

Pacific herring, *Clupea pallasii*, recruitment in the Bering Sea and north-east Pacific Ocean, II: relationships to environmental variables and implications for forecasting

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ABSTRACT

Previous studies have shown that Pacific herring populations in the Bering Sea and north-east Pacific Ocean can be grouped based on similar recruitment time series. The scale of these groups suggests large-scale influence on recruitment fluctuations from the environment. Recruitment time series from 14 populations were analysed to determine links to various environmental variables and to develop recruitment forecasting models using a Ricker-type environmentally dependent spawner–recruit model. The environmental variables used for this investigation included monthly time series of the following: southern oscillation index, North Pacific pressure index, sea surface temperatures, air temperatures, coastal upwelling indices, Bering Sea wind, Bering Sea ice cover, and Bering Sea bottom temperatures. Exploratory correlation analysis was used for focusing the time period examined for each environmental variable. Candidate models for forecasting herring recruitment were selected by the ordinary and recent cross-validation prediction errors. Results indicated that forecasting models using air and sea surface temperature data lagged to the year of spawning generally produced the best forecasting models. Multiple environmental variables showed marked improvements in prediction over single-environmental-variable models.

Key words: Bering Sea, environmental variable, forecasting, north-east Pacific Ocean, Pacific herring, recruitment, spawner–recruit model

INTRODUCTION

Pacific herring, *Clupea pallasii*, is a wide-ranging species with a long history of exploitation. This member of the clupeoids is commonly found along the eastern coast of the Bering Sea and north-east Pacific Ocean (Williams and Quinn, 2000). Herring populations and/or management units are typically defined by springtime spawning aggregations of fish returning from wintering grounds (Hay, 1985). Generally the age of first spawning for Pacific herring in the Bering Sea and NE Pacific Ocean is at age 3. The abundance of age-3 Pacific herring is the measure usually used for Pacific herring recruitment estimates.

An understanding of the recruitment dynamics of Pacific herring is essential to determining optimal harvesting strategies (Quinn *et al.*, 1990). Density-dependent spawner–recruit relationships for many Pacific herring populations seem inadequate for explaining the changes in year class strength. For many herring stocks, the method for forecasting Pacific herring recruitment is to simply use the historical median recruitment (Schweigert and Noakes, 1991; F. Funk, Alaska Department of Fish and Game, Juneau, pers. comm.). However, the clupeoids are notorious for their large population fluctuations, which seem to be the result of cycles possibly driven by density-independent processes (Cushing, 1982). Development of forecasting models including spawning biomass and the environment should be an improvement.

Density-independent influences of Pacific herring recruitment have been studied in a few British Columbia and Alaska populations to improve recruitment forecasting. Several British Columbia herring recruitment time series have been found to be influenced by local environmental conditions including: sea surface temperature, sea surface salinity, river discharge, Ekman transport, and sea level (Stocker *et al.*, 1985; Stocker and Noakes, 1988; Schweigert and Noakes, 1991; Beamish *et al.*, 1994; Schweigert,

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1995). Only the Bering Sea and Sitka herring populations have been analysed for associations between recruitment and the environment (Wespestad, 1991; Zebdi and Collie, 1995). Bering Sea herring recruitment appears to be correlated with wind-driven transport and sea surface temperatures (Wespestad, 1991), while Sitka Sound herring population fluctuations were correlated with sea surface temperature and an index of upwelling (Zebdi and Collie, 1995). Some of the recruitment forecasting models developed for Pacific herring have not survived the test of time, and on occasion have contradicted one another with respect to the nature of the relationship (Schweigert, 1995). One factor generally agreed upon in these studies of Pacific herring recruitment is the relationship of recruitment to temperature.

Many studies linking Pacific herring recruitment to the environment tend to focus on coastal variables corresponding to sites close to herring spawning grounds. This assumes that the environmental influence on recruitment occurs during the spawning and early life history stages of herring, which is the most commonly held belief for fisheries in general (Hjort, 1914; Cushing, 1975, 1990; Iles and Sinclair, 1982; Wooster and Bailey, 1989). Recent studies have pointed toward similarities in recruitment patterns for Pacific herring at distant sites, leading to the possi-

bility that herring may be responding to larger-scale influences (Schweigert, 1995; Zebdi and Collie, 1995).

A study of several fish stock–recruitment patterns, including Pacific herring, indicated that recruitment success is synchronous across large areas of the NE Pacific Ocean (Hollowed *et al.*, 1987; Hollowed and Wooster, 1995). A more detailed multivariate analysis of the recruitment patterns of Pacific herring in the Bering Sea and NE Pacific Ocean confirms the existence of large-scale groups of herring populations with highly correlated recruitment time series (Zebdi and Collie, 1995; Zheng, 1996; Williams, 1999). The geographical ranges of the herring population groups imply large-scale environmental influences (Williams and Quinn, 2000).

Pacific herring groups appear to follow the location of oceanographic domains delineated by the location of ocean currents and differences in sea surface temperatures (Ware and McFarlane, 1989; Williams, 1999). It appears that the major Pacific herring populations in the north-east Pacific Ocean and the Bering Sea can be placed into the groups indicated in Table 1 (Williams and Quinn, 2000). The purpose of this paper is to analyse recruitment time series for 14 herring populations from the Bering Sea and north-east Pacific Ocean to determine important correlations with large-scale and local environmental variables.

Table 1. Ricker-type spawner–recruit model fits and cross-validation prediction errors for Pacific herring populations in the Bering Sea and north-east Pacific Ocean.

Groups*	Pacific herring populations	n	Ricker parameters		Prediction error	
			a	β	Ordinary	Recent
BS	Norton Sound (NOR)	13	3.38	0.0780	1 493	699
	Togiak Bay (TOG)	16	2.65	0.0076	212 630	112 979
OGOA	Kodiak/Kamishak Bay	38	1.40	0.0087	83 660	8 220
	Prince William Sound	47	1.96	0.0138	102 174	14 329
	Sitka Sound	24	2.05	0.0051	214 027	78 140
	South-east Alaska	65	2.55	0.0158	299 589	191 947
IGOA	Seymour Canal	18	4.73	0.6928	1 463	4 423
	Craig	20	4.07	0.1403	66 315	10 655
	Kah-Shakes	18	3.51	0.1421	7 526	2 299
	Prince Rupert	43	3.77	0.0517	144 772	835 799
BC	Queen Charlotte Islands	43	3.96	0.0865	140 895	22 271
	Central Coast	43	3.29	0.0616	43 723	1 332
	West Vancouver Island	43	3.35	0.0346	69 450	48 046
	Strait of Georgia	43	3.73	0.0225	159 054	51 084

* BS, Bering Sea; OGOA, Outer Gulf of Alaska; IGOA, Inner Gulf of Alaska; BC, British Columbia (minus Prince Rupert).

