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A top-down survival mechanism during early marine residency explains coho salmon year-class strength in southeast Alaska

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ABSTRACT

Coho salmon (*Oncorhynchus kisutch*) are a vital component in the southeast Alaska marine ecosystem and are an important regional fishery resource; consequently, understanding mechanisms affecting their year-class strength is necessary from both scientific and management perspectives. We examined correlations among juvenile coho salmon indices, associated biophysical variables, and adult coho salmon harvest data from southeast Alaska over the years 1997–2006. We found no relationship between summer indices of juvenile coho salmon growth, condition, or abundance with subsequent harvest of adult coho salmon in the region. However, using stepwise regression, we found that variation in adult coho salmon harvest was largely explained by indices of juvenile pink salmon (*Oncorhynchus gorbuscha*) abundance (67%) and zooplankton abundance (24%). To determine if high juvenile pink salmon abundance indicates favorable "bottom-up" lower trophic level environmental conditions for juvenile coho salmon, we plotted abundance of juvenile pink salmon against growth and condition of juvenile coho salmon. No change in growth or condition of juvenile coho salmon was observed in relation to the abundance index for juvenile pink salmon. Therefore, we hypothesize that coho salmon year-class strength in southeast Alaska is influenced by a "top-down" predator control mechanism that results from more abundant juvenile pink salmon, which serve as a predator buffer during early marine residency.

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1. Introduction

Coho salmon (*Oncorhynchus kisutch*) are a vital component in the southeast Alaska (SEAK) marine ecosystem and are an important regional fishery resource. Over the last decade, commercial coho salmon harvests in SEAK averaged 2.5 million fish, with an estimated $20 million dollar ex-vessel value (ADF&G, 2007). Because of their high commercial and recreational value in SEAK, understanding the biophysical variables that influence their regional abundance is important. Identifying the mechanisms governing coho salmon survival will improve our ability to conserve and manage this resource and will provide a broader understanding of ecosystem relationships.

Throughout their life cycle, coho salmon survival may be influenced by multiple factors. These factors vary over spatial (rivers, estuaries, and oceans) and temporal (seasonal, interannual, and longer) scales. The coho salmon life cycle can be partitioned into several stages: a juvenile freshwater stage (1–2 years), an early marine coastal stage (3–5 months), an overwintering ocean stage (1 year, except for precocious males that return as jacks), and an adult freshwater spawning stage (Sandercock, 1991). In the ocean, coho and pink salmon spend one winter at sea before returning to spawn, whereas chum, sockeye, and Chinook (*Oncorhynchus tshawytscha*) salmon generally spend 2–5 years at sea. Consequently, habitat utilization patterns may reflect a shared ocean experience of coho and pink salmon, particularly during their early marine life history (Briscoe et al., 2005). This study focuses on the biophysical conditions experienced by juvenile coho salmon in the early marine coastal stage.

Within the life cycle of Pacific salmon, in general, most mortality at sea occurs during the early marine stage (Ricker, 1976; Quinn, 2005). For coho salmon, in particular, environmental conditions during the early marine stage have been related to overall survival and year-class strength (Nickelson, 1986; Pearcy, 1992; Ryding and Skalski, 1999; Koslow et al., 2002). The number of coho salmon that return as jacks (those that do not overwinter

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at sea) is a commonly used indicator of subsequent adult returns and is consistent with the concept that mortality during the early marine stage has an important influence on interannual variation in survival (Pearcy and Schoener, 1987; Pearcy and Fisher, 1988; Young, 1999; Cole, 2000; Briscoe et al., 2005). Growth during this early marine stage may be important to reduce size-selective predation; larger individuals within a cohort of smolts typically have higher survival (Quinn, 2005). Fast growth of salmon during the early marine stage and into the fall may also improve body condition, and therefore determine their ability to survive the subsequent winter at sea when food resources may be limited (Beamish and Mahnken, 2001; Beamish et al., 2004; Moss et al., 2005). Thus, indices of juvenile salmon abundance may be useful as indicators of habitat quality and survival during the early marine stage (Pearcy and Fisher, 1988; Wertheimer et al., 2006; Bi et al., 2007), while information on size and growth during the first summer at sea may be useful as indicators of favorable conditions for survival during both the coastal stage and the subsequent ocean stage (Beamish et al., 2004; Farley et al., 2007).

Bottom-up mechanisms, or lower trophic level environmental conditions, influence salmon survival during the early marine stage. Bottom-up processes begin with the weather that produces the physical environment and results from the climate conditions in a given location. Salmon production has been linked to the physical ocean environment using a number of indices that characterize the long-term climate variability of the North Pacific Ocean (Botsford and Lawrence, 2002; Hunt et al., 2002; Mundy and Spies, 2005). Two commonly used indices are the Pacific Decadal Oscillation (PDO) and the North Pacific Index (NPI). The PDO is a robust, recurring pattern of ocean-atmosphere climate variability centered on the mid-latitude North Pacific basin. The prevailing polarity of the PDO was reversed in 1925, 1947, and 1977. The last two reversals corresponded to remarkable changes in the North Pacific Ocean and in salmon production, including a decrease in Gulf of Alaska salmon survival in 1947 and an increase in 1977 (Mantua et al., 1997; Hare et al., 1999). The atmospheric counterpart to the PDO, the NPI, is defined as the area-weighted sea-level pressure over the region extending between 30°N–65°N and 160°E–140°W (Trenberth and Hurrell, 1994). The parallel trends in catches of pink (*Oncorhynchus gorbuscha*), chum (*Oncorhynchus keta*), and sockeye (*Oncorhynchus nerka*) salmon across the entire North Pacific Ocean suggest that climate events can influence salmon production across wide areas (Beamish and Boullion, 1993; Beamish et al., 1997; Downton and Miller, 1998). Similarly, zooplankton abundance in the subarctic North Pacific and in SEAK has been linked to climate variability (Brodeur and Ware, 1992; Mackas et al., 1998; Anderson and Piatt, 1999; Park et al., 2004). The relationship of both salmon catches and zooplankton abundances to climate forcing factors suggests that interannual changes in salmon abundance may be mediated via the lower food web. Climate also could affect differences in diet and survival of juvenile salmon over time (Landingham et al., 1998; Brodeur et al., 2007).

