REX WORKSHOP ON TEMPORAL VARIATIONS IN SIZE-AT-AGE FOR FISH SPECIES IN COASTAL AREAS AROUND THE PACIFIC RIM

(Co-convenors: William T. Peterson and Douglas E. Hay)

A one-day REX Workshop on *Temporal variations in size-at-age for fish species in coastal areas around the Pacific Rim* was convened October 5, 2001, immediately preceding the PICES Tenth Annual Meeting in Victoria, British Columbia, Canada. The workshop was very popular with more than 50 scientists attending. In total, 11 papers were presented by speakers from Canada, Japan, Russia and the United States. Four presentations discussed salmon size-at-age, five considered herring (one paper was on sardine-herring comparison), one - sablefish and one - chub mackerel. In addition, several posters presented data on size-at-age of other herring stocks as well as data for pollock and yellowfin flounder.

The keynote paper by Nikolay Naumenko summarized vast amounts of data on length-at-age and weight-at-age for 19 populations of herring from the western Bering Sea. The overall conclusion of his work was that herring growth is controlled by two main factors, food abundance (zooplankton biomass) and total fish biomass (density-dependent effects). A similar conclusion was reached by other authors as well.

Several general themes were common to many papers. One was the need to understand better the spatial scales of co-variation in size-at-age for species of fish with populations distributed along great distances of the coast. Prime candidates for such analysis are of course the salmonids and herring. Peterman showed that there was strong co-variation in size-at-age time series for sockeye salmon from Bristol Bay and Fraser River; however there was even stronger co-variation at regional scales. Eight Bristol Bay stocks were far better correlated with each other than with Fraser stocks; the same was true for 20 Fraser River stocks. This suggests the hypothesis that similar stocks are more likely to occupy a similar habitat (*i.e.*, feed in the same region of the ocean). Though no data of this type were presented for other salmon species, it is known from ongoing work (NOAA/NMFS/Northwest Fisheries Science Center) that coho salmon from the Columbia River system and coastal Oregon streams tend to spend their entire lives in continental shelf waters off Washington and Oregon state. Also, there are indications that some Sacramento River chinook salmon reside chiefly in coastal waters off central California (MacFarlane). A recommendation of the workshop participants was that REX scientists should purse analysis of co-variation and spatial autocorrelation of size-at-age of other salmon stocks and of herring stocks. An alternate approach would be to use cluster analysis, as shown by Naumenko.

The second common theme was the high degree of correlation between time series of size-at-age and various environmental (explanatory) variables. Temnykh showed the declining trends in size-at-age for Okhotsk pink salmon from the 1970s through 1985. However after 1985, pinks have gotten heavier. This is in contrast to other North American pinks which continued to grow smaller through the 1990s. She noted correlation between size-at-age of pink salmon stocks from the Sea of Okhotsk and sardine and zooplankton biomass. The period of time when pink salmon were small in size was the time when sardines were abundant and zooplankton biomass was low. The simultaneous collapse of the Japanese sardine and increased size of pink salmon, though not necessarily causal, suggests the possibility of some common forcing mechanism related to zooplankton. Positive correlations between zooplankton biomass and both length-at-age and weight-at-age were found for several herring populations as well including the Korf-Karaginsk (western Bering Sea) stock (Naumenko; Balykin and Buslov), Prince William Sound (Brown), and stocks from British Columbia (Schweigert; Tanasichuk). Finally, Tarasyuk showed that biomass of yellowfin sole from the Tatar Strait (Japan/East Sea) was correlated with zooplanton biomass.

Temporal and special changes in pattern in size-at-age were examined relative to climate variability and climate change. Good correlations were also found with climatic variables such as the Pacific Decadal Oscillation, Aleutian Low Pressure Index, or water temperature alone (Peterman, MacFarlane, Brown, Schweigert, Bonk, Tarasyuk). Competition with other pelagic species was suggested as a possible mechanism explaining changes in growth of chub mackerel (Watanabe). Ecosystem change was implicated as a factor explaining stock fluctuations in Hokkaido-Sakhalin herring whereas the co-occurring sardines stocks appear to be largely density dependent (Watanabe).

Many papers demonstrated density dependence of size-at-age. When population size was large, size-at-age was small and *vice versa*. Discussion at the workshop centered on the need to think more and work harder at identifying mechanisms that might control density dependence, with studies of the forage base being one of the prime candidates.

Discussion was also focused on the need to make better use of existing samples to study size- and weight-at age through use of scales and otoliths to generate new data sets on size- and weight-at-age. There are many data on length and weight of fishes but not as much data on age and weight at length. Through analysis of otoliths and scales, one could determine age of fishes that have already been measured.