DATA AND METHODS

Time series of Pacific herring recruitment and spawning biomass were assembled for the Bering Sea, Gulf of Alaska, and eastern Pacific Ocean from assessment models or analyses performed by the authors (Reid, 1971; Funk *et al.*, 1992; Schweigert *et al.*, 1997; Williams and Quinn, 1998). The available herring data span seven decades and two fishery types and a more detailed description of this data may be found in Williams and Quinn (2000). Recruitment estimates used in this study are for age-3 fish for all the stocks, except for Togiak, which are for age-4 fish.

The typical pattern of Pacific herring recruitment time series is highly variable, with large year classes occurring at occasionally regular intervals of between 3 and 9 years. The large year classes can dominate the recruitment time series, with the ratio of the largest year class to the weakest being as high as 429 (Zheng, 1996). The dominance of large year classes in herring recruitment time series suggests environmental influences are more likely to occur on an annual scale. This is contradictory to recent studies indicating that biological variables exhibit more correlation with physical variables at the decadal scale (Francis and Hare, 1994; Hare and Francis, 1995; Francis *et al.*, 1998). However, these analyses have primarily focused on salmon and groundfish populations and rarely, if ever, are Pacific herring implicated in the hypothesized 'regime shift' of the North Pacific.

Monthly environmental time series for air temperature, sea surface temperature, North Pacific atmospheric pressure (a measure of the Aleutian low pressure system), southern oscillation (negative values are associated with El-Niño – Southern Oscillation events), and coastal upwelling were collected for analysis with the Pacific herring recruitment time series as described below. Additional data specific to the Bering Sea included monthly ice cover, monthly wind anomalies, and annual bottom temperatures (Niebauer, 1988; Niebauer and Day, 1989; Quinn and Niebauer, 1995). A recent interdecadal climate index for the North Pacific has been developed based on eigen-analysis of sea surface temperatures (Mantua *et al.*, 1997). Because this index has been shown to be closely associated with both the North Pacific pressure and southern oscillation indices, and the sea surface temperatures used for its calculation are the same ones in this study, it was not used in this analysis.

Air temperatures were obtained from the Global Historical Climate Network database for various coastal cities corresponding to the location of herring

spawning sites. Sea surface temperatures were collected from the Comprehensive Ocean–Atmosphere Data Set (COADS) (Woodruff *et al.*, 1987). The COADS data consist of a 2°latitude by 2°longitude grid of averaged ship observations of sea surface temperatures. The North Pacific atmospheric pressure index, southern oscillation index, Bering Sea ice cover, and Bering Sea wind data were obtained from H. J. Niebauer (Niebauer, 1988; Niebauer and Day, 1989; Quinn and Niebauer, 1995). The Bering Sea bottom temperatures are from an annual survey performed aboard the RV *Oshoro Maru* (Ohtani and Azumaya, 1995). The coastal upwelling data series was obtained from the Pacific Fisheries Environmental Group (Internet address: <http://upwell.pfeg.noaa.gov/products/upwell.html>).

The interrelationship of environmental and oceanographic variables in the Bering Sea and NE Pacific Ocean is complex. On a global scale it appears that the southern oscillation index is related to the whole North Pacific environment owing to the link between El Niño events and the Aleutian low pressure system (Niebauer, 1988). Variability in the Aleutian low appears to drive as much as 30–40% of the oceanographic variability in the Bering Sea. Negative signals in the southern oscillation index (El Niño event) are associated with an intensification of the Aleutian low pressure system (as measured by the North Pacific pressure index), which in turn draws warm, moist air northward along the north-east Pacific coast. The North Pacific pressure index tends to lag behind the southern oscillation index by 2 months (Niebauer, 1988; Niebauer and Day, 1989).

Most of the North Pacific environment can be linked to the southern oscillation index and the North Pacific pressure index. Air temperatures, wind and ice cover appear to lag behind the southern oscillation index and North Pacific pressure index by 5–6 and 0–6 months, respectively. Sea surface temperatures appear to lag behind air temperatures by 0–3 months (Niebauer, 1988; Zebdi and Collie, 1995). This highly generalized view of the North Pacific environment on a large scale probably does not reflect smaller-scale associations, which are certainly more variable.

Relationships of Pacific herring recruitment and the environment were determined through correlation analyses. The presence of autocorrelation in time series of data can affect the inferences of a correlation analysis owing to spurious correlations (Haugh, 1976; Brockwell and Davis, 1995; Pyper and Peterman, 1998). The standard method of preventing spurious correlation in the presence of autocorrelation is to 'prewhiten' the time series by fitting an autoregressive

model and using the model residuals for the correlation analysis (Box and Jenkins, 1976). Removal of the autocorrelation in a time series by prewhitening prior to correlation analysis may increase Type II error rates (Pyper and Peterman, 1998). Furthermore, the theory behind prewhitening is based on large sample sizes ($n = 50\text{--}200$) (Haugh, 1976; Brockwell and Davis, 1995). Because most of the herring population data sets in this study are shorter than 50 years, prewhitening was not used in this study.

For this study, correlation analysis was performed in an exploratory setting. Because correlation analysis assumes some level of normality and herring recruitment data appear to be lognormally distributed, the time series were ln-transformed (Williams, 1999). The exploratory correlation measure consists of the ln transformation of the inverse of the computed P -value from Kendall's τ , a rank-based correlation measure. Generally, rank-based correlation measures are preferable in determining significance levels, because they are not as sensitive to outliers and non-normality as the standard Pearson estimate (Hollander and Wolfe, 1973; Zar, 1984; Dowdy and Wearden, 1991). A ln transformation of the inverse P -values was required based on the highly skewed distribution. The sign of the exploratory measure was changed to correspond to the direction of the relationship. To include robustness, the exploratory correlation measure was repeated with 10% of the outlying data trimmed (Rousseeuw and Leroy, 1987). The final measure to be used in the exploratory analysis was computed by taking the average of the full and trimmed exploratory correlation measures, as shown here:

$$P\text{-value}_{\text{raw}} = \frac{\pm \ln\left(\frac{1}{P\text{-value}_{\text{raw}}} + 1\right) \pm \ln\left(\frac{1}{P\text{-value}_{10\%\text{trim}}} + 1\right)}{2}.$$

Based on this 'conservative' correlation measure, an average P -value of 0.05 for the raw and trimmed data, indicating a potentially significant correlation, will result in an exploratory correlation measure of ± 3 .

The exploratory correlation analysis was applied similarly to the cross-correlation function used in time series analysis, in which time series are lagged at sequential time intervals to determine relationships. In this analysis, only lags allowing for the environmental variable to be a possible predictor of recruitment were explored. Thus the extent of the lags was limited to 1 year prior to spawning. This corresponds to four-year lags for all the herring populations except Togiak Bay, which was extended to cover five-year lags because of its greater age of recruitment. Subsets of the air and sea surface temperature data sets were selected based on

the nearest locations to the spawning grounds of the particular herring population. For the air temperature and sea surface temperature data, two city locations and five grids were selected, respectively.