Through a series of trophic interactions, both the physical habitat and its associated biota influence salmon growth and marine survival rates and thus the return strength of adults (Francis and Sibley, 1991; Francis and Hare, 1994). For example, upper ocean temperature and salinity gradients influence the mixed-layer depth (MLD) (Bathen, 1972; Kara et al., 2000; Alexander et al., 2001), which is an important factor in phytoplankton production, the first link in bottom-up trophic interactions (Cullen and Lewis, 1988; Mann and Lazier, 1991). The production of secondary prey resources depends on this primary production, and results from changing physical environmental conditions. Juvenile coho salmon feed on larval and small fish and invertebrates such as euphausiids, crab larvae, and hyperiid amphipods (Macdonald et al., 1987; St. John et al., 1992; Landingham et al., 1998; Brodeur et al., 2007; Weitkamp and Sturdevant, 2008), many of which are found synchronous with the growth of phytoplankton concentrated in the MLD (St. John et al., 1992; Landingham et al., 1998; Sturdevant et al., 2002; Brodeur et al., 2007). Thus, this food source for juvenile coho salmon can change with the environment.

Food supply and other habitat factors such as temperature may play key roles in the determination of brood year strength for coho and other Pacific salmon. In the subarctic Pacific, zooplankton prey are seasonally abundant in spring and summer, then decline in the fall and winter (Frost, 1983; Brodeur and Ware, 1992; Cooney et al., 2001; Park et al., 2004). Beamish and Mahnken (2001) identified the first fall and winter as a critical time period for coho salmon survival because food supplies are low. Beamish et al. (2004) found evidence of size-specific mortality at that same time, resulting from earlier bottom-up mechanisms, which determined growth and influenced coho survival over the winter. Thus, the relationships of early ocean conditions to marine survival and year-class strength may also indicate the importance of bottom-up processes (Solazzi et al., 1991; Coronado and Hilborn, 1998; Edsall et al., 1999; Ryding and Skalski, 1999).

In addition to bottom-up processes, early marine mortality of juvenile coho salmon may also be driven by predation intensity, a top-down process. Juvenile coho salmon survival may be linked to the presence and abundance of salmon predators, such as the Pacific hake (*Merluccius productus*), spiny dogfish (*Squalus acanthias*), and river lamprey (*Lampetra ayresi*) (Holtby et al., 1990; Beamish et al., 1992; Beamish and Neville, 2001; Emmett and Sampson, 2007), and to the presence of alternative prey that are potential buffer species. The predator buffering hypothesis asserts that abundant alternative prey species divert predators away from consuming juvenile salmon (Fisher and Pearcy, 1988). For example, in Prince William Sound, Alaska, when large copepods and pteropods were abundant, pink salmon fry experienced less predation by Pacific herring (*Clupea pallasi*) and walleye pollock (*Theragra chalcogramma*) (Willette et al., 2001). Similarly, Briscoe et al. (2005) reported that numbers of hatchery pink and chum salmon released near Juneau had the strongest correlation with marine survival of an adjacent coho salmon population in Auke Creek. The authors concluded that marine survival of coho salmon was more strongly associated with biological variables than physical variables, and suggested that when juvenile pink and chum salmon are abundant, predation upon coho salmon is lessened. Their conclusion is consistent with observations that early marine growth of Auke Creek coho salmon has little or no relationship to marine survival (Briscoe et al., 2005; Robins, 2006). Thus, top-down mechanisms may be as important, or more important, than bottom-up (production) processes to coho survival in SEAK.

Because neither bottom-up nor top-down mechanisms consistently explains variation in coho salmon year-class strength, to gain insight into both types of mechanisms operating in SEAK and to identify the dominant mechanism, we examined the relationship of coho salmon year-class strength with a suite of biophysical variables. Data on juvenile salmon and their environment were collected from Icy Strait and Upper Chatham Strait in SEAK, from 1997 to 2006. We included juvenile pink salmon abundance as a biological variable because adult coho and pink salmon exhibit synchrony in ocean year-class strength in SEAK. This synchrony could derive from similar conditions encountered during their marine life history (Shaul, 1994; Briscoe et al., 2005), and could be linked to either mechanism. We chose correlation and regression as complementary and unbiased analyses that could detect the driving mechanisms that explain variation in year-class strength.

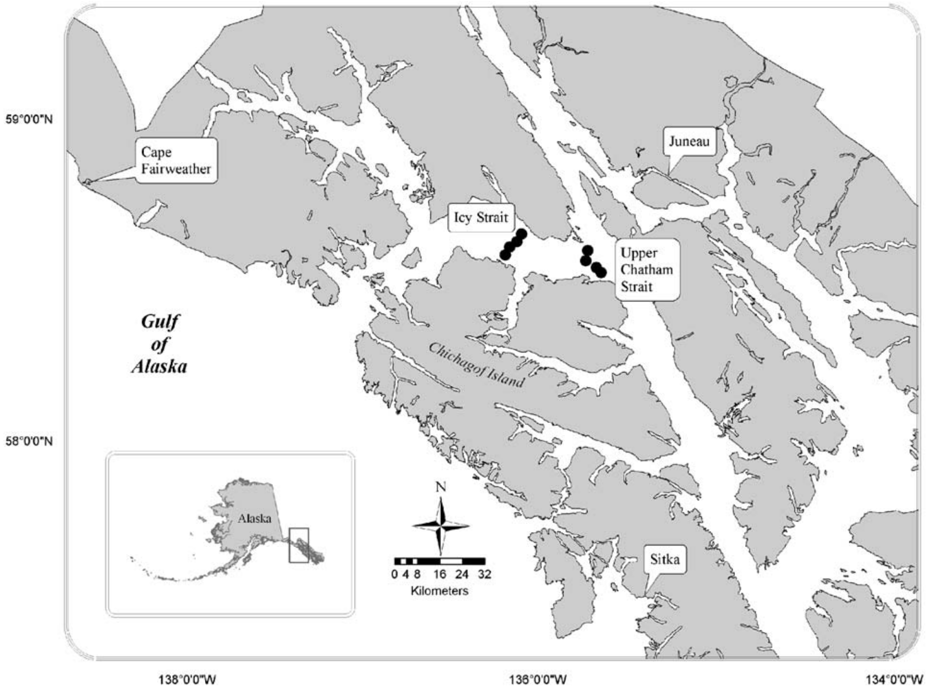

Fig. 1. Strait habitat stations sampled for juvenile coho salmon and their biophysical variables during the Southeast Coastal Monitoring project in the northern region of southeast Alaska, USA, May–September, 1997–2006.

