

Bottom-up and top-down controls of walleye pollock (*Theragra chalcogramma*) on the Eastern Bering Sea shelf

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Abstract

Control of walleye pollock (*Theragra chalcogramma*) recruitment in the Eastern Bering Sea involves complex interactions between bottom-up and top-down processes, although the mechanisms are poorly understood. We used statistical models to test the leading hypotheses linking recruitment variability to biotic and abiotic factors. Consistent with a “cold-pool hypothesis”, recruitment of pollock was significantly stronger if winters preceding the larval (age-0) and juvenile stages (age-1) were mild. However, our results did not support the proposed top-down mechanism (cannibalism) underlying this hypothesis. Several empirical relationships support an “oscillating control hypothesis”. As predicted by it, the effect of ice conditions on survival during the larval and early juvenile stages was modified by the abundance of adult pollock, implying stronger bottom-up control when adult abundance (hence cannibalism) was low. The proposed bottom-up mechanism predicts that the survival of pelagic-feeding walleye pollock (benthic-feeding yellowfin sole), should be higher during years with an early (late) ice retreat, which was confirmed by our analysis. Our results also provide additional evidence for a “larval transport hypothesis”, which states that cannibalism of larval and juvenile pollock is reduced in years when strong northward advection separates juveniles from cannibalistic adults.

In addition to testing existing hypotheses, we identified new relationships between spawner-to-recruit survival rates of walleye pollock and several indicators of mixed layer dynamics during the spring and summer. Survival rates and recruitment were significantly reduced when larval or early juvenile stages experienced a delay in the (non-ice-associated) spring bloom as a result of stormy spring conditions, suggesting that the timing of the spring bloom is critical to both first-feeding larvae and age-1 juveniles. Furthermore, a dome-shaped relationship between pollock survival and summer wind mixing at the early juvenile stage is consistent with modeling and laboratory studies showing an increase in survival at low to moderate levels of wind mixing, but a decrease in feeding success at high levels of wind mixing.

Top-down controls also regulate recruitment of walleye pollock. At least one-third of the variability in spawner-to-recruit survival could be accounted for by predation mortality at the early juvenile stage (age-1). Predation of juvenile pollock can be attributed largely to cannibalism, which varies with the abundance of adult pollock and with the availability of juveniles to adult predators. A simple index reflecting the spatial overlap between juvenile and adult pollock explained 30–50% of the overall variability in recruitment, similar to the variability explained by the best environmental predictors. Although environmental effects are difficult to separate from the effects of predation, we conclude that bottom-up and top-down processes are equally important in controlling the survival of pollock from spawning to recruitment at age 2.

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However, the magnitude of top-down control is itself modified by environmental factors that control the availability of juvenile pollock to adults (through impacts on spatial distribution) and the abundance of adult predators (through effects on productivity and carrying capacity).

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1. Introduction

There is general agreement that changes in the climate and oceanography of the Northeast Pacific influence the recruitment of walleye pollock (*Theragra chalcogramma*) and other groundfishes in the Bering Sea (Holmwood et al., 2001). Although a number of potential relationships among large-scale climate change, the oceanography of the Bering Sea, and walleye pollock recruitment success have been reported (Ohtani and Azumaya, 1995; Quinn and Niebauer, 1995; Wespestad et al., 2000), reliable predictive relationships have not been established to date. Similarly, the importance of predation, primarily in the form of cannibalism, to the population dynamics of walleye pollock has long been recognized (Wespestad and Quinn, 1996). However, the relative importance of top-down and bottom-up controls of walleye pollock in the eastern Bering Sea remains poorly understood. Therefore, we undertook a comprehensive analysis of environmental influences and predation on pollock survival and recruitment in the eastern Bering Sea to improve our understanding of the processes that determine recruitment and to develop better predictive models. To identify models that can serve as useful predictors of pollock recruitment, we examined, in a unified and rigorous statistical framework, the major hypotheses that have been put forward to explain variations in pollock recruitment.

Most of the variability in pollock recruitment is believed to occur during the first years of life, in particular during the early ocean life of larvae and age-0 fish. For example, recruitment of walleye pollock in Shelikof Strait is largely determined by the end of the larval period (Kendall et al., 1996), although predation at the juvenile stage may have played a larger role in more recent years due to the high abundance of predators (Bailey, 2000). In Shelikof Strait, survival is enhanced by strong freshwater runoff in the spring prior to spawning, which enhances productivity, and by weak mixing in the summer, which enhances retention on the shelf (Megrey et al., 1995; Megrey et al., 1996). Processes determining recruitment of pollock in the eastern Bering Sea are not well understood, but ice extent (Ohtani and Azumaya, 1995; Quinn and Niebauer, 1995), the timing of ice retreat, advection on the shelf (Wespestad et al., 2000), water temperature (Bulatov, 1989; Ohtani and Azumaya, 1995), and summer stratification (Hunt et al., 2002) all are believed to influence recruitment success.

Marine populations respond to environmental variability in complex, non-linear ways that may not be adequately described by linear correlations (Cury et al., 1995). It has been suggested that the timing of ice retreat and the abundance of predators interact in complex ways to regulate the survival of juvenile pollock (Hunt et al., 2002). Such complex relationships are unlikely to be captured by linear regression models. Non-linearities, strong interactions, and threshold relationships may drive much of the dynamics in the Bering Sea, as evidenced by the highly unusual conditions in 1997 when sea surface temperatures (SST) were anomalously warm, nitrate and silicate were depleted, and the first documented sustained coccolithophore bloom occurred over the Bering Sea shelf (Napp and Hunt, 2001; Overland et al., 2001; Stockwell et al., 2001). The statistical approach we take here takes into account potential non-linearities, interactions, and thresholds in environment–recruitment relationships for Bering Sea pollock.

The primary goals of our study were to improve our understanding of the processes controlling recruitment of walleye pollock in the eastern Bering Sea (Fig. 1) and to develop statistical models linking recruitment to climatic and oceanographic conditions at regional and larger spatial scales. We developed a series of models that reflect our current understanding of potential mechanisms underlying environment–recruitment relationships for walleye pollock. These models were used to assess the strength of evidence for and against several general hypotheses that have been proposed to explain variability in pollock survival and recruitment. Specifically, we modelled the proposed relationships between recruitment, stock size and relevant environmental

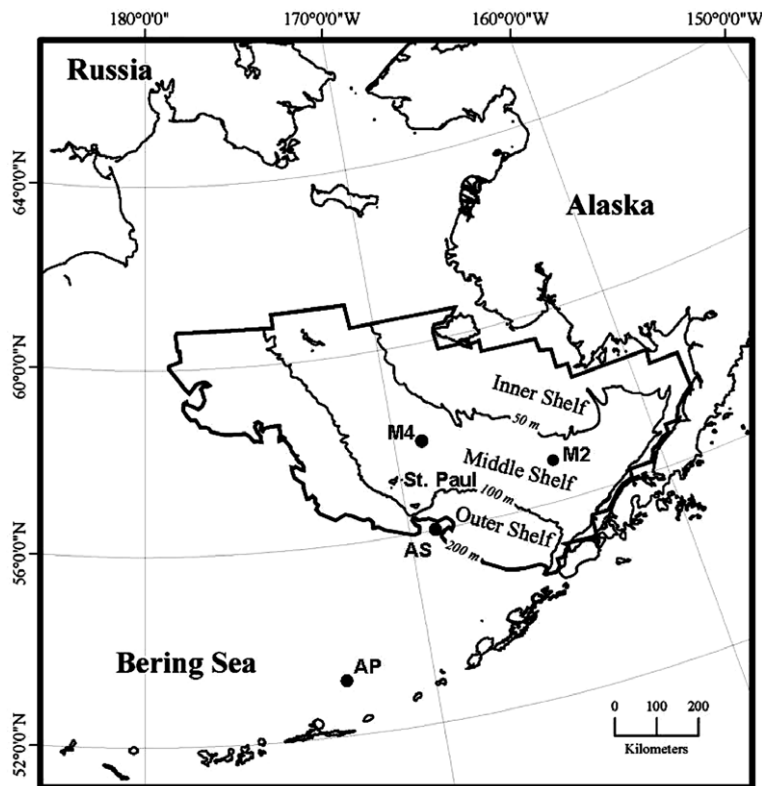


Fig. 1. Map of the eastern Bering Sea showing the NOAA Fisheries standard bottom trawl survey area (heavy line), FOCI mooring 2 location (M2, 56.9°N, 164.1°W), mooring 4 location (57.9°N, 168.9°W), along-Peninsula wind stress location (AP, 53°N, 173°W), along-shelf wind stress location (AS, 56°N, 169°W), and three hydrographic domains (inner, middle and outer shelves) separated by the 50 m and 100 m isobaths.

variables at lags corresponding to the larval (age-0), early juvenile (age-1), and late juvenile (age-2) stages. A secondary goal was to identify environmental indicators that best reflect the potential mechanisms driving pollock recruitment. We updated existing indicators to reflect the most recent conditions and developed new indicators to reflect our best understanding of walleye pollock recruitment dynamics. Finally, we attempted to quantify the relative importance of bottom-up and top-down controls in determining the recruitment of walleye pollock.

2. Hypotheses linking pollock recruitment to environmental variables

Based on previously established or proposed relationships, we examined four general hypotheses related to the major sources of environmental variability that may affect recruitment of walleye pollock in the Bering Sea. We briefly summarize the hypothesized mechanisms linking variability in the physical environment to pollock recruitment and discuss relevant environmental variables that will be used as potential predictors of recruitment.

2.1. Winter ice conditions and the cold pool (cold-pool hypothesis)

The extent of ice cover on the eastern Bering Sea shelf has previously been shown to be related to pollock recruitment (Fair, 1994; Quinn and Niebauer, 1995), and the cold-pool hypothesis of Wyllie-Echeverria and Wooster (1998) suggests one potential mechanism. Following cold winters with extensive ice cover, a cold pool of water remains on the middle shelf and concentrates juvenile pollock (age-1) on the outer shelf, where they

are exposed to increased mortality from cannibalism (Ohtani and Azumaya, 1995; Wyllie-Echeverria and Ohtani, 1999).

To test the cold-pool hypothesis, we updated an index of the spatial extent of the cold-pool, estimated average summer bottom temperatures on the shelf, and compiled several climate indices that reflect winter atmospheric conditions and drive variability in temperature and ice conditions. In addition, we constructed measures of “cannibalism potential” to examine relationships between the size of the cold pool and the estimated intensity of cannibalism on juveniles. These indices are described in detail below. Specific questions to be examined with respect to winter ice conditions and the cold pool include: Are recruitment and/or survival rates of pollock related to the severity of ice conditions or the size of the cold pool? Is cannibalism more likely to occur if the cold pool is large? What life stage or stages (age-0, age-1, or age-2), if any, are most strongly affected by ice conditions and the cold pool?

2.2. *Advection (larval transport hypothesis)*

Advective processes in the basin and advection onto the shelf exert a strong influence on both the supply of nutrients and the distribution of pollock eggs and larvae (Napp et al., 2000). While little is known about interannual variability in sub-surface flows onto the shelf, model results suggest considerable interannual variability in surface layer flows (Ingraham et al., 1991; Wespestad et al., 2000). This variability leads to interannual variations in the food supply of larval pollock, particularly on the outer shelf (Napp et al., 2000), and therefore affects the growth and survival of larval walleye pollock. In addition, certain patterns of surface flow on the shelf may separate larval pollock from adults, thus reducing cannibalism (Wespestad et al., 2000). Strong year-classes of walleye pollock are produced in years with strong onshore transport (to the north and east), while weak year-classes are produced in years of minimal onshore transport during the larval stage (Wespestad et al., 2000). We refer to the latter hypothesis as the larval transport hypothesis. We obtained indices of surface currents and atmospheric conditions to examine relationships between advection and year-class success. In addition, we modified and updated an index of separation between juveniles and adults (Wespestad et al., 2000) and constructed an alternative index of cannibalism potential to examine whether advection influences survival by altering the amount of cannibalism. Specific questions to be examined include: Are surface currents (distance and direction of flow) in the spring and early summer related to the survival and recruitment of walleye pollock? Is the relative distribution of juveniles and adults, and hence the potential for cannibalism, related to surface transport? Are indices of advective processes over the shelf and shelf-slope exchanges related to recruitment success?

