point Road, Nanaimo, BC V9T 1K3, personal communication). Southeast Vancouver Island produces small runs of pink salmon that return in approximately equal numbers during both odd- and even-numbered years (Fig. 2). Spawning-escapement estimates were four times larger during 1984–1997 (average 44 000) than during 1972–1983 (average 10 300), largely because of efforts to rebuild the runs.

Puget Sound chinook salmon

During release years 1984–1997, release-to-recovery survival of Puget Sound chinook salmon was significantly lower among fish released from hatcheries during even-numbered years than among those released during odd-numbered years (two-factor ANOVA (odd/even year, stock); $F_{[1,74]} = 25.548$, $P < 0.001$). This pattern was consistent among chinook salmon originating from all 10 drainages (Fig. 3) and there was no significant interaction between the effects of odd/even year and stock (ANOVA factor interaction; $F_{[9,74]} = 0.376$, $P = 0.94$). On average, juvenile chinook salmon released during

Fig. 2. Average spawning escapement (solid bars) and harvest (open bars) of pink salmon (*Oncorhynchus gorbuscha*) originating from (a) Puget Sound rivers, (b) the Fraser River, and (c) southeast Vancouver Island rivers during odd- and even-numbered years of return. Values correspond to juvenile migrations during 1972–1983 and 1984–1997. Few pink salmon return to the Washington coast and west Vancouver Island.



even-numbered years, corresponding to years of abundant juvenile pink salmon, experienced 62% lower survival than those released during odd-numbered years.

Puget Sound chinook salmon were recovered after spending from one (age-2 fish) to five (age 6) winters at sea. Recovery rates of age-2 ($F_{[1,74]} = 14.086$, $P < 0.001$), age-3 ($F_{[1,74]} = 23.763$, $P < 0.001$), age-4 ($F_{[1,74]} = 24.006$, $P < 0.001$), and age-5 ($F_{[1,74]} = 20.468$, $P < 0.001$) chinook salmon were significantly lower among fish released during even-numbered years than among those released during odd-numbered years. Few age-6 chinook salmon were recovered and they were not tested. Lower age-specific recovery rates of fish released during even-numbered years were observed among chinook originating from all 10 drainages (Fig. 4), and percent reductions were similar among the age groups, ranging from 56% among age-4 fish to 65% among age-3 fish. Of these age groups only age-2 chinook salmon did not interact with both odd- and even-year pink salmon.

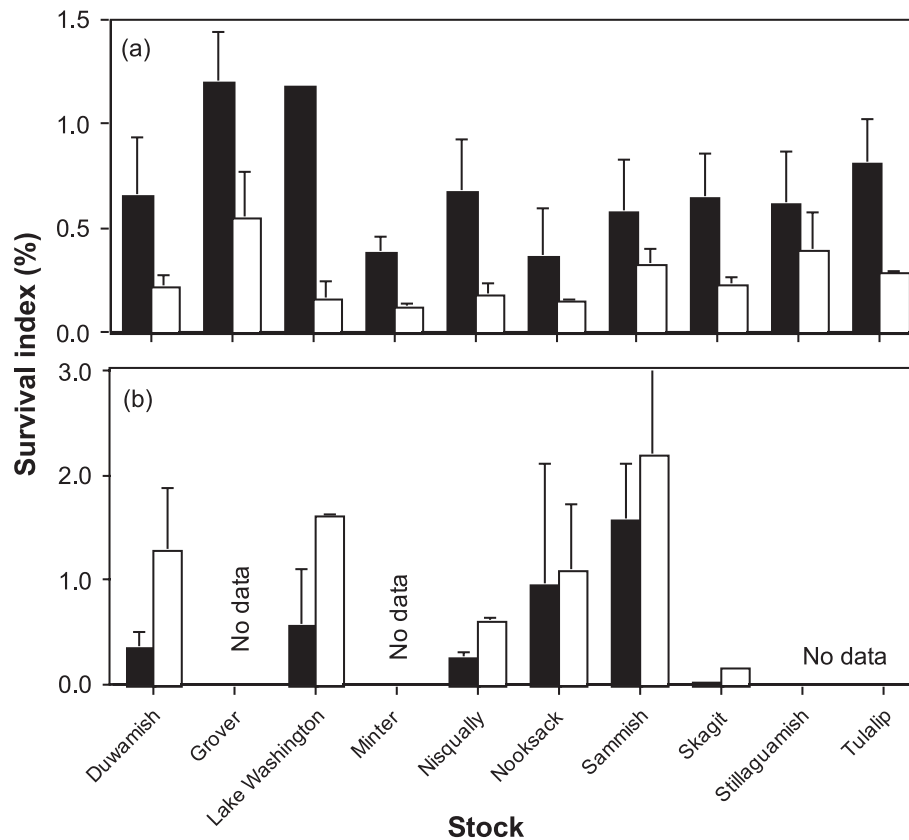
No interaction effect between odd/even-numbered year and stock was detected ($F_{[9,74]} < 1.05$, $P > 0.431$). The consistency in reduced recovery rates of age-2, -3, -4, and -5 chinook salmon released during even-numbered years indicates that the difference in survival occurred during the first year at sea.