Our overall goal was to tie early marine conditions to variation in year-class strength of coho salmon, using commercial harvest as a proxy for year-class strength. Our specific objectives were to: (1) correlate adult commercial coho salmon harvest with indices of juvenile salmon abundance, juvenile coho salmon size, growth, and condition, and with associated biophysical variables over a 10-year period; (2) use a stepwise regression model to determine which of the biophysical variables best explains the variation in adult coho salmon harvest; and (3) generate hypotheses that could explain the variation in coho salmon year-class strength in SEAK.

2. Methods

2.1. Study area

The biophysical data used in this study were obtained in the northern region of southeast Alaska and gathered during the Southeast Coastal Monitoring (SECM) project (Orsi et al., 2000, 2004, 2006) (Fig. 1). All SECM sampling was conducted by the Auke Bay Laboratories, National Marine Fisheries Service, National Oceanic and Atmospheric Administration (NOAA), using the NOAA research vessel *John N. Cobb*. Sampling occurred monthly from May to August from 1997 to 2006 and additionally in September of the first 5 years of this period. This sampling occurred along a primary seaward migration corridor utilized by juvenile salmon that extends 250 km from inshore waters, along Upper Chatham Strait, Icy Strait, and into the Gulf of Alaska (GOA). Juvenile salmon typically spend 1–4 months migrating through this corridor during the spring and summer. For this analysis, physical oceanographic data, zooplankton data, and juvenile salmon abundance data were summarized from eight sampling stations, four in Icy Strait and four in Upper Chatham Strait (Fig. 1).

2.2. Physical oceanographic data

Oceanographic data were collected at each station in Icy Strait and Upper Chatham Strait with a Sea-Bird[1] SBE 19 Seacat conductivity–temperature–depth (CTD) recorder and an onboard thermosalinograph (Sea-Bird SBE 21). Five physical variables were selected to represent indices of summer conditions in the SECM sampling area for each year: sea-surface temperature (SST, °C); salinity (SSS, PSU); 20-m average temperature; 20-m average salinity; and MLD (m) (Table 1). SST and SSS were recorded by thermosalinograph from a 3-m-deep intake port on the vessel. Depth-averaged temperature and salinity were calculated using CTD readings from the surface to a depth of 20 m (the maximum depth fished by the trawl). The MLD was defined as the depth where the temperature was at least 0.2 °C colder than the water at 5 m. This establishes the water-column depth above which surface mixing is active or recent, while waters below are isolated from surface mixing (Kara et al., 2000). In addition, two common large-scale indices of physical conditions in the GOA were used to reflect the conditions that juvenile salmon encounter in the Alaska Coastal Current and the GOA: the Summer (JJA) NPI and the winter (NDJFM) PDO. Data for the NPI was accessed from the University Corporation for Atmospheric Research, Climate Analysis Section, in Boulder CO, (http://www.cgd.ucar.edu/cas/jhurrell/npindex.html). Data for the PDO was accessed from the Joint Institute for the Study of the Atmosphere and Ocean at the University of Washington, in Seattle, WA (http://jisao.washington.edu/pdo/PDO.latest). To calculate the average winter PDO for each year the November and December monthly values were from the previous year. In general, the greater the NPI index, the greater the upwelling in SEAK and the lower the likelihood of

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[1] Reference to trade names does not imply endorsement by the Auke Bay Laboratories, National Marine Fisheries Service, NOAA Fisheries.

Table 1
Summer physical oceanographic indices from Icy Strait and Upper Chatham Strait in northern southeast Alaska and ocean habitat of the Gulf of Alaska varied from 1997 to 2006.

Indices	Months	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	Mean	SE
Strait habitat													
SST (3 m)	June–August	12.7	12.0	11.8	12.0	12.2	10.9	12.1	14.2	13.2	11.6	12.3	0.29
SSS (3 m)	June–August	24.2	26.6	25.8	25.5	25.3	26.9	26.7	24.3	20.1	27.1	25.2	0.66
Avg. temp. (20 m)	June–August	10.2	10.3	9.9	9.9	10.3	9.3	10.5	10.4	11.0	9.7	10.1	0.16
Avg. salinity (20 m)	June–August	28.8	29.2	29.0	29.0	28.9	29.4	29.4	29.0	27.9	29.3	29.0	0.14
MLD (m)	June–August	7.3	8.0	7.7	7.6	7.2	7.6	6.9	6.5	8.9	6.7	7.4	0.22
Ocean habitat													
NPI	June–August	15.6	18.1	15.8	17.0	16.8	15.6	16.1	15.1	15.5	17.0	–	–
PDO	November–March	0.24	1.24	−0.45	−1.24	0.27	−0.6	1.79	0.47	0.36	0.09	–	–

From southeast Alaska strait habitat: 3-m sea-surface temperature (SST, °C) and salinity (SSS, PSU), 20-m average temperature and salinity, and the mixed-layer depth (MLD, m) are shown. From the Gulf of Alaska ocean habitat: the North Pacific Index (NPI) and the Pacific Decadal Oscillation (PDO) winter index are shown.

storms; these conditions result in less precipitation and runoff, increasing plankton/nekton production and creating more forage base close to shore. The PDO index reflects the winter conditions in the GOA prior to juvenile salmon entering the marine environment. These conditions may determine the quality of the marine habitat for juvenile salmon in their first spring and summer at sea. Alaska salmon productivity has been positively correlated with ocean conditions as reflected by the winter PDO (Mantua et al., 1997).