2.3. *Timing of ice retreat and predator abundance (oscillating control hypothesis)*

In addition to the spatial extent of sea ice, the timing of ice retreat has important implications for primary and secondary productivity on the shelf. The timing of retreat is related to the timing of the spring bloom and may regulate growth of forage fish and their pelagic predators through mechanisms that were recently summarized in the oscillating control hypothesis (OCH, Hunt et al., 2002). The OCH builds on recent observations that late ice-retreat (i.e., after light levels have increased sufficiently to allow significant phytoplankton production) typically results in an early, ice-associated bloom in a cold, low-salinity layer along the receding ice edge (Niebauer et al., 1995; Stabeno et al., 2001). Cold temperatures during these ice-associated blooms limit zooplankton production (Coyle and Pinchuk, 2002), such that most of the phytoplankton production is not consumed in the water column and instead sinks to the bottom (Walsh and McRoy, 1986). Therefore, prey limitation is likely to limit the survival of pelagic larvae and juveniles of walleye pollock (bottom-up regulation). When these conditions coincide with high abundances of predators, survival of juveniles will be further reduced due to heavy predation, implying both bottom-up and top-down limitations on survival. In contrast, if ice retreats in early spring, light limitation prohibits an ice-associated spring bloom. Instead, the main spring bloom occurs later in the season when summer stratification commences (Stabeno et al., 2001). As a result, the bloom occurs in relatively warm water, zooplankton production is not limited by temperature, and abundant prey are available for larval and juvenile pollock on the shelf (Hunt et al., 2002). According to the hypothesis, growth and survival of pollock are enhanced by bottom-up

Table 1

Effects of ice retreat and predator abundance on recruitment of walleye pollock as predicted by the oscillating control hypothesis (see text)

Predator biomass	Ice retreat	
	Early (+)	Late (–)
High (–)	+/-	--
Low (+)	++	+/-

The expected response ranges from a strong negative effect (--) over neutral or ambiguous effects (+/-) to strong positive effects (++)

regulation during the onset of a warm regime because the abundance of piscivores tends to be low following a cold, less productive regime. In contrast, survival and recruitment are controlled through top-down processes once the biomass of piscivorous predators, including adult pollock, has increased to high levels. In addition to a shift from bottom-up to top-down control, the OCH may imply a shift from control of larval mortality to control of juvenile mortality. Such a shift has been observed in the Gulf of Alaska (Bailey, 2000), where recruitment of walleye pollock was largely determined by environmentally-driven larval mortality prior to the mid-1980s, and by predation-driven juvenile mortality after the mid-1980s, which resulted from large increases in predatory flatfishes (primarily arrowtooth flounder, *Atherestes stomias*, and Pacific cod, *Gadus morhua*).

The OCH implies that there is a threshold relationship between the timing of ice retreat and survival of pollock that is modified by the abundance of potential predators such as cannibalistic adults, which are responsible for the majority of predation on juvenile pollock. Expected responses of recruitment to the timing of retreat and different levels of predator biomass are summarized in Table 1. To examine the effects of ice retreat and to test the OCH, we constructed several indices that reflect spring ice conditions and the timing of ice retreat, as well as indices of predator biomass and predation mortality. Specific questions to be examined include: Is survival of pollock enhanced if ice retreats early? Is recruitment reduced at high levels of predator biomass? Does the effect of predator abundance (top-down control) depend on the timing of the bloom and conversely, does the effect of ice conditions (bottom-up control) depend on predator abundance?

2.4. Mixed layer dynamics and summer production

While the advance and retreat of sea ice are major seasonal events over the Bering Sea shelf, conditions on the shelf during summer are strongly influenced by solar radiation, wind mixing, and tidal mixing (Overland et al., 1999; Stabenon et al., 2001). The stability of the mixed layer, as determined by temperature and salinity conditions and by the frequency and intensity of storms, controls the supply of nutrients to the surface layer, which modifies the productivity and species composition of the plankton community (Napp et al., 2000). Variability in these processes results in variations in primary productivity on the order of 30–50%, as well as large differences in the species composition of the phytoplankton community (Sambrotto and Goering, 1983), thereby affecting feeding conditions for walleye pollock. The influence of summer conditions on pollock survival and recruitment have not been examined previously, but we hypothesize that recruitment success of walleye pollock will reflect these conditions. Our initial expectation was that survival would increase with the amount of summer primary and secondary production, as determined by the strength and duration of summer stratification and the amount of nutrients mixed into the surface layer during the summer (entrainment). However, intense wind mixing may limit primary production and/or feeding success of larval pollock, which could result in a dome-shaped relationship between pollock recruitment and wind mixing as has been observed in some upwelling systems (Cury et al., 1995), in the laboratory (MacKenzie et al., 1994), and in modelling studies (Megrey and Hinckley, 2001).

To examine relationships between wind mixing, summer stratification, and pollock survival, we obtained wind data from St. Paul, model-based wind indices for the shelf region, and estimates of stratification and entrainment of nutrients into the surface mixed layer based on a simple one-dimensional mixed-layer model. Specific questions to be examined with regard to summer mixed-layer dynamics include: Does recruitment success increase with the amount of new production in the summer, as estimated by entrainment? Is recruitment related to other mixed-layer characteristics such as depth or temperature of the mixed layer or the timing of

the onset of stratification? Is recruitment linearly or non-linearly related to wind mixing? What life stages are primarily affected?

3. Methods

To analyze the above hypotheses statistically we developed a comprehensive set of biological and environmental indicators that relate directly or indirectly to one or more of the hypotheses. These indicators varied in quality and ranged from direct measures of physical environmental variables, such as sea surface temperature, to derived biological indices such as a crude index of cannibalism potential. Physical indices were averaged over the most relevant, biologically meaningful time and space scales, based on convention or on our best judgement. Brief descriptions of each index used in the analysis and of the underlying data sources are included in Appendix 1.

3.1. Walleye pollock data and biological indices

3.1.1. Stock assessment data

Estimates of age-2 recruitment, female spawning stock biomass (SSB), and total adult (age 3+) biomass (*B*) of walleye pollock in the eastern Bering Sea from 1964–2003 (Fig. 2a) were obtained from the most recent

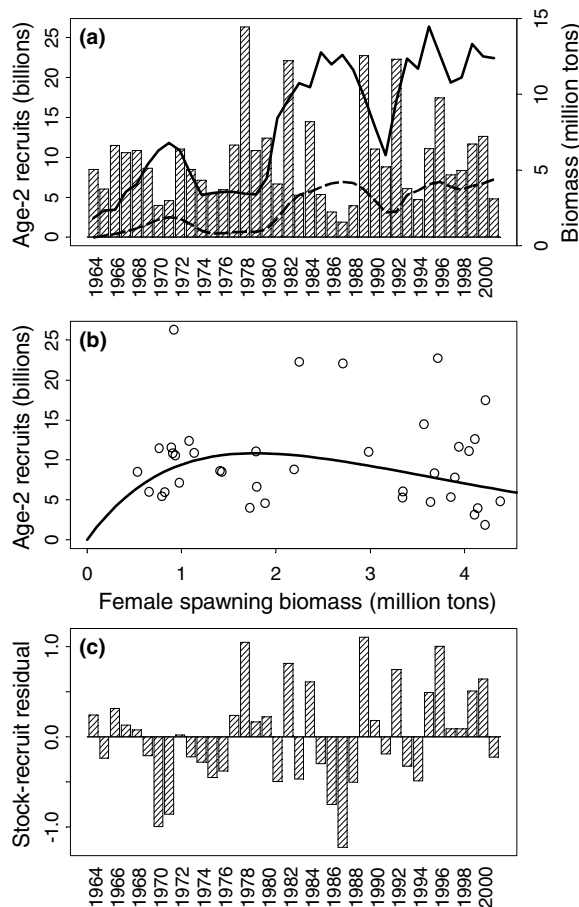


Fig. 2. Time series of (a) age-2 recruitment (bars), age-3+ biomass (solid line), and female spawning stock biomass (dashed line) of eastern Bering Sea walleye pollock, 1964–2001 year classes, (b) stock–recruitment relationship with Ricker model fit, and (c) time series of residuals from Ricker fit.

stock assessment (Ianelli et al., 2003). While stock assessment estimates of biomass and recruitment are highly uncertain, especially for recent years, they represent the best available information on stock size and year-class strength. The recruitment series has been characterized as weak to average year-classes interspersed by sporadic strong recruitment, such as in 1978, 1982, 1989, and 1992 (Fig. 2a). To estimate variability in spawner-to-recruit survival, we fit a Ricker stock–recruitment model that allowed for first-order autocorrelated errors (Quinn and Deriso, 1999) to the relationship between estimated recruitment and female spawning biomass (Fig. 2b). The resulting stock–recruit residuals were used as an index of spawner-to-recruit survival rates (SR index, Fig. 2c). The index reflects variability in survival after adjusting for density-dependent effects of spawner abundance. Much of the observed density-dependence in the spawner–recruit relationship may be attributable to cannibalism of adult pollock on juveniles (Wespestad and Quinn, 1996).

3.1.2. Indices of predation/cannibalism

Three of the four main hypotheses are related either directly or indirectly to predation. To help evaluate these hypotheses, we obtained estimates of total predation mortality for age-0 and age-1 pollock from 1979 to 2002 based on a multi-species virtual population analysis (MSVPA) model for the eastern Bering Sea (Livingston and Jurado-Molina, 2000, Pat Livingston, AFSC, NOAA, personal communication). In addition, two indices of cannibalism potential were constructed. First, we updated an index of spatial separation originally proposed by Wespestad et al. (2000) to include years through 2003. Our index differed from that of Wespestad et al. (2000) in that we only included a fixed set of 306 stations that were sampled consistently between 1982 and 2003 to avoid biases due to differences in sampling locations among years. We found that this index of separation had several shortcomings. In particular, zeroes had too large an influence on the magnitude of the index. Therefore, we constructed an alternative index that measured the degree of association (I_A) between juveniles (<20 cm, predominantly age-1) and adults (>40 cm, predominantly age-5+). The index was computed across the same fixed set of 306 stations within a given year (1982–2003) as follows:

$$I_A = \sum_{i=1}^n \left(J_i / \frac{1}{n} \sum_{i=1}^n J_i \right) \left(A_i / \frac{1}{n} \sum_{i=1}^n A_i \right) / n$$

where J_i and A_i are the CPUE (by weight) of juveniles and adults at station i , respectively, and n is the number of stations. The CPUE values at a given station were standardized by the average abundance across all stations and can be loosely interpreted as the relative likelihood of encountering either juveniles ($J_i / [\sum J_{ji} / n]$) or adults ($A_i / [\sum A_{ji} / n]$) at a given station. The product of these terms, summed across all stations, measures the degree of spatial association between demersal juveniles and demersal adults at the time of the survey and therefore reflects the potential for cannibalism to occur during this period. However, the index does not reflect the potential vertical separation or overlap between pelagic juveniles and adults in the water column and therefore is only a crude measure of cannibalism potential.

3.2. Atmospheric indices

Regional air temperature and wind directly influence ocean conditions on the Southeast Bering Sea shelf.

3.2.1. Air temperature

Monthly averages of measured air temperatures at St. Paul airport as well as at stations in Nome, Bethel, and King Salmon were obtained from the Western Regional Climate Center (Appendix 1) and cover the period from at least 1955–present. Air temperatures tended to follow a regular seasonal pattern with higher variability in the winter months. Two missing values in the St. Paul time series were estimated by fitting a seasonal, auto-regressive time series model to the monthly air temperature series and substituting predicted values. Annual anomalies were computed as weighted annual averages of the January through December means of each year, with more weight on the winter months. The weights used to compute averages were the loadings from a principal components analysis of the annual series of January, February, March, etc., means. The index showed a series of exceptionally low temperatures in the early- to mid-1970s at St. Paul Island, followed by a series of warm years from 1976 to 1982 (Fig. 3a). Annual air temperature anomalies

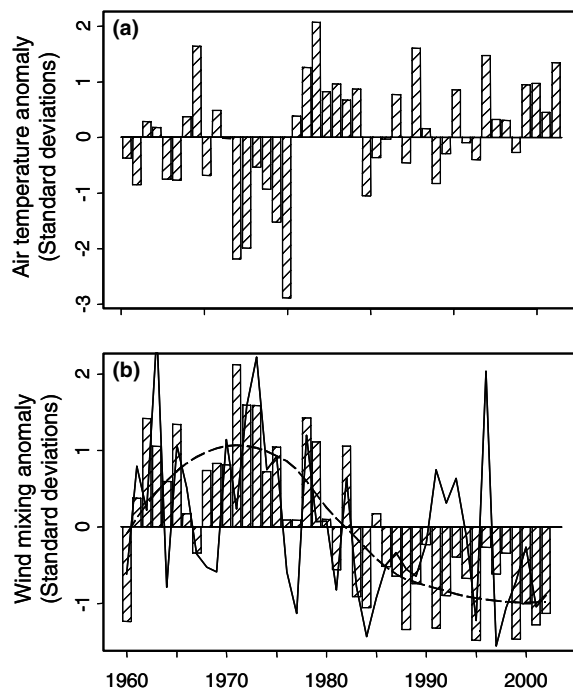


Fig. 3. Time series of (a) standardized annual air temperature anomalies at St. Paul Island, 1960–2003 and (b) standardized summer (May–September) wind mixing averages for St. Paul Island (bars) and at Mooring 2 location (solid line, from NCEP reanalysis) with LOESS fit (dashed line).

at St. Paul Island on the Bering Sea shelf were less strongly correlated with the mainland stations ($r = 0.59$ – 0.68 , $p < 0.05$ in all cases) than the mainland stations were with each other ($r = 0.89$ – 0.93 , $p < 0.01$). St. Paul was most representative of temperatures on the shelf, as evidenced by strong correlations with sea ice conditions (Correlation with combined ice severity index described below: $r = -0.91$) and water temperatures (SST: $r = 0.43$, BT: $r = 0.75$). Hence, we used only the St. Paul air temperature series for further analyses, which should adequately represent annual average air temperature conditions over the eastern Bering Sea shelf.