Finally, the workshop participants discussed the value of comparative studies and of course - this is what REX workshops are all about – providing a forum for discussion on differences in population size, growth, and life history characteristics of species that are distributed widely around the Pacific Rim. This led to the recommendation that PICES scientists need to do more comparisons of populations that are distributed in the coastal zones around the basin, but also need to compare response of fish, nekton and zooplankton populations that are found within the deeper waters of the Kuroshio, Kuroshio Extension, Transition Zone and the California Current. Interesting, this thought arose independently of the inter-sessional symposium proposed on comparative studies of North Pacific transitional areas (the symposium was held April 23-25, 2002, in La Paz, Mexico).

The following section contains extended abstracts of papers given at the workshop.

Spatial patterns of covariation in size-at-age of British Columbia and Alaska sockeye salmon stocks and effects of abundance and ocean temperature

Brian J. Pyper[1], Randall M. Peterman[1], Michael F. Lapointe[2] and Carl J. Walters[3]

[1] School of Resource and Environmental Management, Simon Fraser University, Burnaby, B.C., Canada. V5A 1S6. E-mail: peterman@sfu.ca

[2] Pacific Salmon Commission, 600-1155 Robson St., Vancouver, B.C., Canada. V6E 1B5. E- mail: lepointe@psc.org

[3] Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada. V6T 1Z4. E-mail: c.walters@fisheries.ubc.ca

Introduction

Body lengths of adult Pacific sockeye salmon (*Oncorhynchus nerka*) have decreased significantly in recent years, reducing the reproductive potential of spawners and the economic value of harvests. To understand the causes of these important trends, we pursued three objectives. Firstly, we quantified the extent of spatial covariation among age-specific body sizes of numerous stocks in the Northeast Pacific. The observed spatial scale of covariation could suggest the causes of that variation. Secondly, we compared the extent of covariation among body size and survival rate of sockeye salmon to determine whether these two variables were influenced by similar processes. Thirdly, we tested hypotheses about the relative importance of intraspecific competition and oceanographic conditions on size of adult sockeye salmon. This paper summarizes material already published; see Pyper *et al*. (1999) and Pyper and Peterman (1999) for details.

Methods

We used 72 time series of body length at a given adult age for 31 sockeye stocks from five geographically distinct regions in British Columbia (Fraser River and Skeena River) and Alaska (Upper Cook Inlet, Copper River and Bristol Bay). Ages included were 1.1, 1.2, 1.3, 2.2 and 2.3 fish.

Patterns of covariation. To examine patterns of covariation among length-at-age data both within and between regions, we calculated Pearson product-moment correlation coefficients for pairwise comparisons among the 72 time series of lengths. Size data were aligned to have return years in common (year in which they returned to their natal streams), because Rogers and Ruggerone (1993) and McKinnell (1995) suggest that interannual variability in body size of recruits is largely determined by growth in their final year at sea. However, to estimate the importance of conditions in early ocean life, we also computed correlations after aligning the data series to have a common ocean entry year (OEY) but a different return year (*e.g.* using size data for 1.2 and 1.3 adults).

Positive autocorrelation and time trends were present in many of the time series of body length, indicating that low-frequency (*i.e.*, slowly-changing) variability is important. However, such autocorrelation and time trends increase the chance that statistically significant but spurious correlations will occur in standard inference tests. Therefore, we used two approaches to examine correlations. Firstly, we computed them using the original time series and based significance tests on the method recommended by Pyper and Peterman (1998), which adjusts degrees of freedom to account for autocorrelation and maintains Type I error rates near the specified α in the presence of autocorrelation. Secondly, we first-differenced the time series (subtracting each data point from the next) to remove the low-frequency variation and re-computed correlations. Comparing the results from these two approaches allowed us to quantify the potential importance of low-frequency causes of the positive covariation that we found.

Effects of oceanographic conditions and intraspecific competition. We also used principal components analysis (PCA) to further examine spatial and temporal covariation among lengths for 1967-1997. The PCA was done on 13 regional average length-at-age series, which better depicted the "signal" shared by given age classes and stocks in each region. This method reduced patterns of variability shared by each age class and region to a few defining time series (principal components). Copper River data were omitted due to missing data.

We then used the dominant principal component (PC1) to test hypotheses about the causes of variation in sockeye growth rate. Because our covariation results indicated that adult body size was affected primarily by conditions in the last year of ocean life, we generated indices of oceanographic conditions and intraspecific competition during the final year at sea. These indices were consistent with the area of overlap in ocean distributions of B.C. and Alaska sockeye, which roughly encompasses the Alaskan Gyre and is occupied by sockeye salmon from North America but not Asia (French *et al*. 1976). We used total ocean abundance of maturing North American sockeye salmon as an index of intraspecific competition, based on annual adult recruits (catch plus escapement) summed across the major B.C. (Fraser, Skeena, and Nass River) and Alaska stocks (Copper River, Cook Inlet, and Bristol Bay), which together account for the vast majority of sockeye abundance in the Gulf of Alaska (see Peterman *et al*. 1998 for details).