Because Pacific herring populations can be grouped based on their recruitment time series, the pool of potential time periods for predictions was reduced to those following a pattern of similarity shared by other populations. Patterns in the correlation analysis were used to focus the time period of the environmental data to be used in the spawner–recruit modelling, to avoid potential spurious correlations (Walters and Collie, 1988). The selective process used for determining environmental variables should result in more 'robust' forecasting models of Pacific herring recruitment. The correlation patterns were determined by averaging and summarizing environmental correlations by lags and by months. The populations were grouped as suggested by previous studies and shown in Table 1 (Zebdi and Collie, 1995; Williams and Quinn, 2000).

The monthly environmental time series were standardized into anomalies before use in forecasting models. The use of anomalies rather than raw data is preferred for environmentally dependent spawner–recruit modelling, because the coefficient may be more easily interpreted (Hilborn and Walters, 1992). For simplification, these anomalies were averaged into yearly thirds for use in the forecasting models. Yearly thirds were chosen to correspond roughly to the prespawning, hatching/larval, and juvenile phases of Pacific herring life history.

The Pacific herring recruitment, spawning biomass, and environmental variables were fitted using the linearized form of the Ricker environmental spawner–recruit model:

$$\ln(R/S) = a - \beta S + \gamma_1 E_1 + \dots + \gamma_i E_i, \quad (1)$$

where R is the number of recruits, S is the spawning biomass, E_i is the i th environmental variable, and $\{a, \beta, \gamma_1, \dots, \gamma_i\}$ are the coefficients (Quinn and Deriso, 1999). Initially, only a single environmental variable was fitted. The number of environmental variables applied to each population was limited to the five nearest sea surface temperature grids and the two nearest air temperature stations, along with the remaining variables. Candidate variables for subsequent analysis in multiple-environmental-predictor models were selected based on whether they resulted in an improved fit in single-variable models. Model fitting was accomplished with the linear model fitting algorithm in the S-Plus statistical software package (Mathsoft Inc., Seattle).

Model fit was judged by the use of two types of prediction error. The ordinary cross-validation error was computed by systematically leaving one year of data out of the analysis, fitting the model to the reduced data set, and then calculating the mean of squared differences between each excluded point and its model prediction for each year (Stone, 1974; Efron and Tibshirani, 1993; Venables and Ripley, 1997; Ripley, 1996; Burnham and Anderson, 1998). The recent cross-validation prediction error followed the same basic procedure as the ordinary cross-validation error method, except that just the last 3 years were removed, predicted, and the error computed. The ordinary and recent cross-validation prediction errors are measures of model error for selection of forecasting models. We did not present other model selection criteria such as Mallows's C_p , AIC, or BIC (Efron and Tibshirani, 1993; Ripley, 1996; Burnham and Anderson, 1998), because our primary interest was forecasting. The ordinary and recent cross-validation prediction errors were used for selecting single-environmental-variable models, while only the ordinary cross-validation was used for selecting multiple-environmental-variable models using a stepwise algorithm written by the authors in S-Plus.

Data are missing for many of the environmental time series, resulting in models of various sample sizes. Although the ordinary cross-validation error measure has a correction for sample size, there is still some dependence on the total number of points. Because all the environmental data sets include the three most recent years, the recent cross-validation error is a more comparable measure between competing models of various sample sizes for the same herring populations.

The potential pool of Pacific herring recruitment forecast models was reduced by a series of comparisons of environmental models to the nonenvironmental Ricker spawner–recruit model for each population. In the first step, models with the same sample size as the nonenvironmental spawner–recruit model were analysed based on the ordinary cross-validation error. If there was no decrease in the ordinary cross-validation error, then the model was removed from the pool of potential forecast models. Next, models of differing sample sizes that did not show a decrease in the recent cross-validation error with the addition of environmental parameters were removed.

The final selection of a single-environmental spawner–recruit model for each environmental variable was based on the lowest ordinary cross-validation error. A stepwise fitting procedure was performed to determine the best multiple-predictor model, as men-

tioned above. The final pool of forecasting models consists of a set of single-environmental-variable models for each environmental variable and one multiple-variable forecasting model for each Pacific herring population.

RESULTS

Exploratory correlation analysis

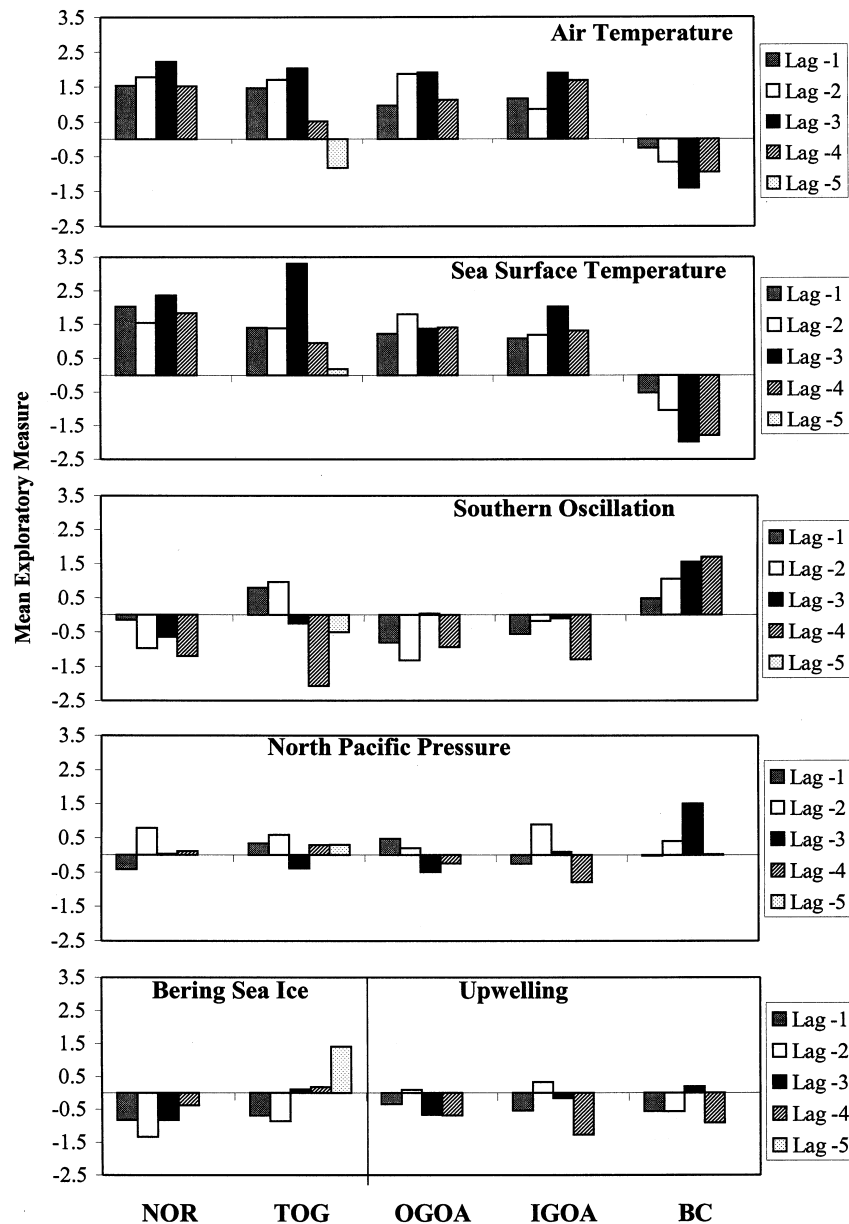
Exploratory correlation measures were summed across months and averaged within groups listed in Table 1. The exploratory correlation analysis of Pacific herring recruitment in Norton Sound and Togiak Bay with Bering Sea wind and bottom temperatures revealed very low correlation levels, so the results are not shown. The Norton Sound and Togiak Bay populations were separated within the Bering Sea group owing to the different ages of recruitment (Fig. 1).