3.2.2. Wind forcing

Indices of wind mixing, along-shelf wind stress, and cross-shelf wind stress were obtained from modelled wind fields and from daily measured winds at St. Paul airport. Bond and Adams (2002) derived several indices from the National Centers for Environmental Prediction (NCEP) reanalysis output (Kalnay et al., 1996). Updated versions of three of their indices through 2002 were obtained from Nick Bond (JISAO, University of Washington, Seattle, personal communication). First, a winter (December–April) average of wind stress at 53°N , 173°W (Fig. 1), rotated into the along-peninsula direction, provides an index of the direct wind forcing of the Aleutian North Slope Current which is related to the flow onto the southern Bering Sea shelf (Bond and Adams, 2002). Second, a summer (May–September) average of along-shelf wind stress near Pribilof Canyon from NCEP (56°N , 169°W , Fig. 1) is an index of water exchange between the slope region and the shelf. Third, the May–September average wind mixing anomaly at the site of a biophysical mooring (Mooring 2, Fig. 1) is an index of summer wind mixing on the middle shelf (Fig. 3b). While the quality of the NCEP output is high in the Bering Sea, it is unclear to what extent these indices reflect biologically important mechanisms, hence analyses using these atmospheric indices are considered exploratory.

Wind data at the St. Paul station were obtained from the National Climatic Data Center (courtesy of Dave Kachel, PMEL, NOAA, Seattle, personal communication) covering the period January 1, 1951 to August 31, 2002. Wind speeds were recorded every three hours through July 1981 and hourly thereafter. Missing values were prevalent throughout the data set, but were usually restricted to missing hours within a day. Despite

these missing values, daily averages could be calculated continuously over the period of interest except for three individual days, which were ignored in computing monthly or seasonal means. We constructed a summer wind-mixing index by computing daily averages of the cube of measured wind speeds, and averaging daily values from May 1 to September 30 (Fig. 3b). Measured wind mixing at St. Paul was reasonably well correlated with the model-based index of summer wind mixing anomalies at Mooring 2 ($r = 0.58$, $p < 0.001$) but shows more consistently negative anomalies in the last two decades. We consider the St. Paul wind mixing index to be representative of wind mixing over much of the shelf and used it in the analyses. Results based on the model-based index were similar and are not shown. Finally, we computed an index of spring and early summer winds in the SW-NE direction (cross-shelf winds) by averaging wind speeds for the April–June period. These may affect larval drift patterns, similarly to a wind index that has been used to predict year-class strength of tanner crab in the Bering Sea (Rosenkranz et al., 2001).

3.3. Indices of ice and temperature conditions

3.3.1. Sea ice extent

While the southernmost extent and timing of sea ice retreat along 169°W has been used in the past to summarize ice conditions on the shelf (Wyllie-Echeverria, 1996), as have observations of sea ice at Mooring 2 (e.g., Stabeno et al., 2001), a single transect or a single point cannot adequately describe sea ice over the 463,000 km² area of ocean contained within the NMFS survey area (Fig. 1). Therefore, we estimated the proportion of the survey area covered by sea ice, averaged over the winter season, based on digital ice charts for the southeastern Bering Sea region (1972–2003, Appendix 1). All digital ice charts had a resolution of at least 0.25 decimal degrees. Sea ice was defined as regions with $\geq 30\%$ ice concentration, following Wyllie-Echeverria (1996). The average weekly percentage of ice-covered ocean was calculated for January–May (approximately corresponding to International Organization for Standardization, or ISO week numbers 1–22) using ArcGIS geographic information system software (Ormsby et al., 2001). Based on weekly averages, we developed indices for the spatial extent of sea ice and for the timing of ice retreat similar to those of Palmer (2003). Spatial ice extent over the NMFS trawl survey region was calculated as a simple average of all weekly ice concentrations (Fig. 4a). This Spatial Sea Ice Index (SSI), agreed closely with an ice cover index (ICI) developed at the Pacific Marine Environmental Laboratory (PMEL), NOAA (Appendix 1, correlation coefficient: $r = 0.84$). The ICI combines a number of disparate indices, but has the advantage of covering a considerably longer time period (1954–2003, Appendix 1).

3.3.2. Timing of ice retreat

A temporal sea ice index (TSI, Fig. 4b) was computed as the standardized anomalies of the first week during which the approximate fraction of the NMFS survey area covered by $\geq 30\%$ ice was less than 20%. This correlated well with a similar but spatially restricted index of ice retreat from a 2° by 2° region centered at 58°N, 164°W (ICT, Appendix 1, $r = 0.73$). Differences between these indices during some periods most likely reflect the restricted spatial extent of the ICT compared to the TSI. Ice retreat at Mooring 2 generally occurred earlier than ice retreat averaged over the entire NMFS survey area. For example, in 1980, 1987, and 1991, the ICT was 2–5 weeks earlier than the TSI, whereas it was later than the TSI in 1985, 1999, and 2002–2003.

3.3.3. Cold pool index

This index was based on the fraction of the NMFS survey area where bottom temperatures were < 2 °C during the summer. For each NMFS survey from 1973–2003 (except 1974 and 1977, when data were insufficient), we first contoured bottom temperature using all measurements available between May 1 and August 31 of a given year. The 2 °C isopleth was estimated using a universal kriging approach implemented in ArcGIS. Because the temperature measurements did not always occur at the same time of year (mean sampling date ranged from June 13 in 1976 to July 21 in 1985), we adjusted for the date of sampling by removing the seasonal warming trend. This trend was estimated by fitting a linear regression of the fraction of the survey area with temperatures < 2 °C on the mean sampling date ($R^2 = 0.68$). Standardized residuals from the regression line were used as an annual index of the cold pool anomaly (CPI, Fig. 4c).

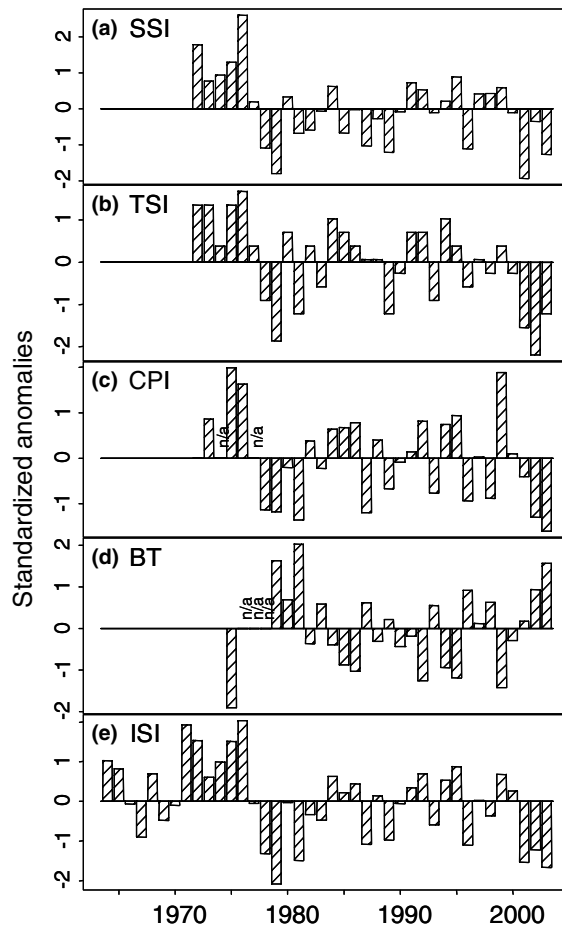


Fig. 4. Standardized time series of (a) spatial sea ice extent SSI, (b) timing of ice retreat TSI, (c) cold pool index CPI, (d) bottom temperature anomaly BT, and (e) combined, reconstructed ice severity index on the eastern Bering Sea shelf (ISI, see text).

3.3.4. Summer bottom temperatures

Like the cold pool index (CPI), average bottom temperatures in the NMFS survey area were estimated from temperature measurements taken during summer trawl surveys. Annual anomalies of bottom temperature across the survey area (Fig. 4d) were estimated by fitting a generalized additive model of measured bottom temperatures on latitude, longitude, depth, and sampling date (day of year) as continuous covariates and year as a categorical covariate. Because day of year was included as a covariate, the estimated annual means are implicitly adjusted for differences in sampling dates across years. The model fit was satisfactory and the index reflected annual means more accurately than a simple area-weighted average of temperatures across survey stations, which can be severely biased in years when sampling occurred much earlier (e.g., 1999) or later (e.g., 1985) than average.

3.3.5. Combined ice severity index

All ice and bottom temperature indices, including the southernmost extent of sea ice, the SSI, TSI, CPI, and average bottom temperature anomaly were highly correlated (Table 2). Therefore, we captured overall variability in winter sea ice conditions between 1972 and 2003 by deriving a single index for ice severity based on a principal components analysis of these 5 variables. The first principal component (PC 1) accounted for 74% of the overall variability in these variables, while the second PC accounted for an additional 16%. A high value of PC 1 corresponded to cold bottom temperatures, large average ice concentrations that extended far to the south, a late ice retreat, and a large spatial extent of the cold pool. The second PC was

Table 2

Cross-correlations among various ice related indices (below diagonal) and corresponding *P*-values (above diagonal)

	168W	SSI	TSI	CPI	BT
168W		<0.001	<0.001	<0.001	0.046
SSI	−0.796		<0.001	<0.001	<0.001
TSI	−0.549	0.790		<0.001	<0.001
CPI	−0.505	0.734	0.820		<0.001
BT	0.464	−0.628	−0.754	−0.942	

Indices include southernmost extent of sea ice along 168°W (168W), spatial sea ice index (SSI), temporal sea ice index (TSI), cold pool index (CPI), and average bottom temperature (BT). See text and Appendix 1 for description of indices.

primarily correlated with the southernmost ice extent. The index was extended back in time (before 1972) by fitting a multiple regression of the 1972–2003 index values on St. Paul air temperatures, the Siberian–Alaskan Index, and the Aleutian low pressure index ($R^2 = 0.87$, see Appendix 1 for description of indices) and using the fitted model parameters to predict ice severity for the period 1964–1971. The resulting reconstructed index covered the period 1964–2003 and was standardized to obtain our final ice severity index (ISI) (Fig. 4e).

3.3.6. Sea surface temperature

Indices of winter and summer sea surface temperature (SST) were based on ship-of-opportunity observations, satellite observations, and measured temperatures from summer bottom trawl surveys. As a monthly measure of SST we used NOAA reconstructed (1900–1981) and NOAA Optimum Interpolation SST version 2 data (1982–2003, Reynolds et al., 2002, Appendix 1). A yearly winter SST index was based on average SSTs from December to February over an area on the eastern Bering Sea shelf between 57–59°N and 163–171°W. Similarly, we constructed a summer index based on May–September averages over the same area. We compared NOAA reconstructed SST to a summer SST index based on direct temperature measurements obtained during summer bottom trawl surveys (1975, 1979–2003). The index was computed using the same approach we used to estimate annual means of bottom temperature described above. The survey-based index agreed well with NOAA reconstructed SST averaged over the May–September period (correlation coefficient: $r = 0.87$).

3.4. Surface transport index

Indices of surface transport during the spring and early summer were based on simulated ocean surface currents. The ocean surface current simulation model (OSCURS, Ingraham and Miyahara, 1988) was used to simulate a 90-day drift of a particle released at the surface at 55.2°N, 164.5°W, corresponding to the historic center of pollock spawning on April 1 (median date of spawning), as described in Wespestad et al. (2000). We used a refined version of the OSCURS model (URL: <http://www.pfeg.noaa.gov/products/las/OSCURS.html>) to update drift trajectories for each year from 1967 to 2003, resulting in indices somewhat different from those used by Wespestad et al. (2000). The northernmost latitude of the 90-day drift trajectory and the final latitude and longitude of the trajectories on June 30 were used as indices of egg and larval drift during their first 3 months of life. These indices are relatively crude measures of larval transport because they do not account for the vertical distribution of larvae and it is unclear how well the OSCURS model captures upper layer circulation on the Bering Sea shelf.

3.5. Model-based indices of mixed layer dynamics in the summer

In summer, after the spring bloom has depleted the surface water of nutrients, vertical mixing over the shelf entrains nutrients into the surface layer resulting in further production. To quantify variability in spring/summer stratification and mixing on the shelf we used the results of a one-dimensional mixed layer model (Ladd, unpublished manuscript). The model calculates the density and wind-driven velocity profile in response to imposed atmospheric forcing and was run from May 1 to September 30 for the years 1951–2002. Model runs were validated by comparison with data from two moorings on the southeast Bering Sea shelf (Moorings 2

and 4, Fig. 1). The model reproduced well the temperature, mixed layer depth, and timing of mixing events in mooring data during the summers of 1995–2002.