To reflect ocean conditions that might affect growth, we generated time series of annual sea-surface temperature (SST) deviations from the long-term mean. We used monthly SST data (ºC) on a 5-by-5 degree latitude-longitude grid across the area stated above of general overlap in ocean distributions of B.C. and Alaska sockeye (see Pyper and Peterman 1999 for details). Deviations were computed for a given grid cell and month by subtracting its long-term mean SST for 1947 through 1997. These deviations were then averaged to create two time series, with each corresponding to a different period preceding the return (generally in July) of sockeye salmon to their rivers: 1) winter months (November through February), and 2) a combination of winter and spring months (November through June). Climatic forcing during winter months is thought to be an important determinant of ocean productivity in the subsequent spring and summer (*e.g.*, Brodeur and Ware 1992), while in spring, maturing sockeye are feeding and growing at high rates before and during migrations back to their natal streams.

We then used multiple regression to examine relationships among the dominant pattern of covariation for length (PC1), total sockeye abundance in millions of fish (A), and ocean temperature (SST) for either November-February or November-June:

$$PC1 = a + b_1A + b_2SST + \varepsilon$$

Because of positive autocorrelation in the residuals, we simultaneously computed maximum likelihood estimates of the lag-1 autocorrelation coefficient and regression parameters. Due to time trends in the data, we first computed regressions using the original data and then repeated the regressions using detrended data (deviations from a linear time trend fit to each data series) to test for effects at shorter time scales.

Results and discussion

Patterns of covariation. There was widespread positive covariation among the 72 body-length time series, aligned by return year, across ages and across stocks. Of the 2,556 correlations, 91.4% were positive (and 43%, or 1,006, of the positive ones were significant at $p<0.05$, whereas only 3 negative cases were significant). There was strong evidence of positive covariation in age-specific body size among sockeye stocks even between distant regions, as indicated by the predominance of positive correlations in these comparisons (*e.g.*, Bristol Bay vs. Fraser River; Fig. 1C). However, there was a stronger positive covariation among body length of stocks within regions (*e.g.*, among the 8 stocks in Bristol Bay and among the 20 in the Fraser River; Fig. 1A and 1B). Generally, the percent of variation in length shared by stocks in the same region was about twice that shared by stocks from different regions (see Pyper *et al.* (1999) for detailed results).

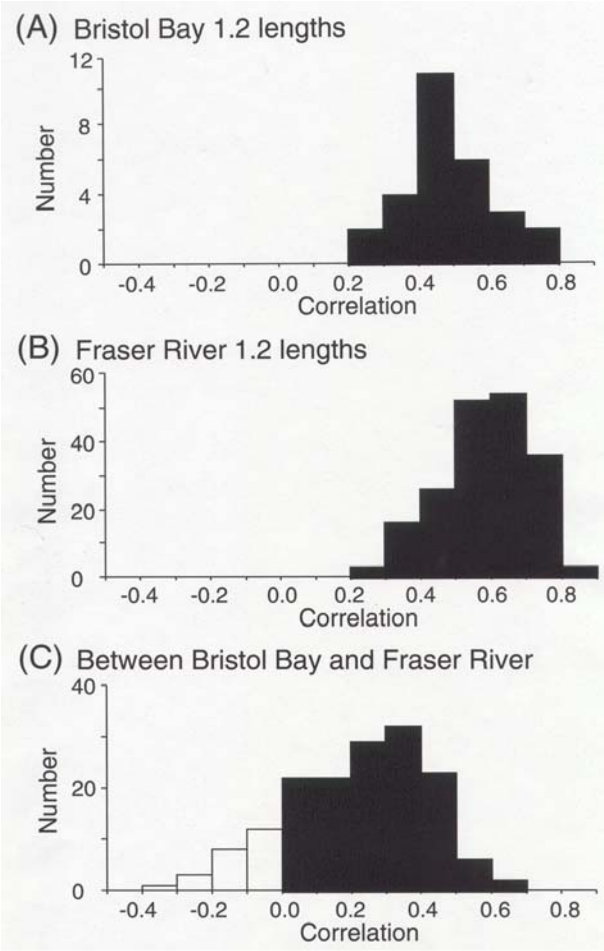


Fig. 1 Histograms of correlations between lengths of age 1.2 sockeye: A) among Bristol Bay stocks (all 28 correlations positive; 23 significant at $p<0.05$); B) among Fraser River stocks (all 190 correlations positive; 161 significant); and C) between Bristol Bay and Fraser River stocks (136 of 160 correlations positive; 25 significant positive correlations). Open bars represent negative correlations; solid bars are positive correlations. Reprinted from Pyper *et al.* (1999).