During release years 1972–1983, release-to-recovery survival rates of Puget Sound chinook salmon did not differ significantly between even- and odd-numbered years ($F_{[1,22]} = 1.964$, $P = 0.175$). No significant difference in survival was detected among age-2 ($F_{[1,22]} = 2.413$, $P = 0.135$), age-3 ($F_{[1,22]} = 1.826$, $P = 0.183$), and older chinook salmon ($P > 0.28$) (Fig. 5). However, average survival rates during odd-numbered years tended to be lower among all six stocks for which data were available (Fig. 3), a pattern that was opposite to that during 1984–1997. The lack of a statistically significant difference in survival among odd- and even-numbered-year releases was largely due to the exceptionally high survival of chinook salmon released in 1975 (Fig. 1). Excluding 1975, chinook survival was significantly less during odd-numbered years ($F_{[1,19]} = 5.257$, $P = 0.033$). No interaction between odd/even-numbered year and stock was detected ($F_{[5,19]} = 0.127$, $P = 0.98$).

Mean release-to-recovery survival declined 50% from 1972–1983 (average 0.88% survival) to 1984–1997 (average 0.44% survival) (excluding Stillaguamish, Grover, Minter, and Tulalip stocks, which had few data during the early period). However, survival of odd-numbered-year releases was relatively constant across the two time periods (0.61% and 0.68%, respectively), whereas survival of even-numbered-year releases experienced an 82% decline from 1972–1983 to 1984–1997 (1.15% and 0.21%, respectively; Fig. 1; paired t test, $df = 5$, $t = -3.287$, $P = 0.028$). This suggests that the decline in survival of Puget Sound chinook salmon during the 25-year period of investigation was associated with releases of chinook salmon during even-numbered years, not releases during odd-numbered years.

Length at age of CWT chinook salmon recovered at Puget Sound hatcheries was examined to determine whether salmon released in even-numbered years experienced reduced growth compared with those released in odd-numbered years during the 1984–1997 release period. Age-2 chinook salmon released during even-numbered years (mean \pm SE = 436 ± 7.9 mm) were significantly smaller than those released during odd-numbered years (453 ± 8.3 mm; Fig. 6; two-factor ANOVA (odd/even-numbered year, stock); $F_{[1,45]} = 4.860$, $P = 0.033$). Age-3 chinook salmon released during even-numbered years (659 ± 8.5 mm) tended to be smaller than those released during odd-numbered years (672 ± 7.9 mm), even though these fish experienced growing seasons during both even- and odd-numbered years ($F_{[1,55]} = 3.862$, $P = 0.054$). Lengths of age-4 and age-5 chinook salmon were not significantly different when they were released as juveniles during even- versus odd-numbered years ($P > 0.32$). The odd/even-numbered-year growth pattern of age-2 and age-3 chinook salmon was consistent among stocks, as indicated by the insignificant ANOVA interaction values ($P > 0.05$). Too few data were available to evaluate length at age during 1972–1983. These data indicate that growth reduction occurred during the first year, and that growth and mortality

Fig. 3. Release-to-recovery survival of subyearling coded-wire-tagged (CWT) chinook salmon released into Puget Sound streams in odd- (■) and even-numbered (□) years during (a) 1984–1997 and (b) 1972–1983. Values are given as the mean + 1 standard error.



during subsequent years masked the differential growth during early marine life.

Age composition of recovered chinook salmon was examined to determine whether even-numbered-year releases led to an older age at maturation during 1984–1997, as might be expected if growth of these fish was reduced. Most Puget Sound chinook salmon mature at ages 3 and 4, thus the percentage of fish recovered at age 4 and older was used to test the hypothesis. The percentage of chinook salmon recovered at age 4 and older tended to be greater ($12.3 \pm 3.2\%$) among fish released during even-numbered years than during odd-numbered years (two-factor ANOVA (odd/even-numbered year, stock); $F_{[1,74]} = 3.674$, $P = 0.059$). This pattern was consistent among 8 of the 10 stocks (Fig. 7); there was no significant interaction between the effects of odd/even year and stock ($F_{[1,74]} = 0.270$, $P = 0.980$). In contrast, age composition during 1972–1983, a period when pink salmon abundance was low, did not vary between odd- and even-numbered release years ($F_{[1,22]} = 0.101$, $P = 0.754$).

For the 1984–1997 period, VPA was used to estimate the proportion of chinook salmon mortality that was associated with delayed maturation as opposed to mortality during the first year at sea. Delayed maturation explained approximately 1% of the difference in mortality between odd- and even-numbered-year releases, indicating that most mortality associated with the alternating-year pattern occurred during the first year in marine waters. This finding is also apparent in Fig. 4, which shows that the survival pattern was established during the first year and was apparent among chinook salmon of all ages. Although delayed maturation was appar-