Mixed layer dynamics have at least two important implications for biological production. First, the shoaling of the mixed layer in spring due to reduced wind mixing and increased insolation determines the timing of the spring bloom, which may affect feeding success of early larvae and determines the total length of the summer production season. Using the model output, we defined a spring bloom date as the first day when the depth of maximum stratification shoaled to less than 25 m and the temperature difference across the thermocline remained stronger than $0.2\text{ }^{\circ}\text{C m}^{-1}$ for more than one day (Fig. 5a), based on Sambrotto et al. (1986). In years when ice was present after March 15, an early, ice-associated bloom occurred (1995, 1997, and 1999), depleting nutrients in the surface layer. Because the model did not simulate ice-associated processes, the bloom date as calculated was an estimate of when conditions were right for a spring bloom assuming that the nutrients had not been depleted by an earlier ice-associated bloom (or, if such a bloom had occurred, that nutrients had been replenished by strong wind mixing). With the exception of 1998, the model-defined spring bloom date was a good estimator of the actual timing of the spring bloom for the six years when fluorescence data were available for comparison.

Mixed layer dynamics affect not only the timing of the spring bloom but also the magnitude of summer production as nutrient-rich bottom waters are mixed into the surface layer during wind events. An estimate of the cumulative amount of mixing (entrainment) over the summer was calculated as the amount of mixed layer deepening measured daily and summed for all mixing events in July and August (Fig. 5b). To examine the influence of mixed layer dynamics on walleye pollock we used the estimated bloom date, the entrainment index, and a summer wind mixing index based on data from St. Paul (see Section 3.2 above).

3.6. Statistical data analysis

We examined the distribution of all variables or indices for extreme outliers or strongly skewed distributions that would require transformation prior to modelling. Linear relationships among the variables were assessed by computing pairwise Pearson product moment correlations among all indices, using all years for which data were available. Pairwise bivariate plots of variables were examined to screen for obvious non-linear relationships. All tests of hypotheses involving the statistical significance of correlations were adjusted for autocorrelation based on the method of Pyper and Peterman (1998).

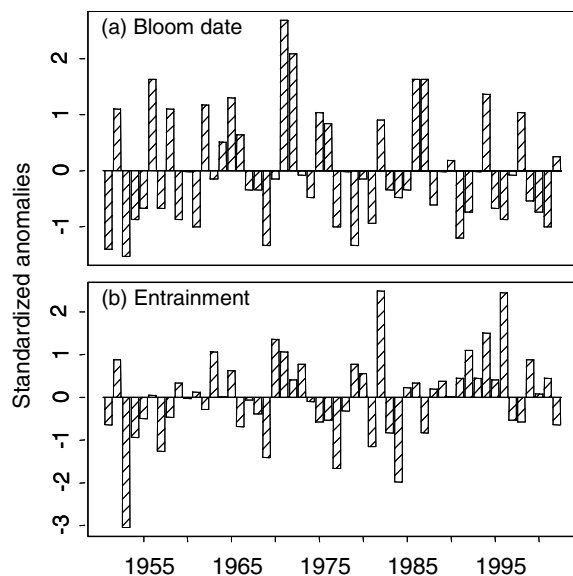


Fig. 5. Standardized time series of (a) bloom date anomaly and (b) entrainment anomaly estimated from mixed-layer model for the middle shelf of the Bering Sea.

For each of the relationships and hypothesized mechanisms described above, we selected a limited subset of potentially important variables or indices from those listed in Appendix 1. We included only variables that either established or reflected conditions during the larval and juvenile periods (ages 0–2). We then selected the best statistical model for predicting walleye pollock survival or recruitment by following a series of steps similar to those recommended by Burnham and Anderson (1998):

We developed first a “global” model that included all of the explanatory variables for a given hypothesis that we believed to be important based on prior knowledge, typically consisting of two or three independent variables. For example, the CPI and an index of predator abundance were used to examine the cold-pool hypothesis. Where several alternative indices were available (for example two indices of summer SST), we fit and examined models using one of the indices at a time and chose the most appropriate index based on the length of the available time series and goodness-of-fit criteria. If no objective choice could be made among several alternative indices, we used data reduction techniques such as principal component analysis to combine similar indices into a single index for modelling. The selection and processing of variables was somewhat subjective, but was largely based on prior information and was intended to minimize the risk of identifying spurious relationships.

In the second step, we constructed generalized additive models (GAM), which can accommodate non-linear relationships between the predictor variables and pollock recruitment or survival (Hastie and Tibshirani, 1990). The model had the following general form:

$$Y_t = \sum_i f_i(X_{i,t+k}) + \varepsilon_t$$

where Y_t was either log-transformed recruitment (R) at age-2 or log-survival ($\log(R/SSB)$) of the walleye pollock year-class spawned in year t , and $X_{i,t+k}$ was the i th predictor variable affecting juvenile pollock during year $t+k$ ($k=0, 1, \text{ or } 2$), f_i denotes a smooth function of the i th predictor variable, and ε_t is the residual error. Models of log-survival always included SSB as an independent variable (generalized Ricker model) to account for density-dependent effects of spawner biomass. Environmental variables were lagged by k years relative to the year of spawning to identify effects that may occur at different times. We fit separate models for each of three early life stages to reflect environmental conditions during the larval ($k=0$), early juvenile ($k=1$), and late juvenile ($k=2$) stages. Generalized additive models use a non-parametric regression approach that uses smooth functions (smoothing splines) of the predictor variables in place of linear functions. A cross-validation approach was used to choose the degree of smoothing for each variable (Wood, 2000), and an approximate F test, in combination with visual examination of the fit, was used to determine whether a relationship was significantly different from linear (Hastie and Tibshirani, 1990). Whenever possible, appropriate linear or quadratic relationships were substituted for smooth fits to facilitate statistical model comparisons. Model residuals were tested for significant (first-order) autocorrelation ($p < 0.05$) and, if present, we accounted for such autocorrelation using generalized least-squares regressions with first-order auto-correlated residuals.

In the third step, the fit of the global model was carefully examined (residual patterns, R^2 , other goodness-of-fit criteria), and we proceeded only if the global model provided an acceptable fit. Otherwise, the general hypothesis was rejected. Fourth, we derived a set of plausible sub-models under each hypothesis, which were simplifications of the global model. The relative weight of evidence for each of the models in this a priori set of candidate models was evaluated, and the best performing model was chosen using the small-sample Akaike Information Criterion (AIC_c) as a model selection criterion (Hurvich and Tsai, 1989).

Because three of the general hypotheses relate to cannibalism of adult pollock on larvae and juveniles, we examined further the potential effects of cannibalism by (1) including adult biomass in models of recruitment and (2) modelling log-recruitment and log-survival as a function of the indices of predation and cannibalism described above. Lastly, we combined the best predictors emerging from the analyses of each hypothesis into a single model, examined the fit of the combined model, derived a set of plausible sub-models, and selected the best overall model or models based on AIC_c .

Results from the statistical analyses were used to assess the strength of evidence for, or against, each of the general hypotheses outlined above and, where possible, to evaluate whether the hypothesized mechanisms had empirical support. Finally, by comparing the estimated effects of cannibalism and predation to the estimated

effects of environmental variables, we assessed the relative magnitude and importance of bottom-up and top-down controls on walleye pollock survival.

4. Results

Walleye pollock recruitment, the dependent variable in most of our models, had a strong positive skew with a number of extreme values, and was log-transformed prior to analysis. The distribution of both log-transformed recruitment and log (recruits-per-spawner), the dependent variable in models of survival, were approximately normal with no obvious outliers. There was no evidence of autocorrelation in the recruitment series and models of recruitment or survival showed no evidence of autocorrelation in the residuals. Most environmental variables had approximately normal distributions and were not transformed. In most cases the environmental variables were used as independent variables in models of recruitment or survival, hence regression assumptions will be met as long as measurement error is small, regardless of their distribution. However, extreme outliers had a strong influence on regression results in some cases.

4.1. Winter ice conditions and the cold pool (cold-pool hypothesis)

Evidence was limited that the extent of sea ice in winter and the extent of the cold pool during the summer, when pollock were 1 year old, were related to subsequent pollock survival or recruitment (Fig. 6a). There was

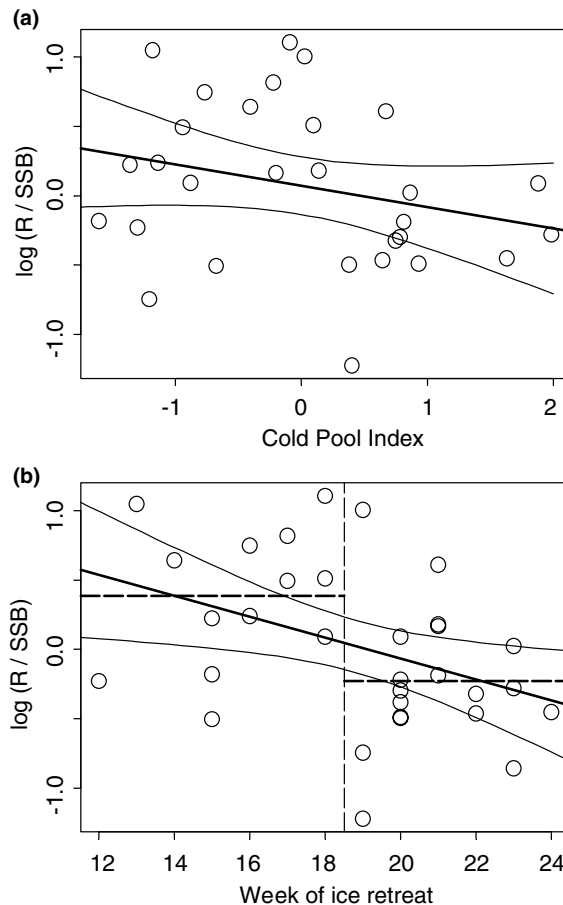


Fig. 6. Partial regression of (a) log-survival of walleye pollock on cold pool index, 1973–2003 with 95% confidence band and (b) log-survival on timing of ice retreat, 1972–2003. Regressions are adjusted for density-dependent effects of spawning biomass. Bottom panel includes fitted means from a one-step intervention model.

no evidence for a non-linear relationship, and the observed linear relationship was primarily due to a large contrast in ice conditions between the early and late 1970s, which coincided with weak and strong year-classes occurring in the early and late 1970s, respectively. The effect was not significant when years prior to 1980 were excluded. There was no evidence of significant effects (95% confidence level) of ice cover, bottom temperature, or cold pool extent on survival during the larval (age-0) or late juvenile (age-2) stages.

There was no evidence that the spatial overlap of juveniles and adults increased during years with a large cold pool, although both the juvenile and adult distributions are affected by the cold pool. The cold pool hypothesis holds that the degree of overlap between juveniles and adults (and hence cannibalism) is larger when the cold pool is more extensive, because juveniles are believed to avoid cold bottom temperatures (Wyllie-Echeverria and Wooster, 1998). However, the linear correlation between our index of the spatial association between juveniles and adults, I_A , and the cold pool index was small and not statistically significant ($r = 0.227$, $p = 0.310$) with no evidence of a non-linear relationship. In years with an extensive cold pool the distribution of all size classes generally shifts toward deeper regions of the shelf and the distribution of adults (but not juveniles) tends to be much farther to the south (Mueter et al., 2004). Finally, there was no evidence that the cold pool index was related to total predation on age-1 pollock (numbers consumed, $r = 0.01$, $p = 0.97$) or to age-1 predation mortality estimated from an MSVPA model for the eastern Bering Sea ($r = 0.10$, $p = 0.63$). Therefore we concluded that there was little empirical support for the cold pool hypothesis.

In addition to examining the effects of the cold pool, and to extend our analysis back in time, we used the combined index of ice severity and several indices of spatial ice extent in models of recruitment and survival. Fits were generally very similar to those based on the CPI, but the ISI index resulted in a better fit in most cases, suggesting that survival of pollock is reduced during periods with generally cold winter conditions (see also below). Due to strong correlations among these indices, it was not possible to separate effects of spatial ice extent from effects related to the size of the cold pool or bottom temperature.

In summary, there was some evidence that cold conditions during the early juvenile stage reduce survival and subsequent recruitment of walleye pollock. However, the observed relationships were not significant after 1980. We found no evidence that the observed relationships were due to increased cannibalism in cold years.