The overall pattern of correlations for Pacific herring recruitment time series with air and sea surface temperatures is strikingly similar within groups. The British Columbia group tends toward having negative correlations with temperature, while the remaining groups show positive correlations with temperature. For the temperature data, it appears that a lag of 3 years is stronger than the remaining lags, except for the outer Gulf of Alaska group with sea surface temperatures. The pattern of lag correlations is similar for both the Bering Sea stocks despite the difference in age of recruitment (Fig. 1).

The relationship of Pacific herring recruitment and the southern oscillation index resulted in a pattern opposite to the temperature pattern. The British Columbia populations show a positive correlation, while the remaining populations tend to be mostly negative. The most important lag for the southern oscillation data appears to be 4 years, except in the outer Gulf of Alaska group (Fig. 1). The North Pacific pressure index reveals no patterns or strong correlations at any of the lags, with the possible exception of a three-year lag in the British Columbia group. The low magnitude of the correlation measures for the North Pacific pressure index indicates that the higher magnitude seen with other variables does not simply arise from random chance (Fig. 1).

All the populations show a tendency toward negative correlations with the upwelling data and a possible pattern emerging with a lag of 4 years. However, the pattern that the British Columbia group has a relationship opposite to those of the remaining populations does not appear with the upwelling data. There were no corresponding upwelling data for the

Figure 1. Mean exploratory correlation measures for various environmental variables lagged from 1 to 4 years for the Norton Sound (NOR), 1–5 years for Togiak Bay (TOG) herring populations and 1–4 years for the outer Gulf of Alaska (OGO), inner Gulf of Alaska (IGO), and British Columbia (BC) herring population associations.

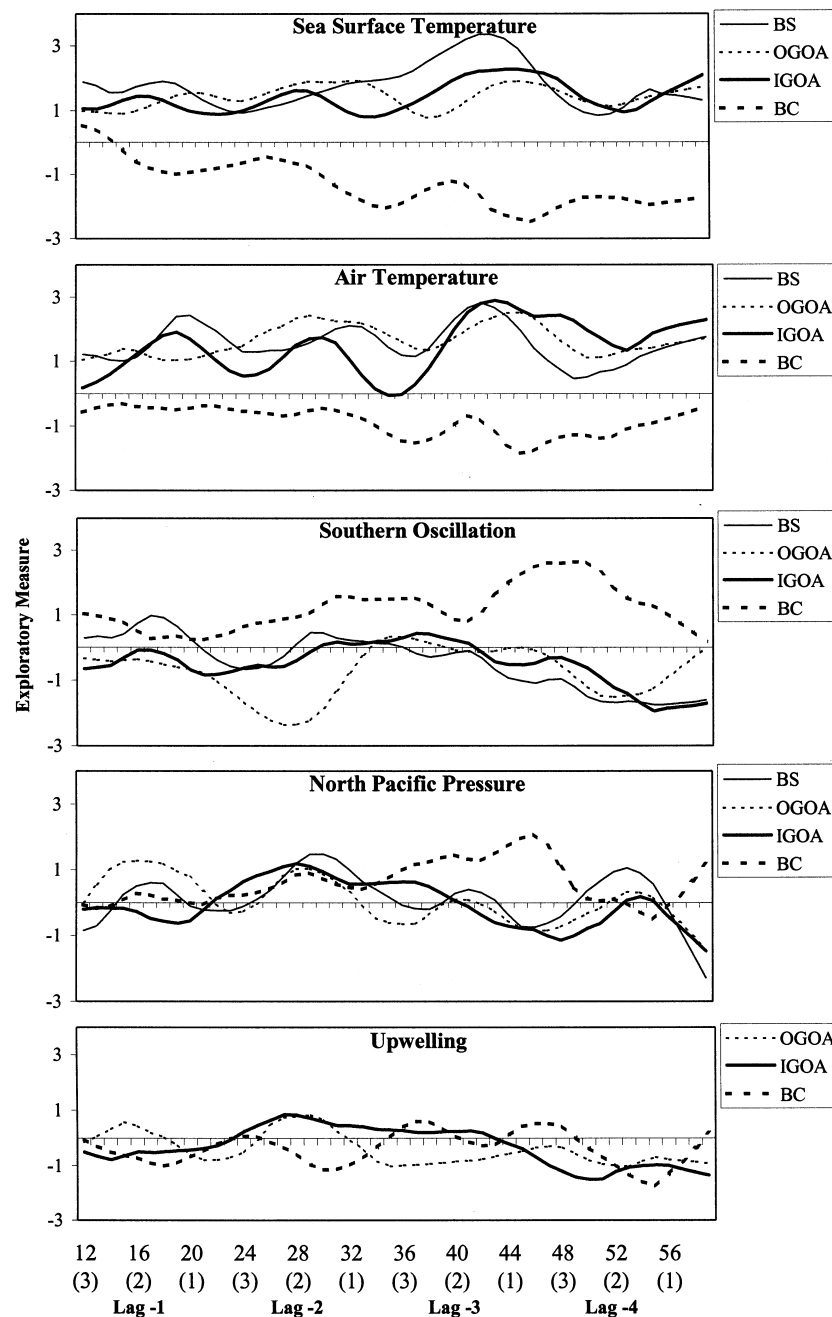


Bering Sea stocks, and exploratory measures are instead shown for Bering Sea ice data. Both Norton Sound and Togiak Bay appear to be correlated with Bering Sea ice cover at a lag of 2 years. The Togiak Bay population resulted in a higher level of correlation with the Bering Sea ice cover at a lag of 5 years (Fig. 1).

In an attempt to elucidate further patterns of correlations between Pacific herring recruitment and environmental variables, the exploratory correlation

measure was examined by months. For air and sea surface temperature data, the average for the two and five selected stations, respectively, was used to examine the correlations by month. For robustness and graphing convenience, a lowess-smoothed line ($f = 0.15$) was fitted to the reverse-ordered monthly correlation measures. Based on the similarity in lag correlations (Fig. 2), the Norton Sound and Togiak Bay populations were combined into a Bering Sea group for the monthly analysis (Fig. 2).