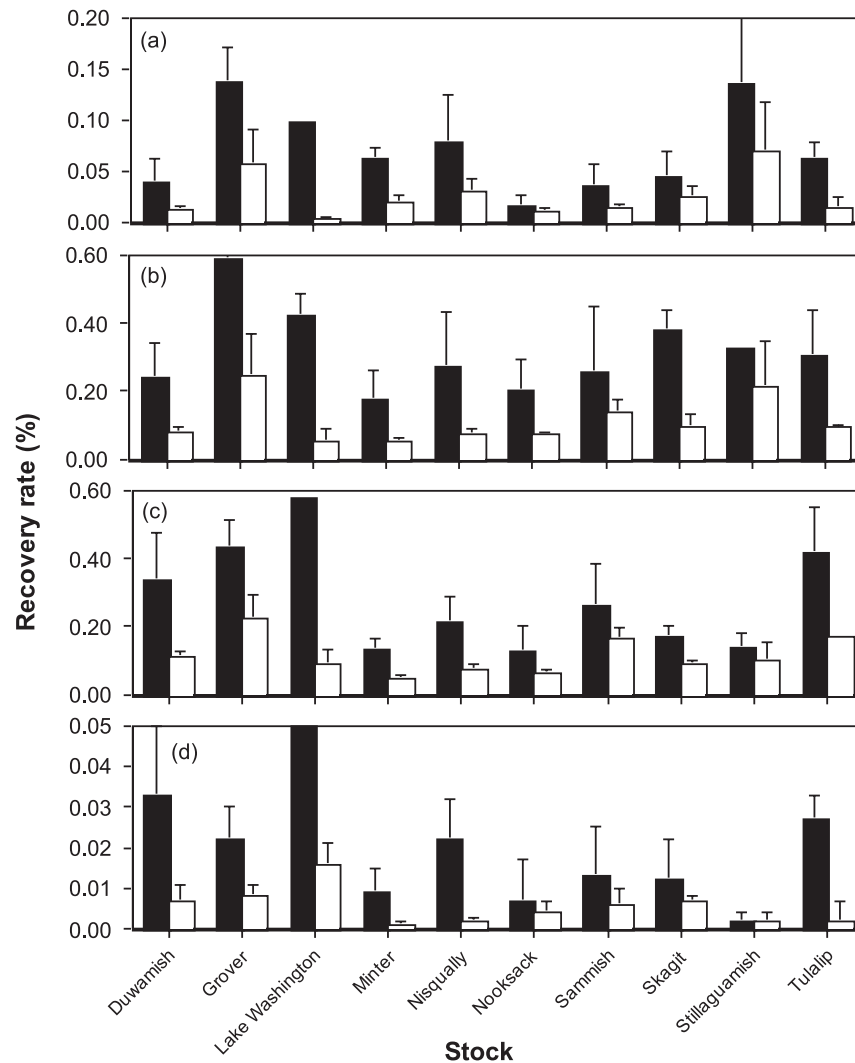
ent among even-numbered-year releases of chinook salmon, its effect on overall survival was minor compared with that which occurred during the first year.

Chinook salmon in the lower mainland of British Columbia

Hundreds of millions of juvenile pink salmon emigrate from the Fraser River, British Columbia, during even-numbered years, but almost none emigrate during odd-numbered years. During 1984–1997, release-to-recovery survival of chinook salmon released into lower mainland streams (Chilliwack, Chehalis, and Capilano) during even-numbered years was 51% lower than that of those released during odd-numbered years (Fig. 8; two-factor ANOVA (odd/even-numbered year, stock); $F_{[1,36]} = 5.547$, $P = 0.024$), a trend that was consistent with that in Puget Sound and among for each lower mainland stock (ANOVA factor interaction: $F_{[2,36]} = 0.224$, $P = 0.80$). The combined average reduction of even-numbered-year migrants in Puget Sound and the lower mainland streams was 59%. Age-specific recovery rates of lower mainland stocks tended to be lower among age-2 ($F_{[1,36]} = 3.812$, $P = 0.059$), age-3 ($F_{[1,36]} = 5.522$, $P = 0.024$), age-4 ($F_{[1,36]} = 3.139$, $P = 0.085$), and age-5 ($F_{[1,36]} = 2.997$, $P = 0.0920$) chinook salmon that were released during even-numbered years, but most relationships were not statistically significant ($\alpha = 0.05$), owing to small sample sizes and the low power of the test. Too few data were available to evaluate changes in length.

The percentage of chinook salmon recovered at age 4 and older (release years 1984–1997) was markedly greater among

Fig. 4. Recovery rates of (a) age-2, (b) age-3, (c) age-4, and (d) age-5 subyearling chinook salmon released into Puget Sound streams in odd- (■) and even-numbered (□) years during 1984–1997. Values are given as the mean + 1 standard error.



those released during even-numbered years ($F_{[1,35]} = 4.914$, $P = 0.048$), a trend that is consistent with that of Puget Sound chinook salmon and for each lower mainland stock (ANOVA factor interaction: $F_{[2,35]} = 0.023$, $P = 0.977$). Greater age at maturity of lower mainland British Columbia chinook salmon during even-numbered years was associated with lower survival and large numbers of juvenile pink salmon.

During 1972–1983, few data were available to test for odd/even-numbered-year survival of lower mainland chinook salmon, and no odd/even-numbered-year pattern was detected (Fig. 8; $F_{[1,9]} = 1.472$, $P = 0.256$).

Washington coast chinook salmon

Essentially no pink salmon are produced by streams along the Washington coast and streams to the south, therefore juvenile chinook salmon originating from these streams would not encounter pink salmon during early marine life. During 1984–1997, release-to-recovery survival of chinook salmon released into coastal Washington streams (Willapa, Humptulips, Quinault, Queets, Sooes) did not differ between odd- and even-numbered-year releases (Fig. 9; two-factor

ANOVA (odd/even-numbered year, stock); $F_{[1,30]} = 0.925$, $P = 0.344$). Recovery rates of age-2, -3, -4, and -5 chinook salmon also did not differ between odd- and even-numbered-year releases ($F_{[1,30]} < 1.15$, $P > 0.30$). No interaction effect between odd/even-numbered year and stock was detected ($F_{[4,30]} = 0.381$, $P = 0.82$).