Correlations using first-differenced data support the suggestion from the PCA reported below that slowly changing, low-frequency patterns of variability, such as the declining time trends in body size, were important sources of covariation among average lengths of stocks. After autocorrelation and time trends in the 72 stock-specific length series were removed by first-differencing, widespread positive covariation was still evident both within and between regions. However, correlations were consistently and often substantially lower than those computed using the original data. The average of the 2,556 correlations was reduced from 0.37 to 0.23, the number of negative correlations increased to 578, and the number of significant ($p<0.05$) positive correlations decreased to 745. Thus, there is little evidence that the general patterns of covariation in lengths could be solely a spurious result of unrelated time trends; instead, to the extent that the observed covariation in length-at-age of sockeye salmon arises from shared processes, such processes appear to be largely characterized by low-frequency patterns of variability.

In contrast to the above analyses, when the body-length time series were aligned to share the same ocean entry year (OEY) but to have a different return year (RY), the correlations among stocks decreased dramatically (*e.g.* for Bristol Bay stocks, the average correlation in the original data series decreased from 0.67 when lined up by RY to 0.29 when lined up by OEY). This decrease was even greater when possible confounding effects of autocorrelation were removed from both analyses (see Pyper *et al*. 1999). Like other analyses, (Rogers and Ruggerone 1993; McKinnell 1995), these findings imply that variable growth conditions during early marine life are not nearly as important a determinant of temporal variation in final sockeye body length as conditions during late marine life.

Comparison of body size and survival rates. We found weak and inconsistent correlations between average length and survival rate, suggesting that different processes drive interannual variability in these components of recruitment. This conclusion is further supported by evidence that environmental processes influence these two variables at different spatial scales. Whereas both adult body size and survival rate show strong positive covariation among stocks within regions, only body size shows strong between-region covariation (*e.g.*, compare Fig. 1C here with Fig. 1C of Peterman *et al*. 1998). These differences in spatial characteristics of covariation suggest that models for body size or forecasting annual salmon abundance (reflecting survival rates and changing age-at-maturity schedules) should be based on appropriate measures of environmental conditions that reflect this information about spatial scales. For example, we found that large, basin-scale SST was significantly associated with variation in body size (see below), whereas Mueter *et al*. (2001) found that smaller, regional-scale SST was much more important in explaining variation in survival rates of salmon.

Effects of oceanographic conditions and intraspecific competition. Principal components analysis (PCA) of the 13 age-specific regional body length series defined the temporal characteristics of variation shared among regions. The PCA yielded three principal components with eigenvalues greater than one; the best one accounted for 65% of the total variance and the other two combined accounted for only 19%. The time series (scores) of this dominant component, PC1, had an obvious declining trend from 1967-1997 ($p<0.001$; linear regression with autocorrelated error) (Fig. 2A). All 13 length series correlated strongly with PC1 (range 0.64 to 0.89), suggesting that much of the covariation among lengths of Alaska and B.C. sockeye salmon resulted from a similar declining trend over this period.

The multiple regression for the PC1 (reflecting shared variation among body size) using the original data was highly significant (multiple $r^2 = 0.71$, $p \ll 0.001$), as was the estimated slope on abundance ($b_1 = -0.03 \pm 0.005$ [±1 standard error], $p \ll 0.001$) (Fig. 2B). The slope on November-February SST was also significant ($b_2 = -0.72 \pm 0.29$, $p = 0.014$) (Fig. 2C). Partial r^2 values were 0.56 for abundance and 0.18 for SST.

The multiple regression using detrended data (to remove possible confounding due to time trends in the original data) showed similar results. Both abundance and November-February SST were significant ($b_1 = -0.035 \pm 0.007$, $p \ll 0.001$ and $b_2 = -0.87 \pm 0.31$, $p = 0.004$). Overall, the multiple $r^2 = 0.54$, $p \ll 0.001$, and multicollinearity was negligible (r = 0.04). Partial r^2 values were 0.48 for abundance and 0.23 for SST.