Figure 2. Lowess-smoothed line fits (fraction smoothed = 0.15) for monthly (tick marks) exploratory correlation measures of environmental variables lagged from 1 to 4 years (labelled as months, yearly thirds in parentheses) for the Bering Sea (BS), outer Gulf of Alaska (OGO), inner Gulf of Alaska (IGO), and British Columbia (BC) herring population associations.



The lowess-smoothed lines in monthly analysis of Fig. 2 confirm some of the patterns seen in the analysis of annual lags. The British Columbia populations and the remaining herring populations show a consistently opposite relationship with sea surface and air temperature data (Fig. 2). The peaks of the smoothed lines seem to be synchronous in these panels and are indi-

cations of time periods useful for herring recruitment forecasting. The highest peaks in correlation for the temperature time series correspond to a three-year lag. During the fourth-year lag, the temperature correlations appear to diminish, but in the first third (last portion of backward time scale) they appear to increase slightly (Fig. 2).

Table 2. Lagged time periods selected for use in forecasting models based on exploratory correlation analysis.

	Yearly third:	Lag – 1			Lag – 2			Lag – 3			Lag – 4		
		3	2	1	3	2	1	3	2	1	3	2	1
Sea surface temperature (SST)								x	x	x			x
Air temperature (AT)								x	x	x			x
Southern oscillation (SOI)											x	x	x
North Pacific pressure (NPPI)								x	x	x			x
Upwelling (UPW)											x	x	x

A pattern similar to that in the temperature time series can be seen in the North Pacific pressure index correlations. For the British Columbia group, the peak correlation corresponds to a four-year lag, and there is a slight increase in the first third of the lag – 4 time period (Fig. 2). The Bering Sea, outer Gulf of Alaska, and inner Gulf of Alaska herring groups do not indicate a strong peak in the lag – 3 time period, but do show increasing negative correlations in the first third of the lag – 4 time period.

The southern oscillation index correlation analysis indicates a consistently positive relationship with the British Columbia populations, which is consistent with the temperature correlations (i.e. negative southern oscillation events are associated with increased temperatures in the North Pacific). Furthermore, the time period of the peak correlation appears to be during the lag – 4 time period, which lags the peak temperature correlations appropriately (Niebauer, 1988; Niebauer and Day, 1989). The Bering Sea, outer Gulf of Alaska, and inner Gulf of Alaska groups indicate a weaker, yet consistent, correlation pattern in the lag – 4 time period of the southern oscillation index time series. The apparent trough in the outer Gulf of Alaska group during the lag – 2 time period does not fit into the overall pattern for Pacific herring recruitment correlations, but may represent a more local phenomenon (Fig. 2).

The upwelling index indicates no strong correlations with the Pacific herring recruitment. The first and second thirds of the lag – 4 time period indicate a possible pattern in the correlations, but this does not fit the pattern of an opposite relationship between the British Columbia group and the remaining populations (Fig. 2). Given the low magnitude of the exploratory correlation measure relative to analyses of other variables, it appears that upwelling (at least as calculated here) may not be useful in forecasting herring recruitment.

The life history stages at which the peak correlations occur are important in determining if the

observed pattern is appropriate. The temperature and North Pacific pressure correlations indicate that the lag – 3 and the first third of the lag – 4 time periods are most important (Fig. 2). Biologically, the lag – 3 time period corresponds to the times just before spawning, during spawning and during early larval development. This period is consistent with the dominating paradigm in fisheries science of the early life history critical stage. The lag – 4 time period corresponds to 1 year prior to spawning, and is not readily reconcilable.

Based on the patterns of the exploratory correlation analysis, a subset of time periods to be explored for use in recruitment forecasting models was developed (Table 2). The time period for all of lag – 3 and the first third of lag – 4 was chosen for the air temperature, sea surface temperature, and North Pacific pressure index time series (Table 2). For the southern oscillation and upwelling indices, the lag – 4 time period was chosen for exploring potential herring recruitment forecasting models.

Recruitment forecast models

The Ricker spawner–recruit models without environmental data were fitted for comparison with models including environmental data (Table 1). All of these models have a positive β parameter, indicating the presence of overcompensation. Furthermore, the magnitude of the parameters is similar within groups of herring populations. The lowest a and β parameters are found in the outer Gulf of Alaska groups, while the highest a and β -values tend to occur in the inner Gulf of Alaska group (Table 1).

The screening process used for the environmental spawner–recruit models eliminated many candidate variables, particularly those not resulting in an improvement in the recent cross-validation prediction error. The environmental model fits were judged based on the change in the ordinary and recent cross-validation prediction errors relative to the nonenvironmental spawner–recruit models (Table 1). In Tables 3, 4, 5 and 6 the change in model performance was

Table 3. Best Ricker-type spawner–recruit model fits and cross-validation prediction errors for single-environmental-variable models for Pacific herring populations in the Bering Sea group. Prediction error values are percentage changes from Table 1, with model improvements (decrease in error) indicated in bold. See Table 2 for variable abbreviations.

Environmental variable	Yearly third	Lag	n	Ricker parameters			Prediction error (%)	
				α	β	γ	Ordinary	Recent
Norton Sound								
SST (165°W, 55°N)	1	4	13	3.35	0.077	0.276	−8.5	−10.6
Ice	1	3	13	4.16	0.095	−0.635	−7.3	33.4
AT (Nome)	1	4	13	1.68	0.042	0.801	−6.3	44.7
NPPI	3	3	13	3.47	0.080	−0.225	−0.5	−8.2
Togiak Bay								
SOI	2	4	16	2.76	0.00791	−0.595	−30.7	25.8
SST (169°W, 55°N)	1	3	16	2.88	0.00823	0.534	−22.2	72.7
Ice	1	5	16	2.22	0.00644	0.449	−13.8	−65.9
AT (King Salmon)	1	3	15	2.30	0.00637	0.525	1.1	−4.5

computed as the percentage change for the cross-validation prediction error estimates. Inferences about the nature and strength of the influence of the environmental parameters can be judged by the sign and magnitude of the γ parameter in the model (Hilborn and Walters, 1992).

The Bering Sea herring populations are limited by a small sample size relative to the other populations. The best forecasting models for each environmental variable are shown in Table 3. The best forecasting model for the Norton Sound population with sea surface temperature data occurred in lag − 4, and the γ parameter indicated a positive relationship. Improved forecasting models were also obtained using the Bering Sea ice cover, air temperature data from Nome, and North Pacific pressure index, with the γ parameter indicating the direction of the relationship. The Togiak Bay recruitment model resulted in a negative relationship with the southern oscillation index in the second third of the year of the lag − 4 year. Other improved models include positive relationships with sea surface temperature data, air temperature data from King Salmon, Alaska and Bering Sea ice cover. The ice cover fit with Togiak Bay herring seems to be the best single-variable environmental spawner–recruit model with respect to both measures of prediction error (Table 3).