Fewer data were available to test for the odd/even-numbered-year effect on survival of Washington coast stocks during 1972–1983. Release-to-recovery survival of chinook salmon released into coastal Washington streams did not differ between odd- and even-numbered-year releases (Fig. 9; two factor ANOVA (odd/even-numbered year, stock); $F_{[1,10]} = 0.006$, $P = 0.939$), but the power of this ANOVA was weak (0.062).

Lower Vancouver Island chinook salmon

In contrast to survival of chinook salmon released into streams on the lower mainland of British Columbia, release to recovery survival of chinook salmon released into lower Vancouver Island streams (Qualicum, Chemainus, Cowichan, and Robertson) did not differ among odd- and even-numbered-year releases ($F_{[1,40]} = 0.185$, $P = 0.670$). Few

Fig. 5. Recovery rates of (a) age-2, (b) age-3, (c) age-4, and (d) age-5 subyearling chinook salmon released into Puget Sound streams in odd- (■) and even-numbered (□) years during 1972–1983. Values are given as the mean + 1 standard error.

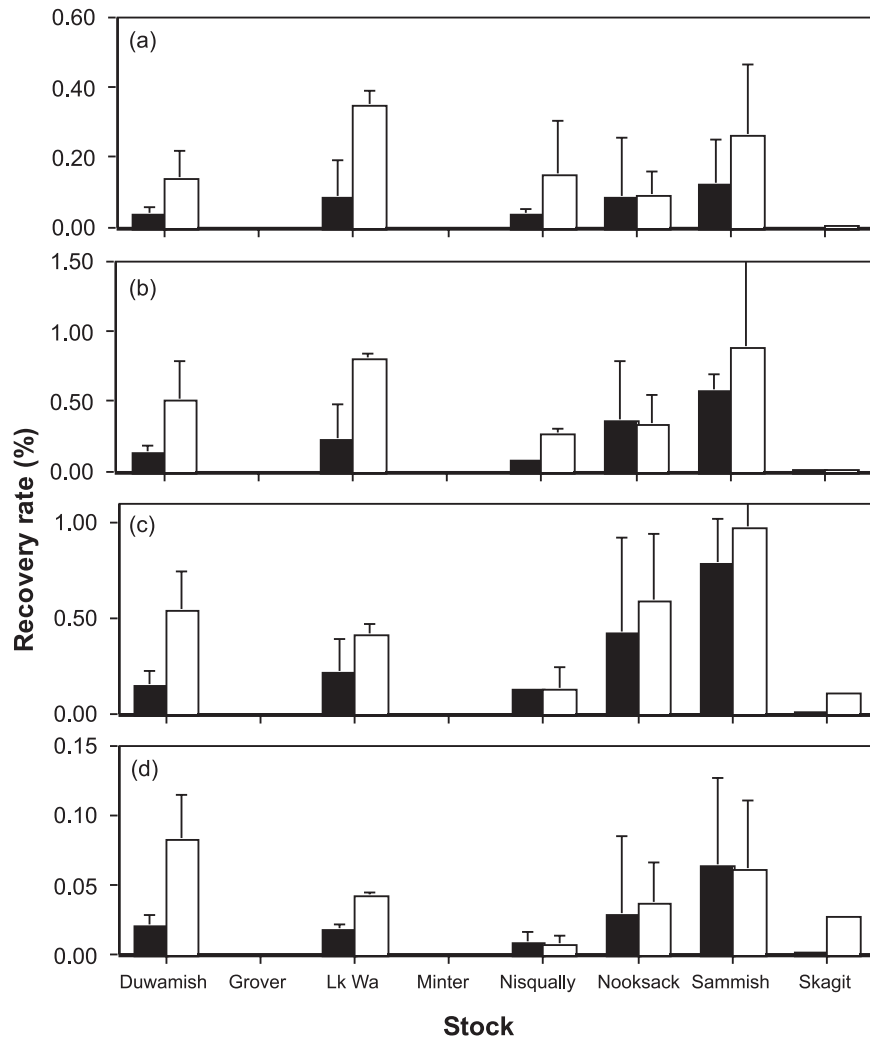
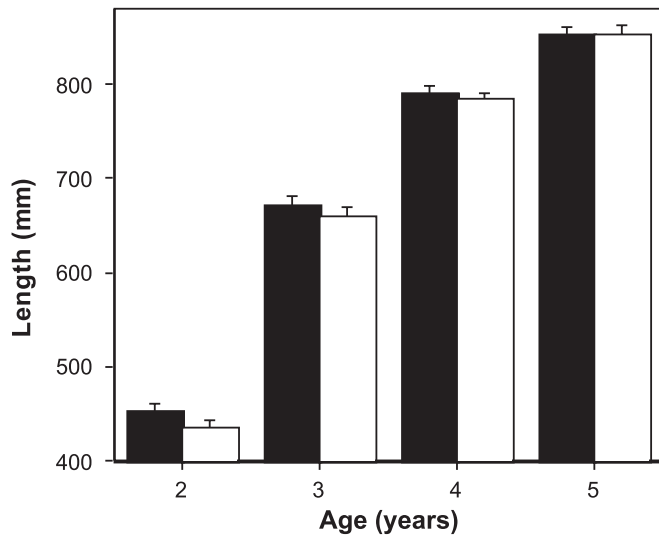


Fig. 6. Mean length at age of chinook salmon recovered at eight Puget Sound hatcheries after release in odd- (■) and even-numbered (□) years during 1984–1997. Values are given as the mean + 1 standard error.



pink salmon originate from lower Vancouver Island, and the small runs returning to southeast Vancouver Island are nearly equal during odd- and even-numbered years.