2.3. *Zooplankton and fish sampling*

Zooplankton was sampled with several net types from May to September. However, since zooplankton biomass peaks early in the summer (Park et al., 2004), only May and June data were used in this study. One shallow vertical tow (20 m) was made at each station with a 50-cm diameter, 243-μm mesh NORPAC net in Icy Strait and Upper Chatham Strait. One double oblique bongo tow was made to a depth of 200 m or to within 20 m of the bottom, using a 60-cm diameter, tandem frame with 505- and 333-μm mesh nets in Icy Strait only. A time–depth recorder and flow meter were used with the oblique bongo tows to record the maximum sampling depth and to calculate the water volume filtered. On board the vessel, zooplankton samples were concentrated and preserved in a 5% formalin–seawater solution. In the laboratory, zooplankton settled volumes (SV, ml) were measured for each NORPAC sample after allowing a 24-h period of settlement in Imhof cones. Zooplankton displacement volumes (DV, ml) were measured for all bongo net samples (333-μm mesh only). Estimates of standing stock (ml/m^3) from these bongo samples were then calculated using DV divided by the volume of water filtered (Table 2).

Fish were sampled at all stations in Icy Strait and Upper Chatham Strait from June to August and sometimes September. Fish sampling was accomplished using a Nordic 264 rope trawl modified to fish the top 20 m of the water column (Orsi et al., 2000). Stations were sampled at the same time each month across years. During each haul, the trawl was fished across a station for 20 min at about 1.5 m/s (3 knots), covering approximately 1.9 km (1.0 nautical mile). After each collection, fish were anesthetized, identified to species, and counted. Usually, all salmon were measured to fork length (FL, mm), but very large catches were sub-sampled due to processing time constraints. Up to 50 individuals of each salmon species from each set were individually bagged and frozen. In the laboratory, frozen juvenile salmon were weighed to the nearest 0.1 g. Fish were processed for weights in the laboratory because accurate shipboard measurement of weight is problematic and frozen weights have been shown to be consistent with fresh weights (Brodeur and Pearcy, 1987; Brodeur et al., 2004).

2.4. *Juvenile salmon size, condition, and abundance indices*

Annual size indices for juvenile coho salmon included June–July growth rate (GR, mm/day) and estimated size (FL, mm) on July 24, the date chosen as a midpoint in the summer sampling period. Average apparent June–July daily GR was calculated separately for each year by regression, using FL data from June and July at Icy Strait and Upper Chatham Strait stations combined. This same procedure was used to estimate the FL on July 24 each year.

An annual index of body condition, the condition residual (CR), was calculated from individual juvenile coho salmon length and weight data (Jakob et al., 1996; Brodeur et al., 2004). We included data from juvenile coho salmon captured at all locations within the larger SECM sampling area (Orsi et al., 2006) from June to September, 1997–2006, to obtain a sample representing a wider range of fish ages and sizes. This extended data set of 3571 fish was used to generate the overall length-to-weight regression equation:

$$\mathrm{Log_e(Weight)} = -12.2 + 3.16\mathrm{Log_e(Length)}$$

with an adjusted $R^2 = 97\%$ ($P<0.0001$). Hereafter, $\mathrm{Log_e}$(Variable) will be referred to as LnVariable. The CR for a given year was calculated as the average of the residuals for all juvenile coho salmon measured in that year from Icy Strait and Upper Chatham Strait, compared to the overall length-to-weight regression equation.

Two annual abundance indices of juvenile coho salmon were calculated from June, July, and August at the eight stations. For the first index, we used the annual frequency of occurrence (FO), calculated as the ratio of the number of hauls in which juvenile coho salmon were caught to the total number of hauls, and then multiplied by 100 to estimate %FO. For the second index, we used catch per unit effort (CPUE) as the number of juvenile coho or pink salmon captured in each haul. These numbers were then transformed by the natural log+1 to calculate the LnCPUE (i.e., LnCPUE = Ln [CPUE+1]). The LnCPUEs were then averaged by month, and the highest monthly average LnCPUE was used as the annual index of abundance (Table 2).

2.5. *Adult salmon harvest data*

Adult coho and pink salmon harvest numbers from 1960 to 2006 for SEAK were collected by the Alaska Department of Fish and Game (ADF&G) (Pers. comm. Steve Heinl, ADF&G, Ketchikan, AK). Because both species only spend one winter at sea, these harvest numbers reflect year-class strength of juveniles from the prior year. These harvest data did not include the relatively small catches from the Yakutat sub-districts northwest of Cape Fairweather because they were outside the study area (Fig. 2).

2.6. Statistical analysis

Correlation analysis was used to examine the bivariate relationships between adult pink and coho salmon commercial harvests and between adult coho salmon harvest and the suite of biophysical variables. Pearson correlation coefficients were generated as an exploratory tool (Minitab, 2003). Time series were examined for autocorrelations, and the significance level was adjusted by the methods of Pyper and Peterman (1998) if autocorrelation was detected. Significance levels of correlations between adult coho salmon harvest and the physical and biological variables were corrected for multiple comparisons using the Bonferroni method with 15 variables (Sokal and Rohlf, 2000). For associated species abundance, juvenile pink salmon peak LnCPUE was also compared with adult coho salmon commercial harvest (Table 3).

Forward–backward stepwise regression (Minitab, 2003) was used to determine the variation of each significant parameter associated with the predicted variable, adult coho salmon harvest. An alpha value of 0.1 was chosen as the criterion for a parameter to enter the model and stay in the model at each step. We defined the best model as the significant stepwise model with the lowest Akaike Information Criteria, corrected for small sample sizes (Shono, 2000) (Table 4).