Each environmental variable resulted in similar forecasting models for the outer Gulf of Alaska group of herring populations (Table 4). All four populations in this group were positively correlated with sea surface temperature data, and in three of the four, the first part of lag − 3 resulted in lower forecast error. The

southern oscillation index resulted in improved forecasting models in three of the four populations, indicating a negative relationship to this variable (Table 4). The addition of air temperature data for lag − 3 resulted in improved forecasting models for Kodiak/Kamishak Bay, Prince William Sound, and particularly south-east Alaska.

Environmentally dependent spawner–recruit models for the inner Gulf of Alaska group showed many improvements in the prediction errors, relative to the nonenvironmental spawner–recruit models (Table 5, Fig. 3). Although the corresponding lag for each environmental variable with the lowest forecast error did not always agree for each population, there was some overlap between populations with shared relations to the same environmental variable. Craig and Kah-Shakes shared positive correlations with the Little Port Walter, Alaska air temperature data and Kah-Shakes shared a sea surface temperature variable with the Seymour Canal population. The Kah-Shakes group indicated a positive relationship with the North Pacific pressure index, while the other members of the group indicated a negative relationship. All the members of the inner Gulf of Alaska herring group had a consistent negative relationship with upwelling data, all corresponding to the lag − 4 year (Table 5).

For the British Columbia group of herring populations, there were many improved forecasting models (Table 6). These spawner–recruit models were all improved with sea surface temperature and southern oscillation index data. In every case, the relationship with sea surface temperature was negative and that with the southern oscillation positive (Table 6). Aside

Table 4. Best Ricker-type spawner–recruit model fits and cross-validation prediction errors for single-environmental-variable models for Pacific herring populations in the outer Gulf of Alaska group. Prediction error values are percentage changes from Table 1, with model improvements (decrease in error) indicated in bold. See Table 2 for variable abbreviations.

Environmental variable	Yearly third	Lag	n	Ricker parameters			Prediction error (%)	
				α	β	γ	Ordinary	Recent
Kodiak/Kamishak Bay								
SST (145°W, 57°N)	2	3	17	2.09	0.0228	0.457	−86.4	−11.0
NPPI	1	3	26	2.31	0.0423	−0.793	−73.0	−8.3
UPW	1	4	26	2.25	0.0404	−0.091	−71.0	−40.4
AT (Kodiak)	3	3	38	1.47	0.0098	0.610	−5.8	−16.0
Prince William Sound								
SOI	2	4	47	1.93	0.0132	−0.327	−2.0	−4.6
AT (Kodiak)	2	3	47	1.99	0.0144	0.175	−1.3	−12.0
SST (143°W, 57°N)	1	3	33	2.30	0.0219	0.533	4.2	−49.5
UPW	2	4	32	2.11	0.0217	−0.196	10.4	−49.9
NPPI	1	3	32	2.03	0.0198	−0.211	10.6	−53.4
Sitka Sound								
SOI	1	4	24	2.32	0.0174	−0.384	−9.2	−38.5
SST (135°W, 55°N)	1	3	24	1.80	−0.0057	−0.310	−4.5	−41.6
UPW	2	4	24	2.23	0.0133	−0.352	−2.0	14.5
South-east Alaska								
AT (Sitka)	1	3	65	2.57	0.0163	0.428	−5.0	−42.9
SOI	2	4	65	2.53	0.0153	−0.149	−0.8	−8.4
SST (133°W, 51°N)	1	3	62	2.54	0.0148	0.323	−0.6	−18.6

from all the populations sharing a relationship with the southern oscillation index, the Queen Charlotte Islands and Central Coast populations shared a relationship with the sea surface temperature data at 131°W longitude and 53°N latitude.

Multiple regression models resulted in improved prediction errors for most herring populations, compared with single-environmental-variable models. The Prince William Sound model resulted in the most improvement in prediction error compared with the best single-environmental-variable model (Table 7). Most of the multiple-predictor models resulted in relatively small reductions in prediction error. The Norton Sound multiple-predictor model did not result in an improvement in the recent cross-validation prediction error. Kodiak/Kamishak Bay, Sitka, south-east Alaska, Craig, and Central Coast population forecasting models reduced to the best single-environmental-variable models (Table 7).

DISCUSSION

The exploratory correlation analysis resulted in the lag patterns in Table 2. The important question is, do these lags correspond to the known information about

Pacific herring, the environment and their interrelationships? The predominating view of the North Pacific environment is that it is dominated by the position and intensity of the Aleutian low pressure system as measured by the North Pacific pressure index. Studies have shown that the North Pacific pressure index is related to the southern oscillation index with a lag of ≈ 2 months (Niebauer, 1988; Niebauer and Day, 1989). The North Pacific pressure index is correlated with air and sea surface temperatures, but the lag at which this occurs ranges from 0 to 6 months (Niebauer, 1988; Niebauer and Day, 1989). However, there is some conclusive evidence that the southern oscillation index lags behind air and sea surface temperatures by about 5–9 months. So, published results are slightly conflicting as to where the North Pacific pressure index fits into the relationship of the southern oscillation index and temperatures.

Our correlation analysis revealed the peak correlation times for air and sea surface temperatures occurred at lag -3 , while the peak correlation for the southern oscillation index appeared to be at lag -4 . If herring are responding to some large-scale environmental forcing, being primarily driven by the southern oscillation, then this is consistent with known relation-

Table 5. Best Ricker-type spawner–recruit model fits and cross-validation prediction errors for single-environmental-variable models for Pacific herring populations in the inner Gulf of Alaska group. Prediction error values are percentage changes from Table 1, with model improvements (decrease in error) indicated in bold. See Table 2 for variable abbreviations.

Environmental variable	Yearly third	Lag	n	Ricker parameters			Prediction error (%)	
				a	β	γ	Ordinary	Recent
Seymour Canal								
AT (Annex Cr.)	1	3	14	4.92	0.744	0.126	−70.3	−82.0
SST (137°W, 57°N)	1	3	18	4.62	0.648	0.283	−19.4	−7.3
NPPI	1	3	18	4.70	0.681	−0.192	−11.5	−12.5
SOI	2	4	18	4.68	0.673	−0.244	−8.2	−8.5
UPW	1	4	18	4.74	0.697	−0.161	−5.2	−1.7
Craig								
SOI	1	4	20	4.17	0.158	−0.654	−24.2	178.4
SST (133°W, 51°N)	1	4	20	4.23	0.162	0.578	−8.9	−49.2
NPPI	1	4	20	4.12	0.147	−0.394	−6.9	−47.2
UPW	1	4	20	4.36	0.180	−0.598	−4.8	−25.2
AT (L. Port Walter)	1	4	18	4.41	0.208	0.922	0.5	−29.0
Kah-Shakes								
SST (137°W, 57°N)	1	3	18	3.65	0.156	0.327	−11.5	−15.6
NPPI	3	3	18	3.39	0.129	0.113	−0.8	−18.8
UPW	2	4	18	3.31	0.121	−0.251	−0.4	−0.4
AT (L. Port Walter)	1	4	16	3.63	0.150	0.013	14.2	−28.9
Prince Rupert								
AT (Prince Rupert)	2	3	40	3.91	0.063	0.521	−50.2	−75.3
SST (135°W, 55°N)	2	3	43	3.84	0.056	0.331	−12.7	−6.0
SOI	1	4	43	3.77	0.052	−0.256	−7.6	−20.4
NPPI	1	4	43	3.79	0.053	−0.187	−2.3	−5.5
UPW	1	4	43	3.93	0.062	−0.289	−0.4	−0.8