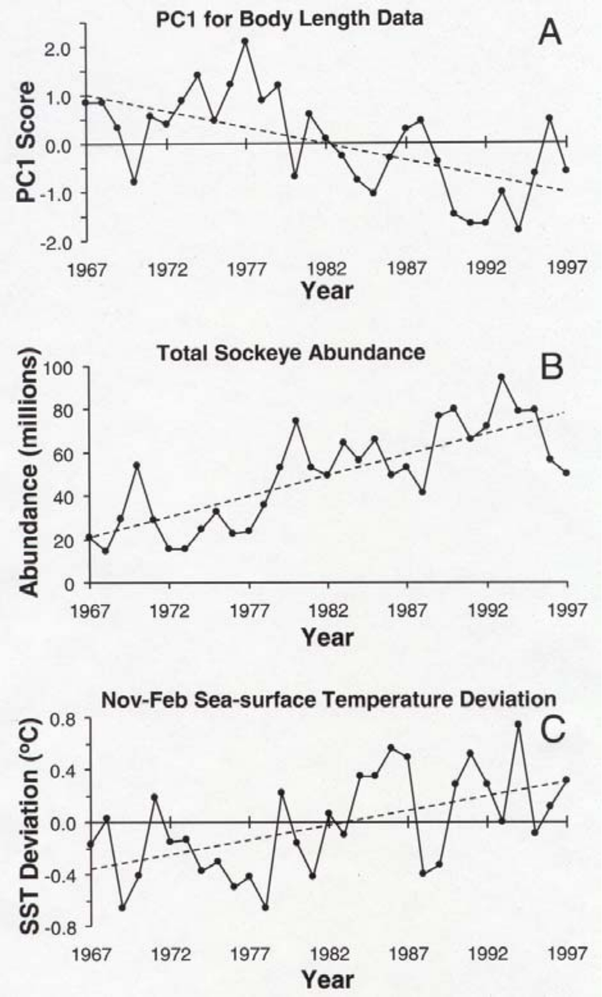


Fig. 2 (A) Scores for the dominant principal component (PC1) of length-at-age data for B.C. and Alaska sockeye salmon -- lower values of PC1, for example, reflect the tendency toward reduced body length that is shared among these stocks; (B) Total annual abundance of adult recruits (catch plus escapement) of the major B.C. and Alaska sockeye stocks; and (C) Average yearly winter (November through February) sea-surface temperature (SST) deviations in °C from the long-term (1947-1997) mean for those months (6.8°C) for the Northeast Pacific Ocean over the region where distributions of B.C. and Alaska sockeye salmon overlap. Dotted lines are the fitted linear time trends used to detrend the data. Reprinted from Pyper and Peterman (1999).

Because November-February and November-June SST data were highly correlated (r = 0.86), all results for the latter were similar to those for November-February, with the exception that November-June SST was not significant in either the multiple regression with original data (p = 0.11) or with detrended data (p = 0.08).

These results indicate that reduced adult body length of both B.C. and Alaska sockeye salmon are associated with increases in total sockeye abundance in the Northeast Pacific and November-February sea-surface.

Abundance and SST together account for 71% of the variability in the first principal component (PC1) of body length among the major sockeye stocks of the northeastern Pacific Ocean during 1967-1997. Furthermore, abundance appears to have a much greater effect on body size than temperature. Its partial r^2 was considerably larger (0.56 vs. 0.18), and when data in each series were transformed into standard deviation units so that slopes were in the same units, the standardized slope for abundance (-0.68) was greater than the slope for SST (-0.27). This indicates that for each standard deviation increase, abundance had about 2.5 times the contribution to reducing adult body size as did November-February SST.

In addition, both abundance and SST were significantly related to the dominant pattern of variability in body length at both long and short time scales (*i.e.*, in the original, as well as detrended data). Thus, although it is possible that relationships among the original data might be coincidental due to their co-occurring time trends (*i.e.*, that some other omitted variable actually explains the trend in PC1), the evidence in support of the effects of abundance and SST was strengthened by their very similar slopes in both the original data analysis and the analysis once time trends were removed.

Although several authors have documented increased secondary productivity in the northeastern Pacific Ocean in recent decades (*e.g.*, zooplankton and squid - Brodeur and Ware 1992, 1995), which should improve growth rates for sockeye salmon, abundance of sockeye recruits also increased (Fig. 2B). We therefore hypothesize that increased food supply was more than offset by increased sockeye abundance, which resulted in greater competition and smaller body size in recent years.

Acknowledgments

We are extremely grateful to the numerous biologists and technicians in various management agencies who gathered, processed, and provided the time series of data analyzed here. Funding was provided by a grant to R.M. Peterman from the Natural Sciences and Engineering Research Council of Canada.

References

Brodeur, R.D., and Ware, D.M. 1992. Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. Fisheries Oceanog. 1: 32-38.

Brodeur, R.D., and Ware, D.M. 1995. Inter-decadal variability in distribution and catch rates of epipelagic nekton in the Northeast Pacific ocean. *In* R.J. Beamish (Ed.) Climate change and northern fish populations. Can. Spec. Publ. Fish. Aquat. Sci. 121, pp. 329-356.

French, R., Bilton, H., Osaka, M., and Hartt, A. 1976. Distribution and origin of sockeye salmon (*Oncorhynchus nerka*) in offshore waters of the North Pacific Ocean. INPFC Bulletin 34.

McKinnell, S. 1995. Age-specific effects of sockeye abundance on adult body size of selected British Columbia sockeye stocks. Can. J. Fish. Aquat. Sci. 52: 1050-1063.

Mueter, F.J., Pyper, B.J., and Peterman, R.M. 2001. Effects of coastal sea surface temperatures on survival rates of sockeye, pink, and chum salmon stocks from Washington, British Columbia, and Alaska. Poster #S11-203 in Session S11: "Results of GLOBEC and GLOBEC-like programs," at the PICES Tenth Annual Meeting, Victoria, B.C., October, 5-13, 2001.

Peterman, R.M., Pyper, B.J., Lapointe, M.F., Adkison, M.D., and Walters, C.J. 1998. Patterns of covariation in survival rates of British Columbia and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. Can. J. Fish. Aquat. Sci. 55: 2503-2517.