4.2. Timing of ice retreat and the spring bloom (oscillating control hypothesis)

The oscillating control hypothesis (Hunt et al., 2002) invokes a relationship linking ice-associated blooms (which depend on the timing of ice retreat), pollock survival, and predator abundance. To examine survival and recruitment in relation to ice retreat, we used the TSI index (described above and in Appendix 1), which reflects the approximate time when much of the ice has left the shelf. Assuming that years with late ice retreat typically have an ice-associated bloom in cold water and reduced pelagic productivity, average survival and recruitment of pollock should be lower if ice retreat occurs late (cold regime) during the larval and/or juvenile stages. This pattern was supported by the observations, which show a relatively abrupt decrease in average survival of pollock if ice cover in the NMFS survey area during the early juvenile phase remains above 20% in early May (Fig. 6b). The difference in average log-survival (residual from stock–recruit relationship) between years with early and late ice retreat at age-1 was highly significant (one-sided t test: $t = 3.376$, $p = 0.0011$), as was the difference in log-recruitment ($t = 2.49$, $p = 0.0094$). A similar threshold between survival or recruitment and the timing of ice retreat was not apparent during the larval or late juvenile (age-2) stage.

While the OCH implies a threshold in the relationship between prey availability and the timing of ice retreat, the retreat of ice from the shelf is a gradual process and the ice typically melts at different rates and times from different areas. Therefore it is not clear what shape the response of pollock survival or recruitment to the timing indices should take. A GAM model showed no evidence that relationships between indices reflecting timing of retreat and pollock survival were non-linear; therefore we used a linear regression model for comparison with a “two-means” model. There was a significant linear effect of the week of ice retreat at age-1 on log-survival ($\beta = -0.252$, $t = -2.46$, $p = 0.020$, Fig. 6b). No significant effect was found on log-recruitment, nor were effects apparent at the larval or late juvenile stages. While these results provide evidence for the potential importance of an ice associated bloom, timing of ice retreat was strongly confounded with the

spatial extent of ice cover, with summer bottom temperatures, and with the cold pool extent in summer (Table 2), suggesting that the observed relationships could also be due to other temperature-related effects on survival and recruitment.

Under the OCH, relationships between ice retreat and survival or recruitment are modified by the presence or absence of predators, such that the predictions in Table 1 should hold. We tested for differences in recruitment and survival between years with an early ice retreat and low predator biomass (recruitment hypothesized to be high) and years with a late ice retreat and high predator biomass (recruitment hypothesized to be low). Recruitment was generally high when ice retreated early and when the biomass of adult pollock was low during the larval stage, as predicted (Fig. 7, bottom left panel). However, recruitment was highly variable when ice retreated late (i.e., when an ice-associated bloom was more likely to occur) and adult biomass was high. Differences in average recruitment between these two states were significant (one-sided *t* test: $t = 2.20$, $p = 0.022$), but were potentially confounded with other temporal trends in the environment because years when ice retreated early and biomass was low occurred almost exclusively in the 1970s and early 1980s, while late ice retreat and high adult biomass generally co-occurred only after the early 1980s (Fig. 7, top right panel).

The OCH further predicts that stronger bottom-up regulation (e.g., effects of temperature on survival) occurs when predator biomass is low. In contrast, stronger top-down regulation should occur during a warm regime (early ice retreat) when survival is not limited by prey availability (Hunt et al., 2002). We tested the first prediction by fitting regressions of the SR index and log-recruitment on ice severity during the early larval stage for low and high levels of adult biomass separately and comparing their slopes (Fig. 8a and b). Both log-recruitment and survival rate (SR index) were significantly negatively correlated with ice severity at low biomass levels ($p = 0.0048$ and $p = 0.0044$, respectively), but not at high biomass levels, suggesting stronger bottom-up regulation when predator biomass was low. Results were very similar when the timing of ice retreat or the cold pool index was used as independent variable. Similar but weaker relationships were also observed between log-recruitment or the SR index and ice conditions during the larval stage.

We found weak support for the prediction that stronger top-down regulation occurs during years with an early ice retreat. Log-recruitment decreased significantly with adult biomass when ice retreated early ($t = -2.12$, $p = 0.043$) but not if ice retreated late, suggesting top-down regulation through cannibalism during mild years (early ice retreat). Slopes for the SR index showed a similar pattern but the slope was not significant during years with an early ($p = 0.123$, Fig. 8c) or late (Fig. 8d) ice retreat.

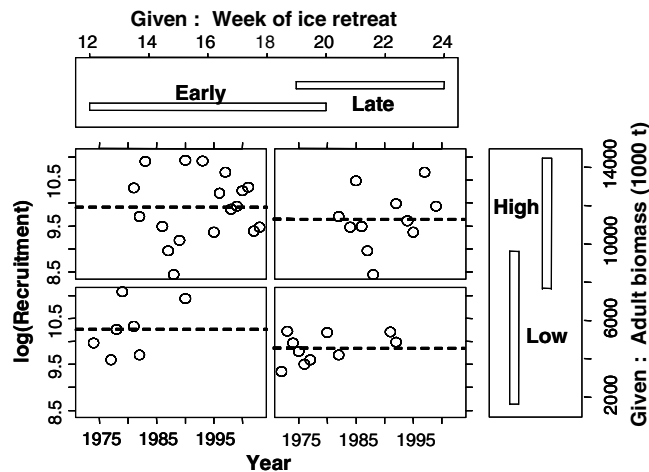


Fig. 7. Log-recruitment of walleye pollock by year class for early and late ice retreat and for two levels of adult biomass. Horizontal dashed lines indicate means across year-classes within each group. Some overlap between early and late ice retreat and between low and high biomass levels was allowed, as indicated by bars, to increase number of observations per quadrant.

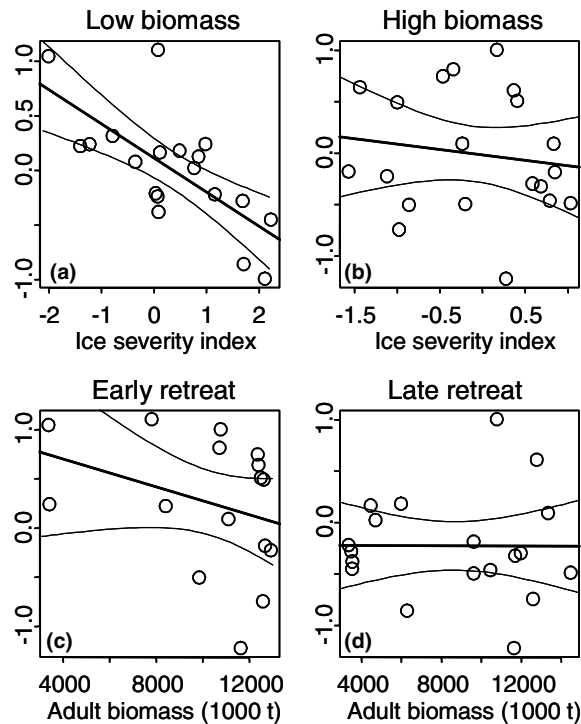


Fig. 8. Partial regressions of log-survival on ice severity index at (a) low and (b) high biomass and partial regressions of log-survival on adult biomass for years with (c) early and (d) late ice retreat. Thin lines indicate 95% confidence bands. Regressions are adjusted for density-dependent effects of spawning biomass.

4.3. Advection (larval transport hypothesis)

We examined potential effects of surface advection on larval and juvenile stages of walleye pollock by modelling log-recruitment and log-survival as a function of simulated surface drift trajectories from the OSCURS model. The AIC_c-best model for predicting recruitment was a simple linear regression of log-recruitment on the final latitude of 90-day drift trajectories (OT.lat) during the post-spawning period (age-0), which was marginally significant ($p = 0.0523$) and explained only 11% of the variability in log-recruitment (Table 3). A positive coefficient implies enhanced survival during years when larvae experience strong northward transport, consistent with the larval transport hypothesis. The model fit was reasonable with approximately normally distributed residuals and no extreme outliers. Models of recruitment as a function of drift trajectories during the juvenile stages (age-1 and age-2) were not significant at the 90% level (Table 3).

Models of log-survival suggest that survival increases with increasing northward transport and with reduced eastward transport (Table 3). There was no evidence for non-linearity in these relationships or significant interactions. The estimated effects of surface transport were very similar during the larval and early juvenile stages, suggesting that similar mechanisms operate during both of these stages (Table 3). In contrast, surface transport variables at the late juvenile stage (age-2) did not significantly improve a Ricker stock-recruitment model. The best models accounted for approximately 25% of the variability in log-recruitment and tended to underestimate strong year-classes and overestimate weak year-classes. Our results agree with previous findings by Wespestad et al. (2000) that pollock survival tends to be enhanced when strong northward surface transport occurs during the first three months after hatching. While strong northward transport is often associated with strong eastward transport (Wespestad et al., 2000), our model results suggest that survival was highest when the component of eastward transport was relatively weak compared to the northward component (negative coefficient for longitude, Table 3).

Table 3

Best multiple regression models of log-recruitment and log(recruits-per-spawner) of walleye pollock on final latitude (OT.lat) and final longitude (OT.long) with interaction term between OT.lat and OT.long

	Age-0		Age-1		Age-2	
	Coefficient	<i>t</i> (<i>p</i> -value)	Coefficient	<i>t</i> (<i>p</i> -value)	Coefficient	<i>t</i> (<i>p</i> -value)
Dependent variable: log(<i>R</i>) (B, OT.long, and interaction term did not improve model fit)						
Intercept	9.934		9.942		9.945	
OT.lat	0.191	2.01 (0.052)				
<i>R</i> ²		0.106		0		0
RSS		11.05		12.46		12.36
<i>F</i> (<i>p</i> -value)		4.04 (0.052)		n/a		n/a
Dependent variable: log(<i>R</i> /SSB) (interaction term not significant)						
Intercept	2.278		2.309		2.340	
SSB	−0.791	−8.14 (<0.001)	−0.796	−8.46 (<0.001)	−0.766	−0.815 (<0.001)
OT.lat	0.335	2.61 (0.014)	0.313	2.44 (0.020)		
OT.long	−0.207	−1.61 (0.117)	−0.254	−1.98 (0.056)		
<i>R</i> ²		0.687		0.694		0.649
RSS		9.51		9.87		11.77
<i>F</i> (<i>p</i> -value)		23.4 (<0.001)		25.0 (<0.001)		66.4 (<0.001)

Female spawning stock biomass (SSB) was included by default as an independent variable in all models of log-survival. Models were fit at three different lags to estimate effects at the larval (age-0), early juvenile (age-1) and late juvenile stages (age-2). Only the models that minimized the small-sample AIC criterion (AIC_c) are shown. Estimated coefficients (Coef) denote change in the dependent variable for a one standard deviation change in the independent variable. The indicated *t* statistic and associated *p*-values are for testing whether individual coefficients differ from zero. The *F* statistic and associated *p*-values measure overall model fit relative to the Null model (intercept only).

The larval transport hypothesis of [Wespestad et al. \(2000\)](#) proposes that larval pollock are separated from adults by surface currents to the northeast during warm years, which tend to be characterized by strong advection. Stronger northward advection during warm years was evident in positive correlations between SST and the final latitude of simulated drift trajectories (OT.lat vs. SST.sum: $r = 0.432$, $p = 0.009$), as well as generally negative correlations between ice variables and OT.lat (ranging from -0.25 to -0.35). Because northward transport and temperature or ice conditions are confounded, it was difficult to separate effects of transport from temperature-related effects on survival. Therefore, we examined relationships between temperature, surface transport, and estimated total predation mortality of pollock at the larval and juvenile stages. Significant negative correlations between the final latitude of 90-day drift trajectories and the estimated total predation mortality of age-0 pollock during the same year (OT.lat vs. M.0: $r = -0.48$, $p = 0.017$) and age-1 pollock during the following year ($r = -0.49$, $p = 0.014$) suggest that northward advection of eggs and larvae may indeed reduce predation on larval and juvenile pollock (from all sources, not just cannibalism). In contrast, we found no significant correlations between the estimated total predation mortality and any of the temperature or ice variables.

The larval transport hypothesis further holds that the degree of spatial overlap between juveniles and adults varies with the spatial distribution of juvenile walleye pollock. Specifically, spatial overlap should be high if juveniles tend to be concentrated on the outer shelf, and should be low if juveniles are concentrated on the middle or inner shelf, away from the adults ([Wespestad et al., 2000](#)). Assuming that our index of association adequately reflects spatial overlap between juveniles and adults, we found the strongest overlap if the center of distribution of age-1 pollock (CPUE-weighted averages of latitude and longitude) was farther south and west from average. The index of association was strongly related to the center of distribution of age-1 pollock as evident in a multiple regression of I_A on the CPUE-weighted averages of depth, latitude and longitude. The regression was highly significant ($p = 0.011$) and all terms were significant at the 95% level, suggesting that the index of association was higher when the average distribution of age-1 pollock was deeper and farther to the south. In contrast, we found no significant relationship between the center of distribution of adults (with respect to depth, latitude, and longitude) and the index of association, suggesting that variability in overlap

between juveniles and adults was primarily driven by variability in the distribution of juveniles, as suggested by Wespestad et al. (2000). However, adult distribution clearly varies among years in response to temperature conditions on the shelf (e.g., Ianelli et al., 2003) and the degree of overlap is a function of the relative distribution of juveniles and adults in a given year.