3. Results

Coho salmon and pink salmon commercial harvests in SEAK were highly correlated over the past 46 years (ADF&G, 2007) (Fig. 2). The Pearson correlation was significant between the two harvest patterns over the entire time series ($r = 0.86$, $P < 0.01$). Autocorrelation was found for both pink and coho salmon harvests at the second and third lags in this series, so the significance level was adjusted (Pyper and Peterman, 1998). The last decade of harvest data for this period, which we used with our companion SECM juvenile salmon data in the correlation and regression analyses, is similarly correlated ($r = 0.88$, $P < 0.05$). However, we did not find any autocorrelation in the subset of harvest data, indicating statistical power may be insufficient to detect autocorrelation in such short time series. During the 1960s and 1970s, pink salmon harvests were low (<20 million) and coho salmon harvests were proportionally low as well

Table 2

Summer biological indices for zooplankton, juvenile coho salmon, and juvenile pink salmon from marine waters of southeast Alaska from 1997 to 2006.

Indices	Months	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	Mean	SE
Zooplankton													
Settled volume (ml)	May–June	27	21	14	20	27	23	37	15	14	27	22	2.2
Standing stock (ml/m^3)	May–June	0.68	0.56	0.58	1.01	1.20	0.72	0.82	0.85	0.86	1.00	0.83	0.06
Juvenile salmon													
Coho GR (mm/day)	June–July	2.5	1.8	2.0	1.5	0.7	1.8	0.8	1.1	0.8	1.0	1.4	0.18
Coho size (mm)	July 24	222.1	215.4	205.1	205.8	183.0	207.6	199.8	201.9	205.6	190.2	203.7	3.36
Coho CR × 100	June–September	−5.27	−3.85	−1.79	1.49	−3.73	−1.91	−3.99	−0.26	−0.21	5.29	−1.42	0.95
Coho FO (%)	June–August	83	96	75	83	96	79	75	75	100	100	86	3.20
Coho LnCPUE	June or July	2.23	2.50	2.27	2.15	2.13	2.30	1.37	1.66	2.28	2.49	2.14	0.11
Pink LnCPUE	June or July	2.48	5.62	1.60	3.73	2.87	2.78	3.08	3.90	2.04	2.58	3.07	0.34

Indices of zooplankton biomass included a surface water-column measure: settled volume (ml per 20-m vertical NORPAC tow) and an integrated water-column (200 m) measure: standing stock (ml/m^3 per 333-μm mesh net double oblique bongo tow). Juvenile coho salmon indices included average apparent daily growth rate (GR, mm/day), size on July 24 (mm), condition residual (CR × 100), percent frequency of occurrence (%FO), and peak average LnCPUE from either June or July. The juvenile pink salmon index used was highest monthly average LnCPUE from either June or July.

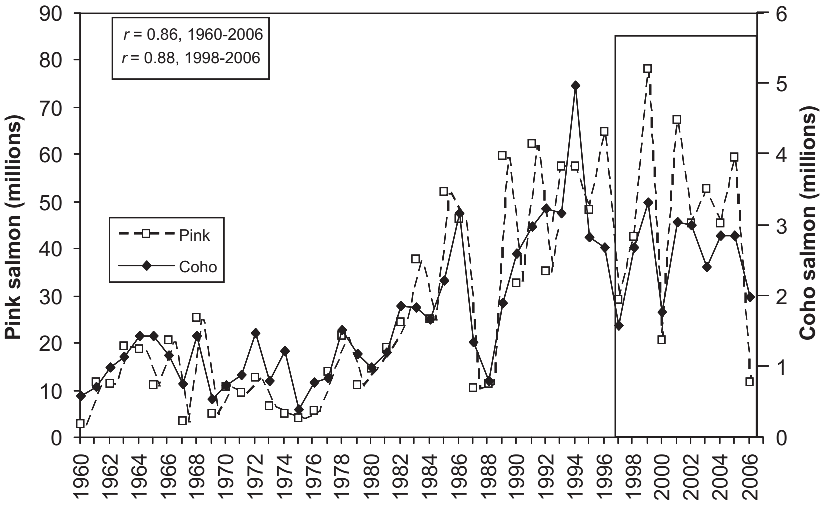

Fig. 2. Total adult coho and pink salmon commercial harvests in southeast Alaska, 1960–2006 (Pers. comm. Steve Heinl, ADF&G). The Southeast Coastal Monitoring (SECM) project study interval, 1997–2006, is shown inside the rectangle. Correlation, r, is shown for the entire 46-year time series and the 10-year SECM time series.

(<1.5 million); conversely, during the 1990s, pink salmon harvests were high (~50 million) and coho salmon harvests were proportionally up as well (~3.5 million) (Fig. 2).

Physical environmental indices for the study area varied over the 10-year time series, and no significant autocorrelation was detected for the variables (Table 1). The 3-m SST ranged from 10.9 °C in 2002 to 14.2 °C in 2004, with a mean of 12.3 °C. The 3-m SSS ranged from 20.1 PSU in 2005 to 27.1 PSU in 2006, with a mean of 25.2 PSU. 20-m average temperature ranged from 9.3 °C in 2002 to 11.0 °C in 2005; with a mean of 10.1 °C. The 20-m average salinity ranged from 27.9 PSU in 2005 to 29.4 PSU in 2002 and 2003, with a mean of 29.0 PSU. MLD ranged from 6.5 m in 2004 to 8.9 m in 2005, with a mean of 7.4 m. Overall, temperature and salinity exhibited inverse interannual patterns and trends were similar at the two depths, but 3-m SST and SSS were more variable than measures over the 20 m depth. For basin-scale environmental indices, the NPI ranged from 15.1 in 2004 to 18.1 in 1998, while the winter PDO ranged from −1.24 in 2000 to 1.79 in 2003. These two climate indices showed no common interannual patterns (Table 1).

Table 3
Pearson correlation coefficients (r) between adult coho salmon harvests for SE Alaska and biophysical variables and associated juvenile salmon indices in Icy Strait and Upper Chatham Strait over the years 1997–2006.