Discussion

The key finding of this study was that survival rates of subyearling chinook salmon in Puget Sound and the lower mainland of British Columbia alternated between even- and odd-numbered years during the 25-year period of investigation. During 1984–1997, survival of chinook salmon was significantly less during even- versus odd-numbered years, whereas during 1972–1983, survival tended to be greater during even-numbered years. The transition in salmon survival rate corresponded to the 1982–1983 El Niño event, one of the largest on record (Wolter and Timlin 1998). Below we provide evidence that this major El Niño and subsequent and relatively frequent El Niño events (Wolter and Timlin 1998) contributed to the observed pattern of chinook salmon survival by influencing a shift from predation-based to competition-based mortality. We hypothesize that chinook salmon tended to experience greater survival in even-numbered years during 1972–1983 because prey availability

Fig. 7. Percentages of age-4 and older Puget Sound chinook salmon recovered from releases of CWT subyearling chinook salmon in odd- (■) and even-numbered (□) years during 1984–1997. Values are given as the mean + 1 standard error.

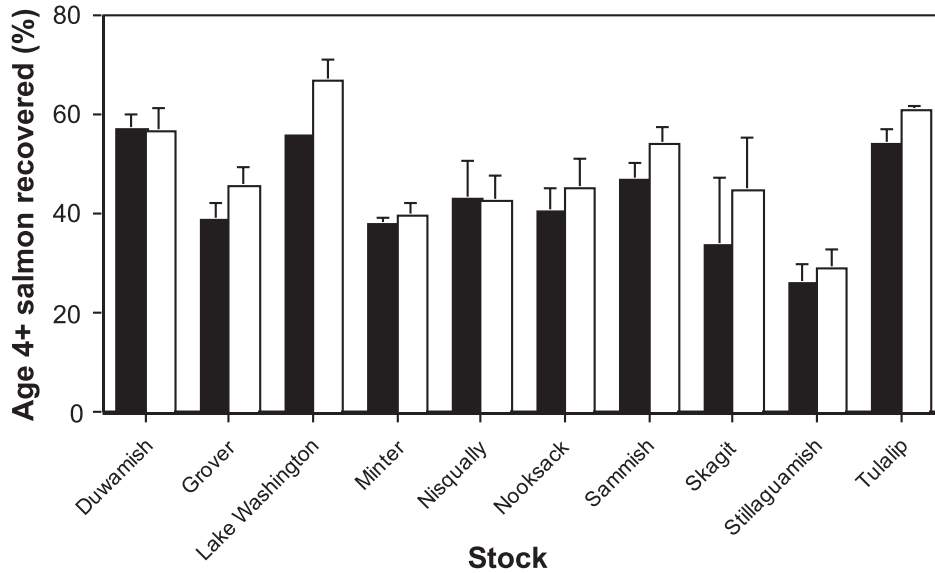
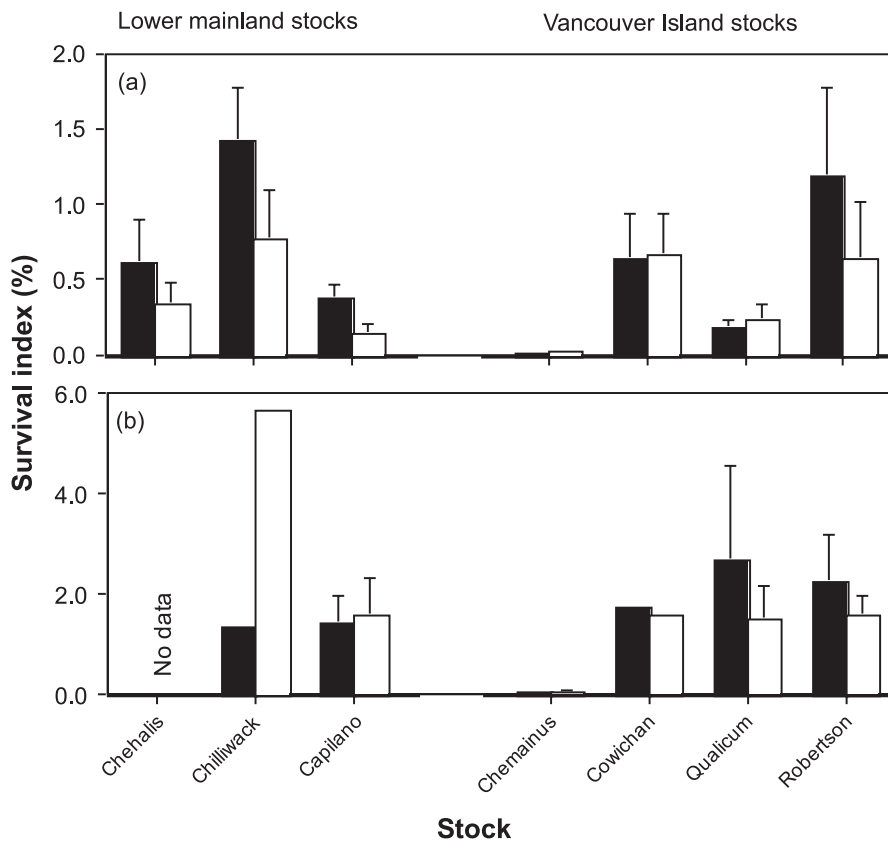


Fig. 8. Release-to-recovery survival of subyearling CWT chinook salmon released into streams in lower mainland British Columbia and lower Vancouver Island in odd- (■) and even-numbered (□) years during (a) 1984–1997 and (b) 1972–1983. Values are given as the mean + 1 standard error.