ships. In our study we used the same lag times for the North Pacific pressure index as we did for the temperature data (Table 2). In a sense, we are assuming that the North Pacific pressure index is closely corre-

lated with temperature. This implies that the southern oscillation index lags behind the North Pacific pressure index by 6–12 months, which does not completely agree with previous correlation studies (Niebauer, 1988; Niebauer and Day, 1989).

We reconcile this disagreement in peak correlation lag times for the southern oscillation and North Pacific pressure indices by indicating that in our analysis the links between herring recruitment and the North Pacific pressure index are weaker than the links with the southern oscillation index. The North Pacific pressure index may not be an accurate representation of the intermediary link between the southern oscillation and temperatures in the North Pacific. The southern oscillation index correlations resulted in a consistent pattern that matched the patterns seen in the temperature data (Figs 1 and 2).

The exploratory correlation analysis did reveal an overall pattern of relationships between herring and the environment. It appears that herring are related to both local- and global-scale environmental variables.

Figure 3. Recruitment values and predictions for Prince Rupert herring using a Ricker-type spawner–recruit model with and without the addition of air temperature data from Prince Rupert.

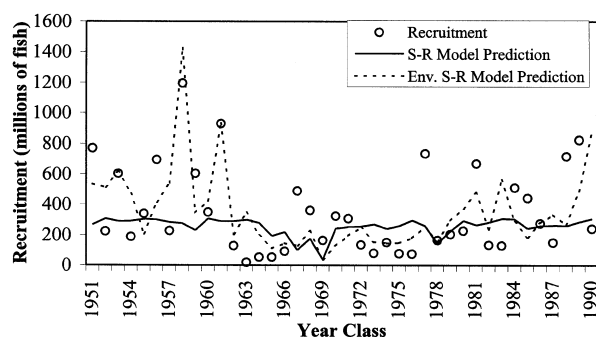


Table 6. Best Ricker-type spawner–recruit model fits and prediction errors for single-environmental-variable models for Pacific herring populations in the British Columbia group. Prediction error values are percentage changes from Table 1, with model improvements (decrease in error) indicated in bold. See Table 2 for variable abbreviations.

Environmental variable	Yearly third	Lag	n	Ricker parameters			Prediction error (%)	
				a	β	γ	Ordinary	Recent
Queen Charlotte Islands								
SST (131°W, 53°N)	3	3	41	3.77	0.079	−0.461	−25.3	−24.3
UPW	2	4	43	4.06	0.093	−0.470	−10.2	−6.7
SOI	3	4	43	3.98	0.087	0.274	−2.7	−30.4
NPPI	3	3	43	4.00	0.089	0.108	−1.2	−9.6
AT (St James)	3	3	40	3.94	0.080	−0.093	4.8	−20.0
Central Coast								
SST (131°W, 53°N)	1	3	41	3.01	0.047	−0.468	−39.4	−81.3
NPPI	1	3	43	3.30	0.062	0.497	−8.2	53.0
UPW	2	4	43	3.43	0.071	−0.308	−3.7	60.0
SOI	3	4	43	3.34	0.065	0.250	−1.5	41.1
West Vancouver Island								
SST (133°W, 51°N)	1	3	43	3.39	0.036	−0.430	−23.6	−42.1
AT (Pachena)	1	3	40	3.37	0.034	−0.360	−21.7	−83.9
NPPI	1	3	43	3.36	0.035	0.376	−16.0	−49.5
SOI	1	4	43	3.43	0.038	0.208	−7.0	−40.0
UPW	3	4	43	3.25	0.031	−0.165	−1.8	−27.3
Strait of Georgia								
SST (129°W, 49°N)	1	3	43	3.71	0.022	−0.179	−7.5	−17.5
SOI	2	4	43	3.75	0.023	0.091	−1.4	−1.8

A fairly consistent pattern emerged in which British Columbia herring showed relationships opposite to those of the remaining north-east Pacific herring populations. This lends credibility to previous studies indicating the grouping structure used in this analysis is a real phenomenon (Zebdi and Collie, 1995; Zheng, 1996; Williams, 1999; Williams and Quinn, 2000). Further, the lags at which these relationships occurred were fairly consistent across all the herring populations, indicating similar responses to the environment (Figs 1 and 2). The dominant pattern of environmental forecasting variables indicated that temperatures during the first third of lag – 3 and the southern oscillation index during the first third of lag – 4 generally resulted in the best forecasting models (Tables 3, 4, 5, 6). Overall, the North Pacific pressure and upwelling indices did not result in the best models and appeared inconsistent in their usefulness for forecasting Pacific herring recruitment.

The multiple-environmental-variable models did not always yield improvements in the recent cross-validation prediction error (e.g. Togiak, Tables 3 and 7), because the model selection was based on the

use of the ordinary rather than recent cross-validation error. In the case of Norton Sound, the recent prediction error was higher than the Ricker model with no environmental information in Table 1. For some populations (Togiak, ordinary error; Prince William Sound, ordinary and recent error; Kah-Shakes, recent error), the multiple-environmental-variable models resulted in large reductions in prediction error, relative to the single-environmental-variable models. It is unclear, however, if such differences will persist with additional years of data, but this result suggests that complex interactions in the environment may influence herring recruitment.

The mechanism by which the environment influences herring recruitment fluctuations may be direct or indirect. The strength of the correlations suggests that temperature is more influential than the rest of the environmental parameters. Air temperatures do occasionally come into direct contact with herring eggs. Previous studies have shown that egg loss through exposure to air can be high, but it is not clear whether this can ultimately determine future levels of recruitment (Jones, 1972; Rooper *et al.*, 1999). Water tem-

Table 7. Best Ricker-type spawner–recruit model fits and prediction errors for multiple environmental variables for Pacific herring populations from the Bering Sea and north-east Pacific Ocean. Prediction error values are percentage changes from Table 1, with model improvements (decrease in error) indicated in bold. See Table 2 for variable abbreviations.