Pyper, B.J., and Peterman, R.M. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. Can. J. Fish. Aquat. Sci. 55: 2127-2140 plus the erratum printed in Can. J. Fish. Aquat. Sci. 55: 2710.

Pyper, B.J., and Peterman, R.M. 1999. Relationship among adult body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon, 1967-1997. Can. J. Fish. Aquat. Sci. 56: 1716-1720.

Rogers, D.E., and Ruggerone, G.T. 1993. Factors affecting marine growth of Bristol Bay sockeye salmon. Fisheries Research 18: 89-103.

Pyper, B.J., Peterman, R.M., Lapointe, M.F., and Walters, C.J. 1999. Patterns of covariation in length and age at maturity of British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*) stocks. Can. J. Fish. Aquat. Sci. 56: 1046-1057.

Influences of the 1997-1998 El Niño and 1999 La Niña on juvenile chinook salmon in the Gulf of the Farallones

R. Bruce MacFarlane, Steven Ralston, Chantell Royer, and Elizabeth C. Norton
NOAA Fisheries, Southwest Fisheries Science Center, Santa Cruz Laboratory, 110 Shaffer Road, Santa Cruz, CA 95060, U.S.A. E-mail: Bruce.MacFarlane@noaa.gov

El Niño, the warm phase of El Niño/Southern Oscillation (ENSO) events, has been shown to produce dramatic effects on marine communities. Alterations in physical oceanographic properties of the marine environment can be observed as far north as Alaska. Less is known of the influences of La Niña, the cool phase of ENSO events that follows an El Niño. During the 1982-83 El Niño, anomalous plankton distributions, altered fish community structure, and reduced fish catch occurred in coastal waters of southern California (Simpson, 1992). Along the central California coast, the 1992-93 El Niño corresponded to delayed phytoplankton blooms, changes in the abundance and distribution of invertebrates, improved recruitment of southern fish species, but recruitment failure in the northerly rockfish species (Lenarz *et al*. 1995). More recently, the largest decline in macrozooplankton abundance off central and southern California in the 50-year series of CalCOFI cruises was recorded during the 1997-98 El Niño (Lynn *et al*. 1998).

In addition to ecosystem impacts, changes in physiology and behavior of fishes, including salmon, have been noted during ENSO events. Poor growth and low condition, ascribed to low fat content, were found in adult rockfish off central California during 1992-93 (Lenarz *et al.* 1995). And in a study of widow (*Sebastes entomelas*) and yellowtail rockfish (*S. flavidus*) in coastal waters of central and northern California, Woodbury (1999) reported reduced otolith growth, a conservative measure of somatic growth history, during the 1982-83 El Niño. Reduced condition and growth of sockeye salmon (*Oncorhynchus nerka*) in the Gulf of Alaska during the 1997-98 El Niño event were related to feeding on zooplankton, prey of lower caloric content than squid, their primary food in 1998 following the El Niño (Kaeriyama *et al.* 2000). In a review of El Niño effects on fisheries, Mysak (1986) detailed other impacts to sockeye, including changes in migration patterns and the timing of returns to streams. Lower survival in juvenile coho salmon (*O. kisutch*) following ocean entry, great mortality in adult coho, and reduced size in both coho and chinook salmon (*O. tshawytscha*) were described off Oregon during the 1982-83 El Niño (Pearcy and Schoener 1987).

We report here the results of a study of juvenile chinook salmon in the Gulf of the Farallones, an embayment on the central California coast. The Gulf of the Farallones, a broad expanse of continental shelf extending from Pt. Reyes to Pillar Pt. out to the Farallon Islands, receives freshwater outflow through the Golden Gate from the Sacramento and San Joaquin Rivers and their tributaries in California's Central Valley. It is also the point of ocean entry for an estimated 50-60 million chinook salmon smolts spawned from four runs (fall, late fall, winter, spring) in streams and hatcheries in the Central Valley. The purpose of the information presented here is to document juvenile salmon development, and how it was influenced by the environment in the Gulf of the Farallones during the 1997-98 El Niño and 1999 La Niña.

Juvenile salmon were captured by surface trawl at locations in the Gulf of the Farallones in June to October of 1998 and 1999. El Niño was evident in the Gulf of the Farallones in August 1997 and persisted to August 1998 (Fig. 3). By late 1998, La Niña was apparent and continued into spring 2000. Plankton samples were taken by Tucker Trawl at 5 m and 15-25 m below the surface to estimate secondary productivity and zooplankton composition.