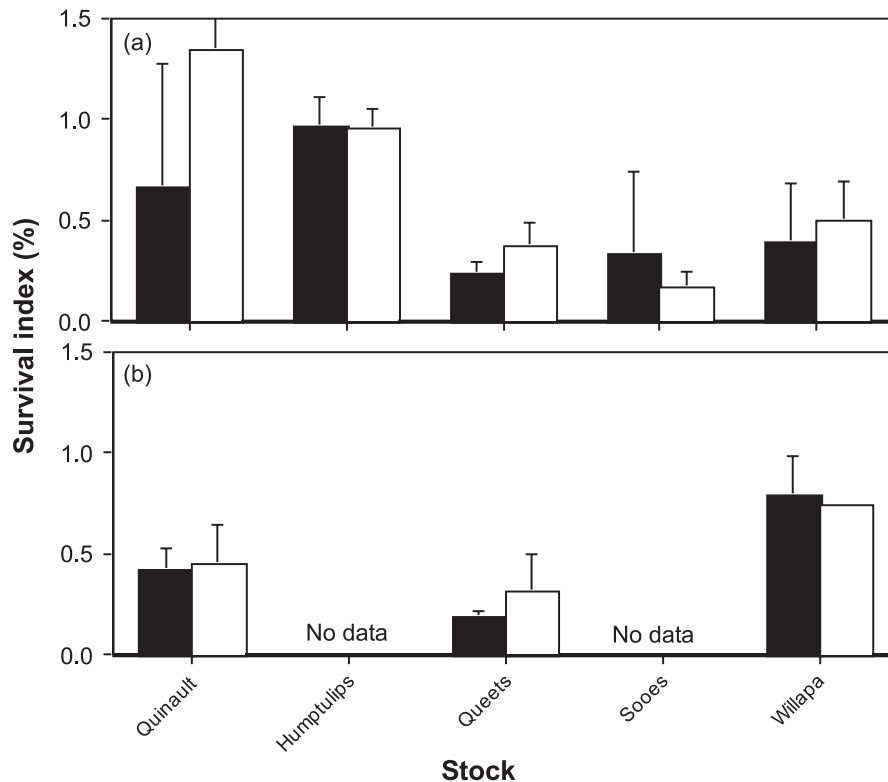


was relatively great and pink salmon provided a buffer against predation. After the 1982–1983 El Niño, low survival of chinook salmon during even-numbered years was related to increased competition with juvenile pink salmon in Puget Sound and the Strait of Georgia. Competition was great during this period because pink salmon abundance was high and

oceanographic conditions had led to low annual prey availability. Size-selective predation likely contributed to chinook salmon mortality through competition and reduced growth.

During 1984–1997, chinook salmon released into Puget Sound streams during even-numbered years experienced reduced growth and survival during the first year at sea and a

Fig. 9. Release-to-recovery survival of subyearling CWT chinook salmon released into coastal Washington streams in odd- (■) and even-numbered (□) years during (a) 1984–1997 and (b) 1972–1983. Values are given as the mean + 1 standard error.



delay in age at maturation. These even-numbered-year migrant chinook salmon entered Puget Sound with the progeny of odd-numbered-year adult pink salmon, which were exceptionally abundant compared with even-numbered-year adult pink salmon. The pattern of lower survival and delayed maturation of even-numbered-year migrants was also observed among chinook salmon released into lower mainland British Columbia streams; these chinook salmon follow the highly abundant Fraser River pink salmon into the Strait of Georgia. In contrast, no alternating-year survival pattern was detected among chinook salmon released into streams along the Washington coast and lower Vancouver Island, where pink salmon abundance was exceptionally low. These observations indicate that the pattern of chinook salmon survival was established while they were rearing in Puget Sound and the Strait of Georgia. Since relatively few pink salmon are found in southern Puget Sound, it is likely that the interaction occurred after chinook migrated into northern Puget Sound. Findings of reduced growth and delayed maturation of chinook salmon provide further support for the competition hypothesis. The magnitude of the interaction was large (an average of 59% reduction in survival among 13 stocks) and explains a significant portion of the decline in chinook salmon survival during 1972–1997.

In contrast to recent studies showing competition between pink salmon and sockeye or chum salmon (Ruggerone et al. 2003), in this study the mechanism of competition between juvenile pink and chinook salmon is not obvious because it apparently involves indirect rather than direct interactions between the species. Pink salmon (30–34 mm in length) rapidly migrate through estuaries, and most enter Puget Sound

and the Strait of Georgia in April, although some fry continue entering marine waters in late May (Heard 1991). Pink salmon fry typically follow marine shorelines for several weeks, then move to epipelagic waters in May (Healey 1980). After rearing in marine waters for nearly 3 months, most juvenile pink salmon leave the lower Strait of Georgia and Puget Sound in July at a length of approximately 100 mm (Healey 1980). However, many still occupy the Strait of Juan de Fuca during August and some remain in inshore waters through fall (Hart and Dell 1986). After leaving inside waters, most juvenile pink salmon migrate northward, primarily within a 40 km wide band along the coast.