Biophysical variables	Coefficients (r)
Physical	
Strait habitat	
SST (3 m)	0.054
SSS (3 m)	0.420
Avg. temp. (20 m)	0.019
Avg. salinity (20 m)	0.439
MLD (m)	−0.428
Ocean habitat	
NPI	0.643
PDO	0.309
Biological	
Zooplankton	
Settled volume (ml)	0.452
Standing stock (ml/m^3)	0.296
Juvenile salmon	
Coho GR (mm/day)	−0.121
Coho size (mm)	−0.062
Coho CR × 100	−0.216
Coho FO (%)	0.162
Coho LnCPUE	−0.172
Pink LnCPUE	0.843*

The biophysical variables are described in the Methods and in Tables 1 and 2. The adult commercial harvest of coho salmon is lagged by 1 year to follow the juvenile cohort. The correlation coefficient that was significantly different from zero is indicated by an asterisk, where *$P<0.1$ after adjusting for multiple comparisons using the Bonferroni correction on 15 variables.

Biological indices for the study area generally varied more than physical variables over the 10-year time series (Table 2). No significant autocorrelation was detected in the time series for these variables. Zooplankton SVs ranged from 14 ml in 1999 and 2005 to 37 ml in 2003, with a mean of 22 ml. Zooplankton standing stock ranged from 0.56 ml/m^3 in 1998 to 1.20 ml/m^3 in 2001, with a mean of 0.83 ml/m^3. Juvenile coho salmon GR ranged from 0.7 mm/day in 2001 to 2.5 mm/day in 1997, with a mean of 1.4 mm/day. The estimated size on July 24 ranged from 183.0 mm in 2001 to 222.1 mm in 1997; with a mean of 203.7 mm. Juvenile coho salmon CR ranged from −0.0527 in 1997 to 0.0529 in 2006, with a mean of −0.0142. Juvenile coho salmon CR did not have the same interannual pattern as GR and size. For example, in the year with the highest GR and size, 1997, CR was the lowest in the series. Juvenile coho salmon %FO was generally very high; it ranged from 75% in 1999, 2003, and 2004 to 100% in 2005 and 2006, with a mean of 86%. The peak LnCPUE was always in June or July of a given year, as higher monthly averages never occurred after that for either juvenile pink or coho salmon. The annual peak LnCPUE for juvenile coho salmon ranged from 1.4 in 2003 to 2.5 in 1998 and 2006, with a mean of 2.1. In contrast, the annual peak LnCPUE for juvenile pink salmon ranged from 1.6 in 1999 to 5.6 in 1998, with a mean of 3.1 (Table 2).

Pearson correlation coefficients (r) between adult coho salmon harvests and the biophysical variables measured within Icy Strait and Upper Chatham Strait are shown in Table 3. Of the biophysical variables considered, juvenile pink salmon LnCPUE had the highest correlation ($r=0.843$) with adult coho salmon harvest. The NPI was also correlated ($r=0.643$) with adult coho salmon harvest. However, only the juvenile pink salmon LnCPUE correlation was significant ($P=0.06$) after adjusting for multiple comparisons; all other variables had an adjusted $P>0.1$. Measures of juvenile coho salmon LnCPUE, FO, GR, and CR were not significantly correlated with adult coho salmon harvest (Table 3).

The stepwise regression analysis revealed that juvenile pink salmon LnCPUE was the strongest predictor of adult coho salmon harvest, explaining 67% of the variation in coho salmon harvest over the past 10 years (Table 4). The full stepwise regression model also included the two zooplankton indices (SV and standing stock), GR, and SST. However, based on the corrected Akaike Information Criteria, the best model included only juvenile pink salmon LnCPUE and the two zooplankton indices. This model explained 91% of the interannual variation in the coho salmon harvest (Table 4).

Juvenile coho salmon LnCPUE was not correlated with adult coho salmon harvest; however, juvenile pink salmon LnCPUE was highly correlated with harvest of both adult pink and coho salmon

Table 4
Results of forward–backward stepwise regression of southeast Alaska coho salmon commercial harvest over the years 1998–2006, with the suite of biophysical variables listed in Tables 1 and 2.

Variable	Step 1	Step 2	Step 3	Step 4	Step 5
Constant	1.52 (0.001)	1.0 (0.017)	0.44 (0.187)	-0.30 (0.355)	-1.28 (0.024)
Pink LnCPUE	0.36 (0.004)	0.35 (0.002)	0.36 (0.001)	0.37 (0.0001)	0.36 (0.0001)
Zooplankton settled volume (ml)		0.03 (0.049)	0.02 (0.031)	0.02 (0.008)	0.02 (0.002)
Zooplankton standing stock (ml/m^3)			0.75 (0.037)	1.24 (0.005)	1.23 (0.001)
Coho growth rate (mm/day)				0.22 (0.033)	0.26 (0.005)
SST (3 m)					0.07 (0.034)
R^2 (adjusted)	67.0	80.8	91.1	96.9	99.3
AIC$_c$	11.1	9.7	8.3	8.9	17.4

The regression coefficients and probability (in parentheses) are shown for each step of the regression. The adjusted R^2 (the coefficient of determination adjusted for degrees of freedom), and the Akaike Information Criterion corrected for small sample size (AIC$_c$), are shown at the bottom of each step. Step 3 was selected as the best model based on the minimization of AIC$_c$.

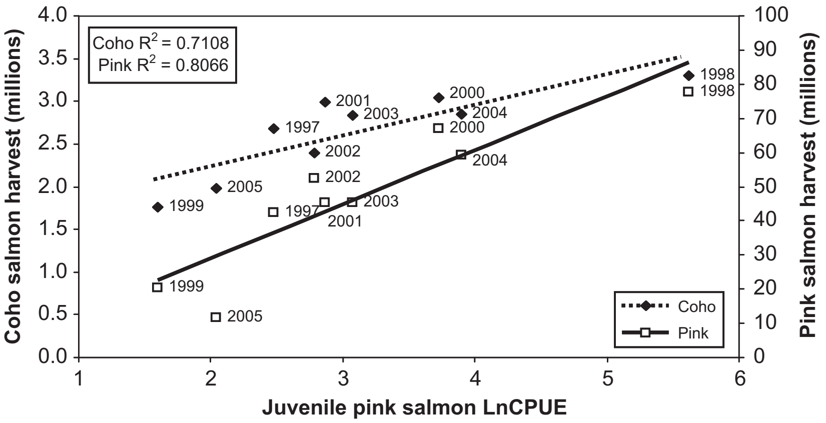

Fig. 3. The relationship between adult coho harvest (diamonds; dashed line) and pink salmon harvest (squares; solid line) with juvenile pink salmon LnCPUE.