Relative growth for juveniles caught in 1998 and 1999 was estimated by microstructural analysis of otoliths. Growth rates and size-at-age of juvenile chinook salmon can be estimated by measuring daily otolith increment widths (Bradford and Geen 1987). We calculated mean otolith increment widths as an index for somatic growth between increments 160 and 260, representing the first 100 days after leaving the estuary. Juvenile salmon exited San Francisco Estuary at 160±1 days old in 1998 and at 168±3 days old in 1999. Growth rate indices for salmon caught in 1998, during the El Niño period, were significantly greater than for fish collected in 1999 ($P<0.0001$). Mean growth rates of otolith increments were 3.37±0.03 μm in fish sampled in 1998 and 3.02±0.03 μm in 1999 (Fig. 4).

Whole body concentrations of triacylglycerols (TAG), the primary metabolically-available form of stored energy in salmonids and other fishes, differed between the two years. Upon entering the Gulf of the Farallones, juvenile salmon had greater levels of TAG in 1999 than in 1998, 30.5±3.1 mg/g and 11.5±1.8 mg/g wet weight, respectively. However, lipid stores of salmon in the gulf were depleted to a greater extent in 1999. Juveniles collected from the gulf in 1999 had TAG levels of 4.4±1.4 mg/g, whereas those from 1998 were 7.9±1.0 mg/g. These data support previous research that found depleted TAG

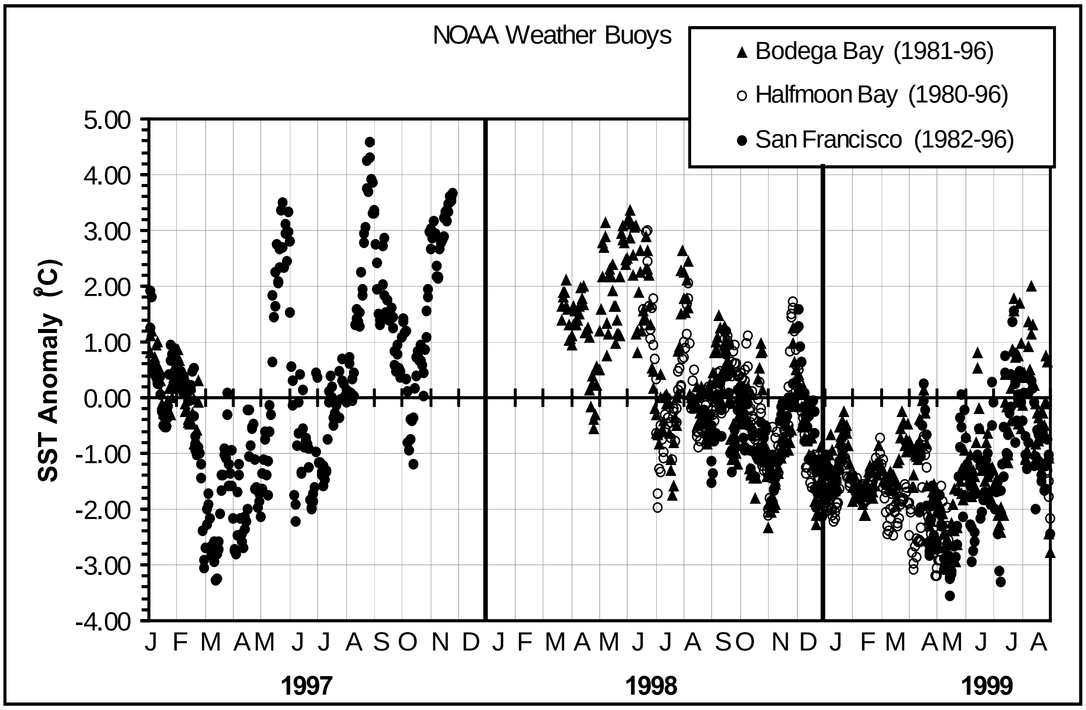


Fig. 3 Sea surface temperature anomalies from buoys at Bodega Bay, San Francisco, and Half Moon Bay. Anomalies were calculated from longer-term averages shown in parentheses in the legend. All three buoys were out of operation from December 1997 to mid-March 1998 when El Niño conditions were most evident.