In addition to the simulated transport trajectories, we examined potential effects of wind forcing, which drives shelf-slope exchanges and circulation on the shelf, on the survival and recruitment of walleye pollock. Exploratory models of log-survival and log-recruitment as a function of cross-shelf and along-shelf wind indices (Wind.AS, Wind.AP, Wind.CS, see Appendix 1) showed no significant effects (F tests: $p > 0.05$ in all cases), suggesting that neither log-survival nor log-recruitment was linearly or non-linearly related to any of these atmospheric variables. Therefore, currently available atmospheric indices of advection onto the shelf or circulation on the shelf do not appear to be useful predictors of pollock recruitment.

4.4. Mixed layer dynamics on the shelf

Although no specific hypothesis has been advanced to relate summer conditions on the shelf to pollock recruitment, summer variability is believed to affect productivity on the Southeast Bering Sea shelf (Stabeno et al., 2001; Hunt et al., 2002). Therefore, we examined potential effects of mixed layer characteristics during the larval and juvenile stages by modeling pollock survival ($\log(R/SSB)$) and recruitment ($\log(R)$) as a function of bloom date, summer sea-surface temperature, wind mixing, and entrainment of nutrients into the surface layer. Generalized additive models suggested a dome-shaped relationship with wind mixing, whereas there was no evidence of non-linearity in relationships with other variables. To facilitate model comparisons, we used multiple linear regression models for selecting the best predictor variables and allowed for a dome-shaped relationship between log-survival and wind mixing by including a quadratic term for wind mixing.

We found the strongest effects of wind mixing and bloom date on log-recruitment and log-survival during the early juvenile (age-1) stage (Table 4). Onset of summer stratification (bloom date) was the only environmental variable included in the best model for the larval stage, while both wind mixing and bloom date were retained for the early juvenile stage (Fig. 9). Survival was generally poor if the estimated bloom date was delayed until early June or later (\sim day of year = 160, Fig. 9a). There was evidence for a dome-shaped

Table 4

Best multiple regression models of log-recruitment and log(recruits-per-spawner) of walleye pollock on wind mixing (St. Paul Island index), squared wind mixing (wind^2), entrainment, summer SST, and onset of summer stratification (bloom date)

	Age-0		Age-1		Age-2	
	Coefficient	T (p -value)	Coefficient	t (p -value)	Coefficient	t (p -value)
Dependent variable: $\log(R)$ (wind^2 , entrainment, and SST not significant at any age)						
Intercept	9.908		9.919		9.923	
Wind			0.179	1.65 (0.108)		
Bloom date	-0.198	-2.05 (0.048)	-0.341	-3.46 (0.001)		
R^2		0.099		0.25		0
RSS		13.04		10.7		14.0
F (p -value)		4.19 (0.048)		6.02 (0.0055)		n/a
Dependent variable: $\log(R/SSB)$ (entrainment, and SST not significant at any age)						
Intercept	3.742		3.382		3.983	
SSB	-0.0006	-9.08 (<0.001)	-0.0004	-4.97 (<0.001)	-0.0007	-7.30 (<0.001)
Wind			0.216	1.48 (0.150)	-0.274	-1.95 (0.059)
Wind^2			-0.260	-2.19 (0.036)		
Bloom date	-0.202	-2.29 (0.028)	-0.307	-3.23 (0.0028)		
R^2		0.705		0.766		0.667
RSS		10.31		7.29		10.52
F (p -value)		43.01 (<0.001)		27 (<0.001)		34.1 (<0.001)

Female spawning stock biomass (SSB) was included by default as an independent variable in all models of $\log(R/SSB)$. See Table 3 for explanation.

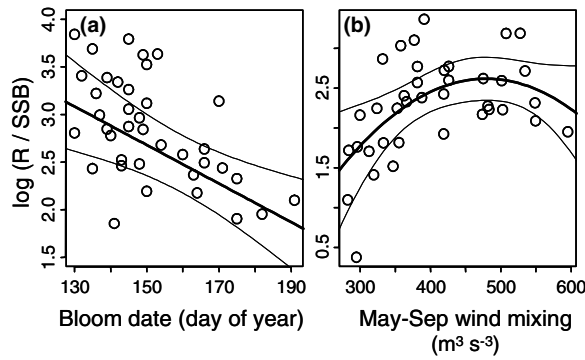


Fig. 9. Partial fits from multiple regression of log-survival (1964–2001 year classes) on female spawning stock biomass (not shown), (a) bloom date and (b) summer wind mixing at St. Paul Island with 95% confidence bands.

relationship between log-survival and wind mixing (*t* test for significance of quadratic term: $p = 0.036$, Table 4), but not between log-recruitment and wind mixing. We found no evidence that either summer SST or the modelled entrainment of nutrients into the surface layer during late summer (July–August) was related to pollock survival or recruitment. Summer SST and entrainment were weakly confounded with bloom date and wind mixing ($|r| = 0.21$ to $|r| = 0.33$), but it is unlikely that this caused spurious results.

4.5. Best combined models of recruitment

Combining the best environmental predictors from each hypothesis into combined models of log-recruitment and log-survival by life stage resulted in multiple regression models with 3–7 independent variables (Table 5). We selected the best predictors among these environmental variables separately at each life stage, and then combined the best predictors at both the larval and early juvenile stages into a single combined model for log-recruitment and log-survival, respectively. No variables at age-2 were included, because we only found one significant variable (wind mixing, Table 4) at this development stage, and it was no longer significant if wind mixing at other ages was included.

The overall AIC_c -best model for log-recruitment suggested (1) a decrease in recruitment when the onset of stratification (bloom date) during the juvenile stage was delayed, (2) an increase in recruitment with summer wind mixing during the juvenile stage, and (3) increased recruitment during years with strong northward transport at the larval stage (as measured by OT.lat). While bloom date at the larval stage did not enter the best model, the estimated coefficients for bloom date were very similar at both life stages. The model for log-survival suggested similar responses in survival rate to bloom date, wind mixing, and OT.lat, but there was strong evidence for a dome-shaped relationship with wind mixing (Table 6). After transforming predicted log-survival rates to log-recruitment, the model accounted for 46% of the overall variability in log-recruitment.

Table 5

Summary of explanatory variables, including adult biomass (B), that were found to significantly affect log-recruitment and log-survival ($\log(R/SSB)$) at the larval (age-0) and early juvenile (age-1) stages

log(recruitment)		log(R/SSB)	
Age-0	Age-1	Age-0	Age-1
B	ISI or TSI	Bloom date	ISI or TSI
ISI	Wind mixing	OT.lat	Wind mixing
B:ISI	Bloom date	OT.long	(Wind mixing)²
Bloom date			Bloom date
OT.lat			OT.lat
			OT.long

Female spawning stock biomass (SSB) was included by default as an independent variable in all models of log-survival. Best predictors (based on AIC_c) of log-recruitment and log-survival at each lag are denoted in bold.

Table 6

Regression results for models of log-recruitment and log-survival using best environmental predictors at the larval and juvenile stages

Independent variable	Coefficient	Standard error	<i>t</i> -value	<i>P</i> -value
Dependent variable: log(recruitment), 1967–2001 year classes				
Intercept	9.052	0.0838	108.03	<0.0001
Bloom date, lag 1	−0.299	0.0883	−3.38	0.0020
Wind mixing, lag 1	0.191	0.0897	2.13	0.0412
OT.lat, lag 0	0.194	0.0851	2.28	0.0295
$R^2 = 0.380$, $F = 6.329$ on 3 and 31 d.f., $P = 0.00179$				
Dependent variable: log(<i>R</i> /SSB), 1967–2001 year classes				
Intercept	1.388	0.0801	17.34	<0.0001
SSB	−0.520	0.1367	−3.80	0.0007
OT.lat, lag 0	0.154	0.0836	1.84	0.0758
Bloom date, lag 1	−0.327	0.0938	−3.49	0.0016
Wind mixing, lag 1	0.253	0.1352	1.87	0.0710
(Wind mixing) ² , lag 1	−0.158	0.0819	−1.93	0.0634
$R^2 = 0.779$, $F = 20.49$ on 5 and 29 d.f., $P < 0.0001$				

All independent variables were standardized to allow comparison of magnitude of coefficients.

The ice severity index or the timing of retreat did not enter any of the best models, although their effects were difficult to distinguish from surface transport (OT.lat) and bloom date due to confounding among these variables, as discussed previously. Both models resulted in a reasonable fit, and model diagnostics suggested that regression assumptions were not violated, although the unusually weak 1987 year-class had a strong influence on both regressions. Re-fitting the models with the 1987 year-class excluded resulted in very similar fits with an improved coefficient of variation for the model of log-recruitment ($R^2 = 0.40$ compared to $R^2 = 0.38$ with 1987 included). Both models captured the pattern of variability in recruitment but tend to underestimate recruitment of extreme year-classes (Fig. 10), which is even more evident on the untransformed recruitment scale.

Finally, we re-fit the best models using only year-classes 1981–2001 to: (1) assess the importance of extreme contrast in recruitment in the 1970s to overall model fit and (2) to compare models using environmental predictors to a model using the index of association as an independent variable (see below). For modeling log-recruitment from 1981 to 2001, the best predictor variables were the bloom date and final latitude of drift trajectories, both at the larval stage (Table 7). The resulting model explained approximately 30% of the variability in log-recruitment. A very similar model resulted if bloom date at the juvenile stage was used instead of, or in addition to bloom date at the larval stage. All estimated coefficients were consistent with those estimated from the longer time series (Table 6) and coefficients for bloom date at both the larval and juvenile stage had the same sign and similar magnitude. The best model of log-survival for the 1981–2001 year classes was very similar to the model for the 1967–2001 year classes, but OT.lat at the larval stage no longer entered into

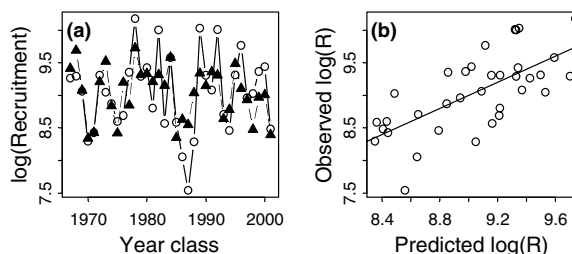


Fig. 10. (a) Time series of observed (open circles) and predicted (solid triangles) log-recruitment by year class and (b) observed against predicted log-recruitment. Predicted values are based on a generalized Ricker model of log(recruits-per-spawner) with wind mixing (linear and quadratic term) during the early juveniles stage (age-1), estimated bloom date during the early juvenile stage, and final latitude of 90-day surface drift trajectories during the larval stage as covariates (1967–2001 year classes).

Table 7

Regression results for best combined models of log-recruitment and log-survival, year classes 1981–2001 only

Independent variable	Coefficient	Standard error	<i>t</i> -value	<i>P</i> -value
Dependent variable: log(recruitment), 1981–2001 year classes				
Intercept	8.943	0.133	67.17	<0.0001
Bloom date, lag 0	−0.276	0.146	−1.88	0.0763
OT.lat, lag 0	0.291	0.154	1.90	0.0738
$R^2 = 0.297$, $F = 3.81$ on 2 and 18 d.f., $P = 0.042$				
Dependent variable: log(recruitment), 1981–2001 year classes				
Intercept	9.035	0.122	74.25	<0.0001
I_A	−0.397	0.124	−3.21	0.0046
$R^2 = 0.352$, $F = 10.3$ on 1 and 19 d.f., $P = 0.0046$				
Dependent variable: log(R/SSB), 1981–2001 year classes				
Intercept	1.393	0.239	5.82	0.0000
SSB	−0.838	0.261	−3.20	0.0055
Bloom date, lag 1	−0.436	0.159	−2.74	0.0145
Wind mixing, lag 1	−0.154	0.348	−0.44	0.6643
(Wind mixing) ² , lag 1	−0.542	0.217	−2.50	0.0238
$R^2 = 0.630$, $F = 6.81$ on 4 and 16 d.f., $P = 0.0021$				
Dependent variable: log(R/SSB), 1981–2001 year classes				
Intercept	1.373	0.212	6.46	0.0000
SSB	−0.668	0.243	−2.75	0.0133
I_A	−0.360	0.129	−2.80	0.0119
$R^2 = 0.547$, $F = 10.87$ on 1 and 19 d.f., $P = 0.0008$				

All independent variables were standardized to allow comparison of magnitude of coefficients. Models using best environmental predictors are compared to models using the index of association between age-1 juveniles and adults (I_A) as independent variable.

the best model (Table 7). Coefficients were larger for the 1981–2001 period and the linear wind mixing term reversed sign. However, this made little difference to the dome shape of the response curve for wind mixing, which was very similar to that in Fig. 9. With three covariates in addition to SSB, the model explained 63% of the variability in log-survival (Table 7), compared to only 35% if a simple Ricker model without covariates was fit to the 1981–2001 year-classes. The model explained 49% of the overall variability in log-recruitment.