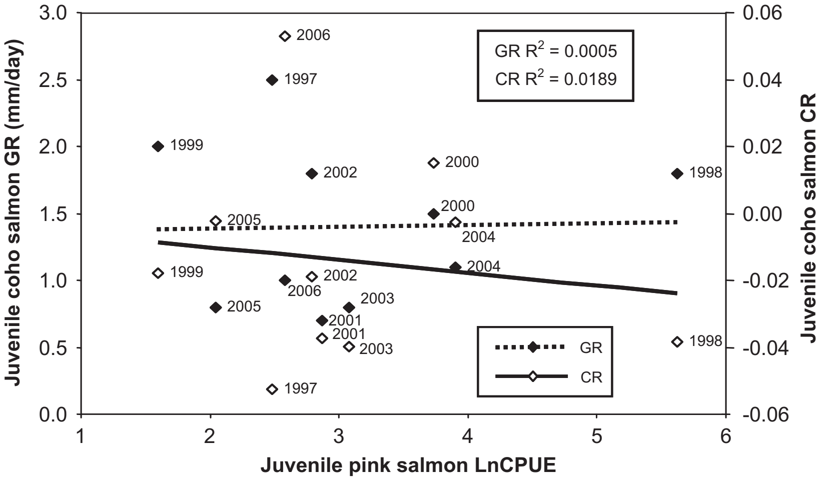

Fig. 4. The relationship between juvenile coho salmon estimated average apparent growth rate (GR, mm/day; filled diamonds; dashed line) and condition residual (CR; open diamonds; solid line) with juvenile pink salmon LnCPUE.

(Fig. 3). Thus, only juvenile pink salmon LnCPUE reflected year-class strengths of these species. If juvenile coho and pink salmon derive similar benefits from positive bottom-up processes while sharing habitats during their early marine residency (even though they do not consume the same prey), then rapid growth and condition of juvenile coho salmon should also be related to the abundance of juvenile pink salmon. We plotted juvenile coho salmon GR and CR over the last 10 years as a function of juvenile pink salmon LnCPUE (Fig. 4), but found no significant relationship between either of these measures and juvenile pink salmon LnCPUE ($R^2 = 0.0005$ and $R^2 = 0.0189$, respectively).

4. Discussion

Bottom-up and top-down processes both undoubtedly influence coho salmon year-class variation in SEAK, but the processes are confounded. To survive, the fish must obtain sufficient prey to meet metabolic and growth demands and must avoid predation. Predation on juvenile salmon is often size-selective (Parker, 1971; Hargreaves and LeBrasseur, 1985; Moss et al., 2005; Wertheimer and Thrower, 2007), so interannual variation in growth conditions can drive variation in survival and year-class strength by mediating size (Holtby et al., 1990; Mortensen et al., 2000). However, Briscoe (2004) found no relationship between early marine scale growth and marine survival of female coho salmon for the Auke Creek stock in SEAK. For the same stock of coho salmon, Robins (2006) also found no relationship of early marine growth and marine survival, and early marine growth explained only a small portion of the variation in marine survival of male coho salmon. Similarly, Fisher and Pearcy (1988) found no relationship of juvenile coho salmon growth off of Oregon and Washington with subsequent survival. The lack of relationship between early marine scale growth and survival could be due to size-related predation after the early marine stage. The size of juvenile salmon prior to the first ocean winter has been related to subsequent survival and year-class strength (Beamish and Mahnken, 2001; Beamish et al., 2004; Moss et al., 2005; Farley et al., 2007). We did not, however, observe any relationship between indices of juvenile coho salmon (size, growth, or condition) with subsequent harvest of adult coho salmon over the past 10 years in SEAK.

In contrast, we did find a highly significant relationship between the abundance of juvenile pink salmon and the regional adult coho salmon harvest in SEAK. Juvenile pink salmon LnCPUE alone explained 67% of the variation in harvest in the multiple regression model. Therefore, because of the synchrony of adult pink and coho salmon harvests in SEAK, juvenile pink salmon abundance also indicates conditions that affect year-class strength of coho salmon. If this synchrony is caused by common environmental conditions that affect growth of both species then it reflects bottom-up forcing of variability in harvest. However, we found no relationship between growth indices of juvenile coho and pink salmon abundance. These results suggest that a top-down, predator buffering mechanism is operating on coho salmon in SEAK (Weitkamp, 2004; Briscoe et al., 2005) and in Oregon (Fisher and Pearcy, 1988).

Predators are considered to be the most significant source of juvenile salmonid mortality in the marine environment (Parker, 1968; Ricker, 1976; Ware and McFarlane, 1989; Beamish and Mahnken, 2001; Beamish and Neville, 2001; Emmett et al., 2006). Fish species that prey on juvenile salmon in neritic habitat according to trawl-caught predator indices include sablefish (*Anoplopoma fimbria*), adult coho salmon, adult Pacific sandfish (*Trichodon trichodon*), and adult spiny dogfish (Beamish et al., 1992; Orsi et al., 2000, 2007; Beamish and Neville, 2001). Juvenile coho salmon are less abundant and larger, on average, than juvenile pink, chum, and sockeye salmon in SEAK marine waters (Jaenicke and Celewycz, 1994; Orsi et al., 2000). Size-selective mortality has been indicated for juveniles of these four species (Parker, 1971; Hargreaves and LeBrasseur, 1986; Koenings et al., 1993; Beamish and Mahnken, 2001; Moss et al., 2005; Wertheimer and Thrower, 2007). The presence of more abundant, smaller juvenile pink salmon available to predators may lower the proportion of juvenile coho salmon eaten in their shared epipelagic habitat.