Environmental variable	Yearly third	Lag	n	Ricker parameters			Prediction error (%)	
				a	β	$\{\gamma_1 \dots \gamma_i\}$	Ordinary	Recent
Norton Sound			13	4.10	0.093		−9.3	24.2
SST (165°W, 55°N)	1	4				0.165		
Ice	1	3				−0.601		
Togiak Bay			15	2.40	−0.007		−54.0	−42.0
SOI	2	4				−0.299		
Ice	3	5				−0.374		
Ice	3	3				0.460		
Ice	1	5				0.772		
Prince William Sound			21	2.92	0.036		−42.9	−81.5
UPW	2	4				−0.710		
UPW	1	4				−0.257		
NPPI	2	3				−0.300		
Seymour Canal			13	4.88	0.741		−78.9	−83.2
UPW	3	4				−0.275		
SST (141°W, 57°N)	3	3				0.062		
SST (141°W, 57°N)	1	3				−0.038		
SST (135°W, 53°N)	1	3				0.013		
Kah-Shakes			16	3.63	0.145		−8.9	−59.8
UPW	3	4				−0.320		
UPW	2	4				−0.222		
AT (Annette)	1	3				−0.047		
SST (135°W, 57°N)	2	3				0.352		
Prince Rupert			38	4.08	0.076		−51.4	−80.2
AT (Prince Rupert)	2	3				0.477		
AT (Langara)	1	4				0.199		
SST (131°W, 55°N)	2	3				0.200		
Queen Charlotte Islands			41	3.82	0.082		−25.4	−33.5
SST (131°W, 53°N)	3	3				−0.462		
UPW	1	4				−0.228		
W. Vancouver Island			38	3.27	0.031		−30.0	−68.5
SST (131°W, 53°N)	1	3				−0.281		
NPPI	1	3				0.258		
AT (Estevan)	3	3				−0.193		

peratures could have direct effects on hatching success, timing of spawning, egg condition, egg mortality, and larval mortality (Taylor, 1971; Hay, 1985; Blaxter, 1992; McGurk *et al.*, 1993; Zebdi and Collie, 1995). However, it is likely that the correlation of herring recruitment with air and sea surface temperatures in this analysis is simply a proxy for some other, more indirect influence. The fact that the direction of the correlations with temperature changes from more

northerly herring populations to more southerly populations suggests an indirect effect. Unfortunately temperature could be seen as a proxy for nearly any mechanism, from predator abundance to food availability.

The most likely indirect scenario is that sea surface temperatures in the first third of the year (the peak time for herring correlations) affect the timing of Pacific herring spawning relative to subsequent physical

ocean conditions. Ocean conditions such as the onset, strength, and/or duration of both the spring bloom and coastal currents may affect herring survival, depending on the relative timing of spawning. The dominant paradigm in fisheries leans toward the larval stage of herring life history as being the most important for determining year class strength (Hjort, 1914; Cushing, 1975; Iles and Sinclair, 1982).

Previous studies have indicated that offsets in timing of herring spawning and set-up of ocean conditions can affect Pacific herring survival (Stevenson, 1962; McGurk, 1984, 1989; McGurk *et al.*, 1993). However, these studies disagree as to the ultimate source of mortality. Both food availability (Cushing's (1975) match-mismatch hypothesis) and retention mechanisms (Iles and Sinclair's (1982) member-vagrant hypothesis) have been implicated in previous studies of Pacific herring recruitment.

The change in the direction of correlations from Gulf of Alaska populations and British Columbia populations suggests that different mechanisms may be operating in each area. Stevenson (1962) and McGurk (1989) studied Pacific herring from British Columbia and suggested that advection may be the most important cause of herring larval mortality. Another study by McGurk *et al.* (1993) examined Pacific herring in south-east Alaska, and indicated that egg condition and predation were more important sources of mortality than the advection of larvae.

There appear to be some differences in coastal current conditions between south-east Alaska and British Columbia. All of the coastal NE Pacific Ocean is affected by freshwater run-off, which is comparable to the discharge from the Mississippi River. The seasonal freshwater discharge from numerous small streams creates a cross-shelf salinity gradient which drives a poleward coastal baroclinic jet named the Alaska Coastal Current (ACC) (Royer, 1982; Freeland *et al.*, 1984; Schumacher *et al.*, 1989). Off the coast of Vancouver Island, the coastal current is named the Vancouver Island Coastal Current (VICC), which appears to undergo seasonal changes in direction (Freeland *et al.*, 1984; Hickey *et al.*, 1991). The flow of the VICC becomes much more variable during the spring months, with a complete reversal in direction developing in southerly areas by May. A little further to the north, around the Queen Charlotte Islands, there appears to be a southerly flowing coastal current, which switches to a northerly flow during the spring months (Freeland *et al.*, 1984). Further north, it appears that the coastal current remains in the northerly direction year-round, with some seasonal weakening (Royer, 1982).

Clearly, there are differences in coastal currents between south-east Alaska and British Columbia. The problem is discerning how temperature anomalies are linked to coastal currents. The currents are clearly affected by seasonal changes in freshwater discharge, with the British Columbia currents experiencing a spring transition (Freeland *et al.*, 1984). Monthly freshwater discharge appears to be at its minimum during the winter months, with a steady increase toward a seasonal maximum in summer/autumn. Perhaps warm temperature anomalies in spring result in increased freshwater discharge, thereby disrupting the spring transition in coastal currents in British Columbia. This implies that the spring transition in coastal currents is favourable to Pacific herring survival in British Columbia, thereby explaining the negative correlation of herring recruitment and temperature. In south-east Alaska, the coastal current remains northward all season long, and perhaps strengthening of this current during the spring months is favourable to herring. Deviations from this relationship of Pacific herring recruitment and coastal currents could further be explained by wind anomalies that also affect the ACC and VICC (Royer, 1982; Freeland *et al.*, 1984; Schumacher *et al.*, 1989).

Despite not knowing the exact mechanism governing year class fluctuations, we have demonstrated that Pacific herring populations in the North Pacific are closely linked to the environment and that this can be used to improve methods of forecasting recruitment. The forecast models contained herein can be applied directly for herring forecasts, but should probably just serve as a template for annual computations of herring recruitment. The time scale of environmental data used for the forecasting models in this research was averaged over yearly thirds for convenience. Further model improvements may be possible by examination on a monthly scale, for which data are typically available.

Clearly, we have not presented evidence of the mechanism by which the environment acts to influence Pacific herring recruitment. In fact, the additional variation explained by the forecasting models in this research is not nearly enough to deter any further research into causes of fluctuations in recruitment of Pacific herring (Fig. 3). It is likely that the actual mechanism by which the environment acts on Pacific herring recruitment changes from time to time and may be highly localized. The dominant pattern for Pacific herring recruitment time series indicates a high degree of variability, with strong year class events occurring every 3–10 years. The strong year classes can be as much as 429 times more than the weakest

recruitment event of the same time series (Zheng, 1996). Perhaps a closer examination of the strong year class events and localized environmental conditions may indicate direct mechanisms that influence Pacific herring recruitment.

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