4.6. The role of cannibalism and predation

Cannibalism is known to be a major determinant of recruitment variability in walleye pollock and increased cannibalism has been shown to be associated with weak year-classes (Wespestad et al., 2000; Wespestad and Quinn, 1996). Based on diet composition data, it has been estimated that approximately 40% of juvenile production (age 0–1) is consumed by age 2+ pollock (Kerim Aydin, AFSC, NOAA, Seattle, personal communication), implying that cannibalism represents a major source of mortality for larval and juvenile pollock. Cannibalism reduces survival rates of pollock when pollock abundances are high, which may account for the strong density-dependence in the stock–recruitment relationship for walleye pollock in the eastern Bering Sea (Fig. 2b, Wespestad and Quinn, 1996). However, the effects of cannibalism are difficult to separate from other density-dependent effects at the larval and juvenile stages.

To quantify the potential effects of total predation on variability in survival rates, we examined the relationship between estimated age-1 predation mortality (M.1, Appendix 1) and stock–recruit residuals, which reflect variability in log-survival after accounting for density-dependent effects. Linear regression results suggest that age-1 predation mortality accounted for approximately 39% of the overall variability in stock–recruit residuals, which may be considered a minimum estimate of the effect of predation on survival. A maximum estimate was obtained by relating log(R/SSB) directly to age-1 predation without first accounting for the effects of

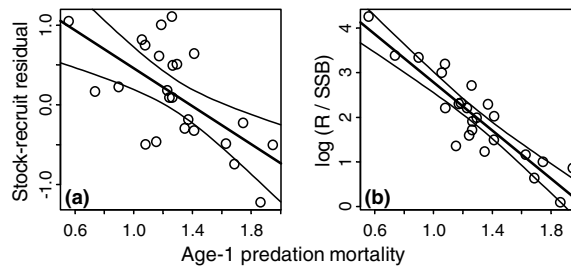


Fig. 11. Linear regressions of (a) residuals from Ricker stock–recruitment model and (b) $\log(R/SSB)$ on total estimated age-1 predation mortality with 95% confidence bands.

spawner abundance (Fig. 11). The resulting relationship suggested that 76% of the variability in log-transformed survival rates ($\log(R/SSB)$) from spawner to age-2 could be accounted for by predation if density-dependence in the stock–recruit relationship is entirely attributed to cannibalism.

Cannibalism mortality depends on the number of adult predators as well as on the availability of juveniles to adult predators. Our index of spatial association between juveniles and adults (I_A) provides a crude proxy for the availability of juveniles to adults, and hence for cannibalism potential. The index was significantly and positively correlated with an independently obtained index of total predation mortality of age-1 pollock (M.1, $r = 0.444$, $p = 0.044$), confirming that increased spatial overlap between juveniles and adults in bottom trawl surveys appears to be associated with increased predation mortality of age-1 juveniles.

Based on this relationship, we assessed the use of I_A as a predictor of recruitment and survival by modeling log-recruitment as a function of biomass and I_A (1982–2002), and by modeling log-survival as a function of SSB and I_A . Biomass was initially included in the model of log-recruitment because both the degree of overlap and the absolute abundance of cannibalistic adults may affect recruitment. However, including biomass did not significantly improve the model. A simple linear regression of log-recruitment of age-2 pollock on I_A during the early juvenile phase resulted in a reasonably good fit that explained 35% of the variability in recruitment for the 1981–2001 year classes. A generalized Ricker model with I_A as a covariate resulted in very similar predictions with R^2 (coefficient of determination) = 0.55, compared to $R^2 = 0.35$ for the simple Ricker model.

4.7. Bottom-up and top-down control

Both bottom-up and top-down mechanisms contribute to the control of walleye pollock survival and recruitment on the eastern Bering Sea shelf. The relative magnitude of bottom-up and top-down controls is difficult to evaluate because predation is dominated by cannibalism, which is confounded with other density-dependent effects and is itself under environmental control. Cannibalism is an important aspect of three of the hypotheses examined here (cold pool, oscillating control, larval transport) and is likely to interact with environmental variability in complex ways, as postulated in the oscillating control hypothesis (Hunt et al., 2002), and as indicated by significant interactions between pollock biomass and ice variables (Fig. 8).

To the extent that effects of environmental conditions operate independently from the effects of predation, we can estimate the relative proportion of variability in pollock survival accounted for by each effect. Empirical relationships from our retrospective analysis suggest that the best environmental predictors may account for up to 46% of overall variability in log-survival. In comparison, age-1 predation accounted for 39% of the variability in log-survival after accounting for other density-dependent effects of spawner abundance, or up to 76% of overall variability, suggesting that bottom-up and top-down effects are of similar magnitude.

However, effects of environmental variability and predation are clearly not independent. For example, both the oscillating control hypothesis and the larval transport hypothesis imply interactions between the prevalence of cannibalism and environmental conditions. Similarly, negative correlations between predation mortality of both age-0 and age-1 pollock and summer wind mixing at St. Paul ($r = -0.42$, $p = 0.041$ and $r = -0.50$, $p = 0.014$, respectively) suggest that the magnitude of predation is affected by summer wind mixing (for example by separating juveniles, which may avoid high turbulence by staying below the mixed layer, from

cannibalistic adults). The importance of cannibalism suggests that an index of cannibalism potential such as the index of spatial association (I_A) may serve as a useful predictor of survival or recruitment. This was confirmed by comparing the best environmental variables to the index of association in models of recruitment, which showed that I_A was a better predictor (lowest AIC_c) of log-recruitment and log-survival than any combination of environmental variables for the 1981–2001 year classes. Combined models including both environmental effects and either predation mortality or the index of association did not significantly improve on models that include only environmental effects or only predation effects, confirming that they are not independent and that they cannot be separated statistically.

5. Discussion and conclusions

The recruitment of walleye pollock displays high interannual variability (Fig. 2a and c) with a coefficient of variation of approximately 61%. Only a relatively small proportion of this variability, ranging from about 10% to 46% for the best predictive models, could be explained by the environmental factors examined in this study. The strongest environmental effects on survival and recruitment typically occurred at the early juvenile stage (age-1), with weaker relationships observed during the egg and/or larval stages (Fig. 12). We found very little evidence of any environmental effects during the late juvenile stage (age-2) on survival or recruitment, suggesting that year-class strength of walleye pollock in the eastern Bering Sea is largely determined at the early juvenile stage. This contrasts with the Gulf of Alaska, where year-class strength is largely determined at the egg and larval stage (Kendall et al., 1996) and may reflect the dominant role of cannibalism in the Bering Sea, which has a strong influence on survival rates at the early juvenile stage.

Our assessment of the four major hypotheses was likely influenced by the availability of suitable data sets, by the quality of the underlying data, and by strong confounding among many of the environmental data series. For example, no direct measures of nutrient availability in the summer were available and we resorted to the use of model-derived indices of entrainment and bloom date to assess the importance of summer conditions. Similarly, the larval advection hypothesis is difficult to evaluate because no direct measures of larval distribution are available, model-based indices of larval transport may be of low quality, and the index of association provides only a crude measure of cannibalism potential. Furthermore, strong confounding among

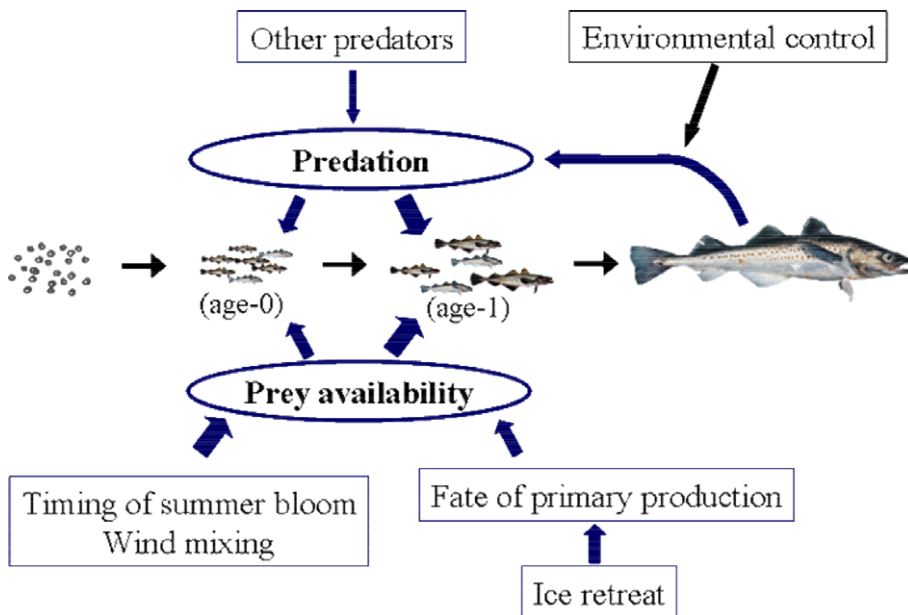


Fig. 12. Schematic of major controls of walleye pollock survival at the larval (age-0) and early juvenile stages (age-1). Width of arrows denotes relative magnitudes of estimated effects.

different indices hampers efforts to statistically distinguish among competing hypotheses. For example, the size of the cold pool (cold-pool hypothesis) is correlated with the timing of ice retreat (OCH), with northward transport on the shelf (larval transport hypothesis), and with summer conditions on the shelf. Nevertheless, we can evaluate the evidence for or against different hypotheses based on the relative strength of observed statistical relationships.

The best environmental predictors of survival and recruitment were related to summer conditions on the shelf and included a modelled estimate of the onset of summer stratification (bloom date) and measured wind mixing at St. Paul Island during the early juvenile phase. In addition, the final latitude of April–June surface drift trajectories during the larval stage appeared to affect significantly both larval and juvenile survival and subsequent recruitment as was previously suggested by [Wespestad et al. \(2000\)](#). However, the relative roles of temperature conditions, advection, and wind mixing are difficult to untangle because these variables are strongly confounded. The estimated environmental effects appear to reflect both bottom-up processes and effects on the availability of juveniles to cannibalistic adults.

Our results provide some evidence in support of the oscillating control hypothesis of [Hunt et al. \(2002\)](#). As hypothesized by the OCH, survival at the early juvenile stage was higher during warm years with an early ice retreat, particularly if the abundance of adult predators was low. In contrast, and in agreement with the OCH, top-down regulation was most apparent during years with an early ice retreat, when feeding conditions were presumably favorable and there was no bottom-up limitation on survival. While several of these relationships were statistically significant, the inclusion of ice retreat or adult biomass in models of log-survival and log-recruitment did not improve their predictive power. Furthermore, the statistical relationships examined here reflect interannual variability in ice conditions, whereas the OCH assumes regime-like shifts between cold and warm conditions that result in a shift from bottom-up control to top-down control following a gradual built-up in the total biomass of piscivorous predators, including pollock, cod, and flatfishes, during a warm regime. To the extent that low- and high-biomass years coincide with cold and warm regimes, the effects of temperature conditions on pollock survival and recruitment are confounded with effects of changes in predator biomass. Currently available data series do not provide enough contrast between regimes to allow a full statistical evaluation of the OCH in the Bering Sea or of the similar “shifting control” hypothesis ([Bailey, 2000](#)) in the Gulf of Alaska. Examination of the shifting control hypothesis is further complicated by the fact that the hypothesized mechanisms not only shift from a bottom-up to a top-down mechanism, but also shift from (bottom-up) control at the larval stage to (top-down) control at the juvenile stage ([Bailey, 2000](#)).

The OCH may be compared to results of [Niebauer et al. \(1995\)](#), who suggested that the contribution of the ice-edge bloom is important to water column production and, by implication, to the survival of larval and juvenile walleye pollock. However, our results clearly suggest that survival of pollock was higher during years with little ice and an early ice retreat, which are characterized by the absence of an ice-associated bloom ([Stabeno et al., 2001](#)). This does not support the importance of an ice-edge bloom to pollock, but is consistent with the OCH, which assumes that production from any ice-associated bloom is not available to pelagic larvae and juveniles because primary production is not consumed in the water column at very low temperatures ([Cooney and Coyle, 1982](#); [Hunt et al., 2002](#)). Instead, much of the primary production sinks to the bottom and may be important to benthic feeders. There is some evidence that benthic feeders, such as flatfishes, benefit from ice-associated blooms. For example, while pollock survival appears to be enhanced during years with an early ice retreat, survival rates of yellowfin sole are significantly higher during years with a late ice retreat ([Fig. 13](#)), resulting in a strong negative correlation between spawner-to-recruit survival rates of these two species ($r = -0.62$, $p < 0.001$). This suggests that walleye pollock and yellowfin sole respond in opposite ways to environmental variability (see also [Palmer, 2003](#)) and supports the hypothesis that benthic productivity is enhanced during cold years with a late ice retreat, while pelagic productivity is enhanced during warm years, as implied by the OCH and suggested by [Walsh and McRoy \(1986\)](#).