Predator buffering of coho salmon by pink salmon is not necessarily limited to the early marine stage of their life history. Our observations of juvenile pink salmon abundance are also highly correlated with adult pink salmon returns. Thus, the relationship of coho salmon harvest to the juvenile pink salmon abundance index may reflect effects on mortality beyond the early marine life history stage of both species. Immature and returning adult salmon are susceptible to substantial predation by large predators such as salmon sharks (*Lamna ditropis*), Steller sea lions (*Eumetopias jubatus*), and killer whales (*Orcinus orca*) (Nagasawa, 1998; Hulbert et al., 2005; Matkin et al., 2007; Trites et al., 2007), but the relative impact on different salmon species remains unknown. It is possible that the predator buffering relationship between pink and coho salmon continues for adults in the open ocean and during their return migrations back through the coastal habitats. However, regional concordance in the marine survivals of pink and coho salmon suggests that regional- and local-scale factors during early ocean life are more important in determining year-class strength (Coronado and Hilborn, 1998; Downton and Miller, 1998; Pyper et al., 2001; Briscoe et al., 2005). Mortality rate estimates for juvenile salmon are typically very high during their early marine residency (Parker, 1968; Ricker, 1976; Karpenko, 1998; Wertheimer and Thrower, 2007). Thus, it is likely that the synchrony of pink and coho salmon harvests is set early on in their marine life history.

In addition to juvenile pink salmon abundance, zooplankton abundance was a significant predictor of the SEAK adult coho salmon harvest in the best regression model. Indices of zooplankton could indicate a bottom-up connection between growth and year-class strength; however, we found that the more directly linked biological metrics, GR, CR, and size of juvenile coho salmon, were not correlated with adult coho salmon harvest. An alternate explanation for the relationship of zooplankton indices, but not juvenile coho salmon growth and condition indices, with adult coho salmon harvest is that abundant zooplankton could divert predation away from juvenile coho salmon just as abundant juvenile pink salmon can. For example, Willette et al. (2001) found that predators of juvenile pink salmon in near-shore habitat switched to zooplankton prey when zooplankton was abundant. Thus, zooplankton may act in either a top-down or a bottom-up process.

The two basin-scale indices, the NPI and PDO, were not significantly correlated with SEAK coho salmon harvest, nor were they significant predictors in the regression model for harvest. Basin-scale indicators have been shown to be significantly related to harvest over long time series (Beamish and Boullion, 1993; Mantua et al., 1997; Hare et al., 1999). The time series used in our analysis may be too short to be affected by longer-term signals of climate variability. Continuously monitoring the biophysical variables of the ocean is the only way to detect if any correlation with climate signals will show up.

Juvenile pink salmon abundance in the northern region of SEAK has been used to forecast regional pink salmon returns the following year (Wertheimer et al., 2006; Eggers, 2007). In contrast, we did not find any correlation between indices of juvenile coho salmon abundance and adult coho salmon harvest the following year. Juvenile coho salmon in SEAK are less aggregated than juvenile pink, chum, and sockeye salmon (Jaenicke and Celewycz, 1994). Agonistic behavioral interactions characteristic of juvenile coho salmon in freshwater habitats can persist in salt water (Paszkowski and Olla, 1984). These behaviors may result in greater dispersal and density-dependent migration rates through the sampling area, which could obscure any relationship between our observed peak LnCPUE and inter-annual variation in either juvenile coho salmon abundance or subsequent harvest.

We used harvest of coho salmon as an indicator of year-class strength that responds to conditions in the marine environment. The harvest data are confounded with unmeasured variability in annual smolt recruitment to the marine environment, and potentially with varying exploitation rates in the commercial fishery of the total regional return. For example, commercial harvest limits are set according to run strength but may be more or less efficient for various reasons. However, SEAK commercial harvest was highly correlated with marine survival of a coded-wire tagged coho salmon stock in northern SEAK (Briscoe et al., 2005). Similar trends in marine survival among additional marked stocks of coho salmon in northern SEAK were found, as well as significant cross-correlation between stocks (Briscoe et al., 2005). These observations support our assumption that much of the variation in harvest was due to marine factors.

We attribute the relationship of SEAK coho salmon harvest with indices of juvenile pink salmon abundance and its synchrony with SEAK pink salmon harvests over the past decade largely to a top-down mechanism: predation buffering by the more abundant and smaller juvenile pink salmon during early marine residency. Two-thirds of the variation in adult coho salmon harvest was explained by juvenile pink salmon LnCPUE. Juvenile coho salmon growth and condition did not respond to the abundance of juvenile pink salmon, indicating no direct connection with bottom-up processes. This does not imply that bottom-up conditions are unimportant for marine survival and productivity of SEAK coho salmon. Marine survival of SEAK pink salmon has been directly linked to early marine growth (Mortensen et al., 2000); environmental conditions that affect growth and survival of juvenile pink salmon could indirectly affect coho salmon by influencing the dynamics of the potential predator buffer. We note that this analysis has occurred during an extended period of generally high abundance of SEAK salmon relative to historical levels (Wertheimer, 1997; Clarke et al., 2006). This high abundance has been associated with changing climatic and oceanographic conditions (Beamish and Boullion, 1993; Mantua et al., 1997; Downton and Miller, 1998), and with high productivity at lower trophic levels (Brodeur and Ware, 1992). Size and condition of juvenile coho salmon may not be a major determinant of interannual variation in SEAK coho salmon harvest during time periods of high productivity, but may become critically important when bottom-up conditions are not favorable. Biological interactions may change with fluctuations in environmental conditions (Nickelson, 1986; Holtby et al., 1990; Bi et al., 2007). Additionally, the correlations between juvenile coho salmon growth indices and adult coho salmon harvest may be weak because the growth indices were measured only on juvenile fish. If significant adult mortality occurs overwinter, year-class strength will not be determined by juvenile survival alone (Hobday and Boehlert, 2001; Fisher and Pearcy, 2005; Wells et al., 2006). Therefore, additional coho salmon research, beyond the juvenile coastal stage, is needed in the GOA.

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