The hatchery-produced subyearling chinook salmon tested here were primarily released into streams during May and June at approximately 6.3 ± 1.41 g (86 ± 5 mm), a somewhat similar size to many pink salmon during May and June because pink salmon had reared in marine waters for approximately 1.5 months. Most hatchery-produced subyearling chinook salmon likely migrate rapidly downstream to marine waters. Like pink salmon, subyearling chinook salmon rear in shallow nearshore waters for days or weeks before dispersing to epipelagic areas (Healey 1991). Most chinook salmon remain inside Puget Sound and the Strait of Georgia until October and November before entering the North Pacific Ocean (Healey 1982). Further, some chinook salmon overwinter in inshore waters. Thus, the period of potential overlap between the two species in Puget Sound and the Strait of Georgia is from approximately May through July. Some naturally produced chinook salmon may leave estuaries and enter nearshore marine waters as early as March and April (Healey 1980) and may therefore have greater overlap

with pink salmon. Hence, large numbers of pink salmon enter marine waters first and may influence prey composition prior to the arrival of most naturally produced and hatchery-produced chinook salmon.

We hypothesize that during 1984–1997, pink salmon primarily influenced prey availability for chinook salmon through food-web dynamics rather than by direct competition for the same prey. Both pink and chinook salmon are opportunistic and generalized consumers of both pelagic and epibenthic prey and will consume similar prey when foraging together (Healey 1980). However, pink salmon typically consume lower trophic level prey (small invertebrates) during early spring and summer, whereas juvenile chinook salmon tend to prefer larger invertebrates and small fishes (Healey 1980; Fresh et al. 1981; Welch and Parsons 1993). Healey (1980) noted that pink salmon in the Strait of Georgia may reduce zooplankton abundance. Likewise, Shiomoto et al. (1997) reported that pink salmon in the central North Pacific Ocean can reduce prey availability for salmon, leading to reduced growth and survival (Ruggerone et al. 2003). Juvenile pink salmon enter Puget Sound prior to most chinook salmon and their impact on lower trophic level prey might reduce growth and survival of larger zooplankton species and small fishes and larvae that are consumed by chinook salmon. Unfortunately, food-web dynamics in this region are poorly understood and the dependence of higher trophic level species on lower trophic level prey has not been quantified (Harrison et al. 1983; Bornhold 1999). We do know that peak zooplankton production in Puget Sound and the Strait of Georgia occurs in April or May and that zooplankton abundance and body size decrease thereafter (Bornhold 1999). Thus, many juvenile chinook salmon enter marine waters during a period of declining availability of invertebrate prey, which may enhance the potential for inter- and intra-specific competition.

The switch in the alternating-year survival pattern of chinook salmon corresponded to the 1982–1983 El Niño. Pearcy (1992) noted that the 1982–1983 El Niño had a significant effect on oceanographic conditions and caused a shift in distribution of many marine fishes in the Pacific Northwest. The 1982–1983 El Niño and subsequent more frequent El Niño events were associated with higher sea-surface temperatures in Puget Sound (Bornhold 1999). Although continuous records are not available, abundances of many species in Puget Sound were markedly different before and after the event and may have influenced the switch in the survival pattern of chinook salmon.

Salmon predator populations appeared to be markedly greater during the 1970s than during the 1990s. For example, abundances of piscivorous birds declined more than 50% from the late 1970s to the 1990s (Puget Sound Water Quality Action Team 2002). Dogfish (*Squalus acanthias*), an important predator on juvenile salmon (Beamish et al. 1992), were also relatively abundant during the 1970s and early 1980s (Ketchen 1986), but their status was considered depressed during the 1990s (Puget Sound Water Quality Action Team 2002). Beamish and Neville (1995) estimated that river lamprey (*Lampetra ayresi*) consumed many chinook salmon in the Fraser River plume during the early 1990s, but in Puget Sound this species is listed as a federal and state species of concern (Washington Department of Fish and

Wildlife 2004), suggesting that its abundance may be relatively low. Hake (*Merluccius productus*) reportedly can consume numerous juvenile salmon (Beamish and Neville 2001); their abundance in Puget Sound declined 97% from the early 1980s to the late 1990s (Puget Sound Water Quality Action Team 2002). Of the key predators on salmon, only harbor seals (*Phoca vitulina richardsi*), which typically consume adult salmon (Zamon 2001), have increased in abundance during the recent period (Puget Sound Water Quality Action Team 2002). These observations support our hypothesis that predation on juvenile Puget Sound salmon was likely greater during the 1970s. Our observation that survival of chinook salmon tended to be greater when they migrated with numerous pink salmon during 1972–1983 was unexpected, and the most likely explanation involves predation. Consumption of numerous pink salmon by subyearling chinook salmon is unlikely because the species are similar in size at this life stage. We propose that pink salmon provided a buffer to predation on juvenile chinook salmon, leading to greater survival of chinook salmon entering Puget Sound during even-numbered years from 1972 to 1983.