Our findings further support the importance of mixed layer dynamics during the spring and summer to the survival of juvenile pollock. Considering that most of the production from ice-associated blooms may not be available to pelagic consumers, as evidenced by low secondary production during cold years ([Coyle and Pincuk, 2002](#)), the timing of the open-water spring bloom may be critical to both first-feeding larvae and to juveniles emerging from their first winter. For example, when the open-water bloom during the early juvenile stage was delayed past the beginning of June (approximate day of year = 160, [Fig. 9](#)) survival was generally below

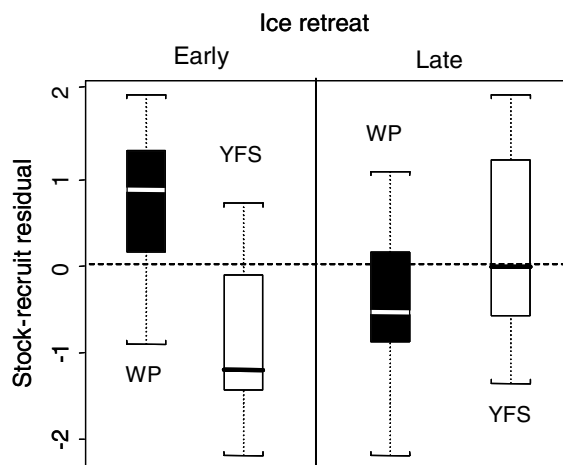


Fig. 13. Boxplots denoting median (heavy white or black line), central 50% (box), and extremes (whiskers) of the distribution of stock–recruit residuals for walleye pollock (WP) and yellowfin sole (YFS) during years with an early and late ice retreat.

average, possibly resulting from increased starvation. In contrast, an early spring bloom extends the summer production season and hence the critical feeding season for larvae and juveniles, which need to store sufficient lipids to survive the following winter (Sogard and Olla, 2000). However, total entrainment during July and August had no apparent effect on survival, suggesting that either the timing of the bloom or the duration of the production season is more important than the magnitude of new production (as estimated by entrainment), or that entrainment is a poor indicator of production.

Consistent with our expectation, we found a dome-shaped relationship between survival and summer wind mixing (Fig. 9). However, the dome-shaped relationship was weak and was not evident in models of log-recruitment. Furthermore, previous work predicts a dome-shaped relationship at the larval stage (MacKenzie et al., 1994; Megrey and Hinckley, 2001), while we found a significant dome-shaped relationship only at the early juvenile stage. Reduced survival during periods of high wind mixing can result from reduced feeding success associated with high levels of turbulence (MacKenzie et al., 1994). While these relationships have only been confirmed for larval fishes, our results suggest that feeding success of juvenile pollock may also be limited by strong turbulence (wind mixing). Alternatively, strong turbulence may reduce juvenile mortality if juveniles reduce vertical overlap with cannibalistic adults by avoiding the turbulent surface layer (Olla and Davis, 1990). However, the dome-shaped relationship is relatively weak, whereas survival rates of pollock increase significantly with increasing wind mixing during the larval stage and, up to intermediate values of wind mixing, during the early juvenile stage. Summer wind mixing may enhance survival by increasing prey availability through increased productivity associated with mixing nutrients into the surface layer. The lack of a significant relationship between July–August entrainment and pollock survival suggests that other mechanisms must be responsible for the apparent positive effects of wind mixing on survival or that wind mixing is a better index of nutrient enrichment than entrainment.

We confirmed a previously described relationship between surface advection in the post-spawning period and recruitment of walleye pollock (Wespestad et al., 2000). However, we found a significant relationship between northward transport of surface waters not only at the larval stage, but also at the early juvenile stage. At the larval stage, advection within the surface layer presumably transports eggs and larvae onto the shelf and away from cannibalistic adults during years with strong northward transport (Wespestad et al., 2000). Although larvae (and age-0 pollock) are generally found on the shelf and along the slope (Brodeur et al., 1999; Matarese et al., 2003), interannual differences in their distribution are poorly understood. The spatial distribution of age-1 juveniles, based on annual bottom trawl surveys, was not related to surface transport at either the larval or juvenile stage (Mueter, unpublished data), therefore other mechanisms besides passive transport must control their distribution. Regardless of the environmental or behavioral factors involved, the spatial distribution of juveniles is closely related to the degree of overlap between juveniles and adults, as

measured by the index of association. Spatial overlap, in turn, appears to affect predation mortality and overall pollock survival, suggesting that juvenile mortality from cannibalism, although a top-down process, is ultimately controlled by environmental factors that determine the spatial overlap of juveniles and adults. Advection of larvae may be one of the environmental factors controlling this spatial overlap, although we found no convincing empirical evidence that larval transport determines the extent of overlap between juveniles and adults (Mueter et al., 2004).

One hypothesis not considered in our analysis is the prey-switching hypothesis, which was developed for Prince William Sound based on observations that adult pollock eat copepods and euphausiids when available in spring and switched to salmon fry and age-0 herring only when adequate supplies of copepods were not available (Cooney et al., 2001). It is unclear whether such prey switching occurs in the eastern Bering Sea or what its implications for larval and juvenile survival of walleye pollock would be. Adequate data to examine the hypothesis were not available.

In general, the observed relationships between environmental variables and survival or recruitment were relatively weak and explained only a moderate proportion of the variability in recruitment. In particular, recruitment of strong year-classes was often greatly underestimated. Nevertheless, environmental effects at the larval stage, such as the estimated effects of surface transport, have been included in current stock assessment models (Ianelli et al., 2003). Similarly, environmental effects at the early juvenile stage, such as the estimated effects of bloom date and wind mixing, could be incorporated into stock assessment models to account for some of the unexplained variability in survival from spawning to recruitment at age-2. Additional insights may be gained and improved predictive models may be obtained by focusing on exceptionally strong year-classes and the environmental conditions associated with these year-classes. Exploratory analyses using logistic regression and regression trees suggested that ice conditions during the first two winters and surface currents during the larval stage were the best predictors of unusually strong (>15 billion recruits, Fig. 2a) year-classes (Mueter, unpublished results). Such models, which predict the probability of strong or weak year-classes, provide a promising tool to improve further our understanding of pollock recruitment dynamics.

In addition to environmental effects, cannibalism can explain much of the variability in pollock recruitment, as was evident in models relating the index of association to log-survival or log-recruitment. Indeed, the index of spatial association between juveniles and adults was at least as good a predictor of recruitment as any of the environmental variables examined. The dominant role of cannibalism in the recruitment dynamics of walleye pollock has long been recognized (e.g., Laevastu and Favorite, 1988; e.g., Livingston and Lang, 1996; Wespestad and Quinn, 1996) and several of the above hypotheses include mechanisms related to cannibalism. The magnitude of cannibalism is related to the abundance of adult pollock, as well as to the spatial overlap between juveniles and adults, which reflects the vulnerability of juveniles to predation. The importance of this spatial overlap was evident in a positive relationship between the index of association and the estimated predation mortality of age-1 pollock. Our results did not support an effect of either the cold pool or larval transport on the spatial association between juveniles and adults, therefore it remains unclear which factors control their relative distribution. Nevertheless, the index of association was a useful predictor of survival, in spite of the fact that it is based on bottom trawl surveys and therefore only captures the horizontal overlap of the demersal component of the pollock population.

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Appendix 1. List of all variables and indices used in this study

Name	Description	Begin	End	Source
R	Pollock recruitment (age-2) by year class	1963	2002	Ianelli et al. (2003), stock assessment estimate
S	Female spawning biomass of pollock	1964	2003	Ianelli et al. (2003), stock assessment estimate
SR	Survival rate index (residual from Ricker stock–recruit model) by year class	1963	2002	This study, based on data in Ianelli et al. (2003)
B	Total pollock biomass (Age 3+)	1964	2003	Ianelli et al. (2003), stock assessment estimate
M.0	MSVPA-based estimates of total predation mortality for age-0 pollock	1979	2002	Pat Livingston, Alaska Fisheries Science Center, NOAA (personal communication)
M.1	MSVPA-based estimates of total predation mortality for age-1 pollock	1979	2002	See M.0
Separation	Index of separation between juveniles (<20 cm) and adults (>40 cm)	1982	2003	Modified and updated from Wespestad et al. (2000)
Association	Index of association between juveniles and adults (see text)	1982	2003	This study
airT.StPaul	First principal component of monthly series (January–December) of air temperatures at St. Paul	1950	2002	This study, data provided by Western Regional Climate Center: http://www.wrcc.dri.edu/summary/climsmak.html
RACE.SST	Estimated mean sea-surface temperature during summer based on trawl survey data, corrected for differences in date of sampling	1982	2003	This study, data provided by RACE division, Alaska Fisheries Science Center, NOAA, Seattle
RACE.BT	Estimated mean bottom temperature during summer based on trawl survey data, corrected for differences in date of sampling	1982	2003	See RACE.SST
SST.sum	May–September average sea-surface temperature in region 57–59°N, 163–171°W	1900	2002	Based on Optimum Interpolation Version 2 data (Reynolds et al., 2002) provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, CO, USA (http://www.cdc.noaa.gov/)
SST.win	Winter (previous November–February) average of SST in region 57–59°N, 163–171°W	1901	2003	See SST.sum
Ice.168W	Southernmost ice extent along 168°W	1972	2003	Updated from Wyllie-Echeverria (1996)
SSI	Spatial Sea-ice Index: Average percentage of NMFS trawl survey area covered by ice between January and May	1972	2003	Modified and updated from Palmer (2003) data provided by Arctic Climatology Project, National Ice Center, NOAA (http://www.natice.noaa.gov/)

(continued on next page)

Appendix 1 (continued)

Name	Description	Begin	End	Source
TSI	Temporal Sea-ice Index: ISO week during which average ice concentration in NMFS trawl survey area first drops below 20%	1972	2003	See SSI
CPI	Cold pool index: spatial extent of the cold pool (<2 °C) during summer trawl survey, corrected for differences in date of sampling	1973	2003	This study, data provided by RACE division, Alaska Fisheries Science Center, NOAA, Seattle (missing data in some years)
ISI	Index of ice severity combining RACE.BT, Ice.168W, SSI, TSI, and CPI, reconstructed values prior to 1972	1964	2003	This study
ICI	Multivariate ice cover index	1954	2003	PMEL, NOAA (http://www.beringclimate.noaa.gov/)
ICT	Weeks after March 15 where ice cover in 56–58°N, 163–165°W exceeds 10%	1973	2003	PMEL, NOAA (http://www.beringclimate.noaa.gov/)
Wind.AP	Winter (Dec–Apr) average of along-peninsula wind stress at 53°N, 173°W in $N m^{-2}$	1959	2002	Bond and Adams (2002), updated series provided by Nick Bond, PMEL, NOAA (personal communication)
Wind.AS	Summer (May–September) averages of along-shelf wind stress at 56°N, 169°W in $N m^{-2}$	1959	2002	See Wind.AP
Wind.CS	Average spring/early summer (April–June) cross-shelf (SW–NE) wind speed at St. Paul	1951	2002	This study, data provided by National Climatic Data Center (via Dave Kachel, PMEL, NOAA, personal communication)
Wind.mix1	Summer (May–September) anomalies of NCEP reanalysis wind mixing ($m^3 s^{-3}$) at 57°N, 164°W	1959	2002	See Wind.AP
Wind.mix2	Summer (May–September) anomalies of measured wind mixing ($m^3 s^{-3}$) at St. Paul Island	1951	2002	This study, see Wind.CS
Bloom date	Estimated spring (non-ice-related) onset of bloom (day of year) at Mooring 2 (56.9°N, 164.1°W)	1951	2002	This study
Entrainment	Estimated July–August entrainment of nutrients (deep water) at Mooring 2 (56.9°N, 164.1°W)	1951	2002	This study
OT.N	Northernmost point (°N) of April 1–June 30 OSCURS trajectory started at 55.2°N, 164.5°W	1967	2003	Updated from Wespestad et al. (2000) using OSCURS model (http://www.pfeg.noaa.gov/products/las/OSCURS.html)
OT.lat	Ending latitude (°N) of April 1–June 30 OSCURS trajectory started at 55.2°N, 164.5°W	1967	2003	See OT.N
OT.long	Ending longitude (°E) of April 1–June 30 OSCURS trajectory started at 55.2°N, 164.5°W	1967	2003	See OT.N

Appendix 1 (continued)

Name	Description	Begin	End	Source
SAI	Siberian–Alaskan Index: mean December–March pressure difference between Siberia and Alaska–Yukon	1949	2003	http://www.beringclimate.noaa.gov/
ALPI	Aleutian low pressure index: winter (previous December–March) intensity of Aleutian Low, mean area where sea level pressure is ≤ 1005 hPa	1900	2002	After Beamish et al. (1997), index available at http://www.pac.dfo-mpo.gc.ca/sci/sa-mfpd/downloads/alpi.txt

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