Significant changes in prey species have also occurred since the late 1970s. Bornhold (1999) reported that the timing of peak zooplankton abundance in the Strait of Georgia shifted from May during the 1960s and 1970s to April in the 1990s (no data for the 1980s), apparently in response to higher temperatures. This shift in zooplankton timing may have benefited juvenile pink salmon, which enter marine waters early (April) and were much more abundant during 1984–1997. In contrast, the spawning biomass of Cherry Point herring (*Clupea pallasii*), a spring-spawning stock that was once the largest in Puget Sound, was 60% lower during 1984–1997 than during 1973–1983 (Stout et al. 2001; $F_{[1,23]} = 43.929$, $P < 0.001$), a trend that may have been influenced by the shift in zooplankton timing. Progeny of these late-spawning herring may be important prey of juvenile chinook salmon. Although the spawning biomass of Cherry Point herring has exhibited a gradual decline since the first survey in 1973, it declined sharply in the early 1980s, a trend that corresponds to the switch in juvenile chinook salmon survival and the increase in pink salmon abundance. Potentially, pink salmon may influence growth and survival of larval and small juvenile herring, since the two species consume similar prey, such as copepods (Simenstad et al. 1979; Fresh et al. 1981). In contrast, most early-spawning stocks of herring in Puget Sound have not significantly declined and those in the Strait of Georgia are relatively abundant. Beamish et al. (2001) suggested that herring may compete with coho salmon for prey, especially during the recent period, when prey production appeared to be relatively low. Another source of juvenile chinook salmon prey are groundfish larvae, but most populations in Puget Sound are considered depressed (Puget Sound Water Quality Action Team 2002). Intraspecific competition among hatchery-produced chinook salmon may have contributed to lower prey availability during 1984–1997 because annual numbers of juvenile chinook salmon released into Puget Sound increased from 45 ± 3 million during 1972–1983 to 53 ± 7 million during 1984–1997 (G.T. Ruggerone, unpublished data). Numbers of chinook salmon released during odd- and even-numbered years in each period were nearly identical. We

propose that the shift in peak zooplankton timing, reduced zooplankton abundance, decline in abundances of Cherry Point herring and other larval fishes, and greater abundance of pink salmon have contributed to increased competition between chinook and pink salmon during 1984–1997.

Few data are available to evaluate the growth of juvenile chinook salmon rearing in Puget Sound during the study period. Beamish et al. (2000, 2001) suggested that growth of juvenile coho salmon in the Strait of Georgia might have been low in the 1990s compared with the 1970s in response to shifts in climate, reduced prey availability, and increased competition. Growth of Puget Sound pink and coho salmon after one winter spent at sea was markedly greater before than after the 1982–1983 El Niño event (G.T. Ruggerone, unpublished data). Our analysis indicated that growth of juvenile chinook salmon during their first year at sea was significantly less when they were competing with pink salmon during 1984–1997, but too few CWT data were available to examine age-specific growth rates during 1972–1983. These observations indicate that salmon may have grown less while rearing in Puget Sound during 1984–1997, which suggests lower prey availability and a greater potential for competition.

Our observations suggest that predation-related mortality was relatively great during the 1970s, whereas prey availability and competition may have been more important to survival of chinook salmon in the 1980s and 1990s. This hypothesis is consistent with the “critical size and period hypothesis” proposed by Beamish and Mahnken (2001), which states that predation during early marine life and growth-related mortality late in the first marine year are key to determining year-class strength of salmon. In the Strait of Georgia, the recent decline in survival of coho salmon appeared to be primarily related to lower prey production associated with a climate shift and greater influence of competition for prey (Beamish and McFarlane 1999). However, lower coho salmon survival was associated with climate and ocean changes in 1989 (Beamish et al. 2000; Welch et al. 2000) rather than the 1982–1983 El Niño, which corresponded to the shift in the alternating-year pattern of chinook salmon survival. Both coho and chinook salmon appeared to be influenced by reduced prey availability during the recent period, but they responded differently to specific climate events. This variation may reflect differences in smolt size, timing of migration, habitat and prey preferences, and interactions with predator species.

The findings of this study involved hatchery-produced chinook salmon but have implications for naturally produced chinook salmon in Puget Sound protected by the US Endangered Species Act. Most naturally produced subyearling chinook salmon are somewhat smaller and more variable in size (~60–90 mm) when they enter Puget Sound than hatchery-produced chinook salmon (80–100 mm). This study indicated that reduced growth was associated with reduced survival. Smaller chinook salmon are likely more vulnerable to effects of reduced prey caused by competition. Thus, competition-related mortality in marine waters is linked to conditions in freshwater and estuarine habitats to the extent that these habitats contribute to the size of chinook salmon entering Puget Sound.

While the dynamics of trophic interactions connecting pink

salmon to the alternating-year pattern of Puget Sound chinook salmon survival remain unknown, data show that chinook salmon growth and survival were significantly reduced among even-numbered-year migrants during 1984–1997. These data suggest that prey availability in Puget Sound and the Strait of Georgia was not sufficient to support existing numbers of juvenile chinook salmon in the presence of numerous pink salmon without inducing higher mortality rates. Competition is likely most important during periods when climate and oceanographic conditions limit prey production, such as during 1984–1997. Additional research is needed to evaluate the complex trophic dynamics that we infer from the unique alternating-year survival pattern of Puget Sound chinook salmon.

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