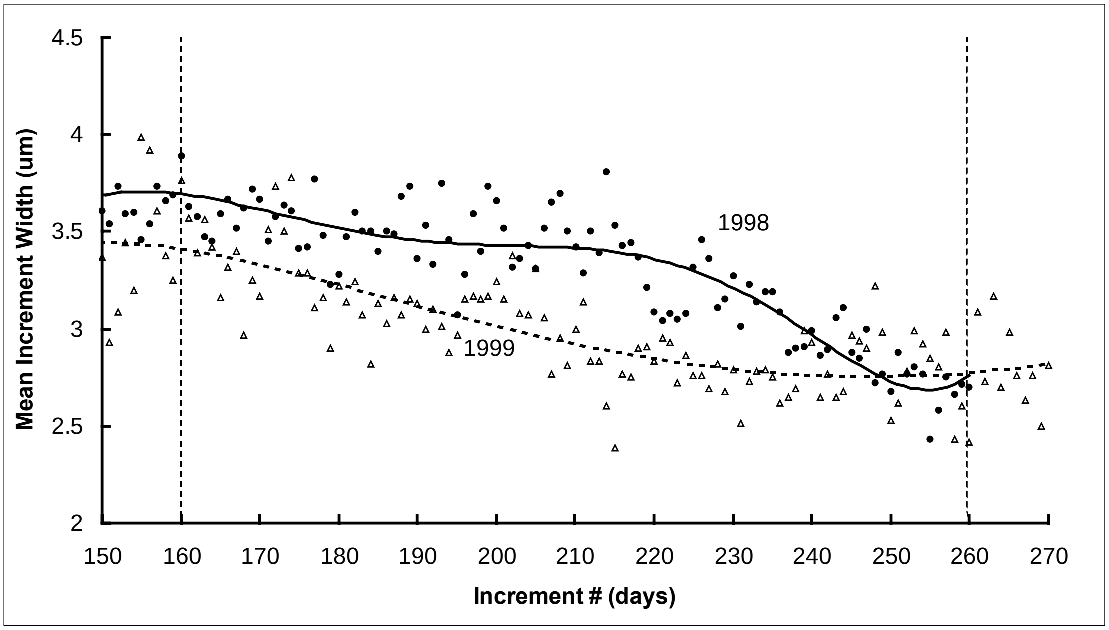


Fig. 4 Mean otolith increment widths for juvenile chinook salmon from the Gulf of the Farallones in 1998 (solid circles) and 1999 (open triangles). Lines represent least squares fit of daily mean increment widths; solid line - 1998, dashed line - 1999. Vertical dashed lines at 160 and 260 increments represent estimated first 100 days in the ocean after leaving the San Francisco Estuary.

concentrations in juvenile salmon after exiting the estuary (MacFarlane and Norton, 2002).

Juvenile salmon in the Gulf of the Farallones not only grew faster and maintained a greater TAG concentration during the 1998 El Niño period, their condition (Fulton's K-factor) was better as well. In 1998, mean K increased to 1.42±0.01 for gulf salmon from 1.03±0.01 at ocean entry, compared with a change from 1.04±0.01 at ocean entry to 1.32±0.01 in the gulf during 1999.

Although there were differences in growth, energy status, and condition between the two years, feeding data did not resolve the disparity. This is not unexpected because stomach contents reflect only recent feeding, whereas growth and lipid accumulation integrate metabolic processes over longer time scales. Stomach fullness was estimated to be 45.5% in juveniles sampled in 1998 and 56.7% in 1999. In both years, fish were the primary food item, comprising greater than 50% of the stomach contents volume. Decapod early life stages were of secondary importance, especially for salmon later in the season in August to October.

The marine environment in the Gulf of the Farallones differed between the two years. From May through August, mean sea surface temperatures were about 1.0°C warmer in 1998 and about 1.3°C cooler in 1999 than long-term averages (Fig. 3). The 1997-98 El Niño was characterized by heavy precipitation in California and this was evident in freshwater outflow from the Central Valley. Freshwater outflow into the gulf averaged 2,940 cubic meters per sec (m^3/s) from January to June 1998, whereas outflow in 1999 was much reduced during the dryer La Niña to 1,330 m^3/s.

The Gulf of the Farallones is buffered from large-scale oceanic influences because it is in the upwelling shadow of Pt. Reyes to the north, bounded by the Farallon Islands and associated marine banks on the west, and subjected to the effects of freshwater outflow from San Francisco Bay. Although El Niño typically produces enhanced poleward flow of the California Current, near-surface current data from an Acoustic Doppler Current Profiler in May and June 1998 did not reveal such a pattern. Currents in the gulf were forced by tidal circulation and persistent northwesterly winds, which also produced positive upwelling index anomalies throughout the summer and fall of 1998 (April - November mean monthly anomaly for 39°N 125°W: +44.5±25.6). As expected, strong northwesterly winds during the summer and fall of the 1999 La Niña event resulted in intense upwelling with a mean April to November monthly index anomaly of 104.6±35.1.

Biological productivity is highly variable in the Gulf of the Farallones region and modulated to varying degrees by upwelling, advection, wind-driven and tidal circulation, and freshwater outflow. Primary productivity, estimated by chlorophyll *a* concentrations in May and June, was similar between the two years, but the distribution of phytoplankton differed. In 1998, phytoplankton were distributed within the gulf on the continental shelf whereas during the 1999 La Niña they were primarily off the shelf, seaward of the gulf. Greater nutrient-rich freshwater influx coupled with higher temperatures in 1998 may have accounted for greater primary productivity within the gulf during the El Niño event. Greater phytoplankton biomass within the Gulf of the Farallones in 1998 was accompanied by greater secondary production. Mean zooplankton biomass in the near-surface waters was 0.30±0.12 ml/m^3 in May and September 1998. In contrast, zooplankton mean settled volume was 0.13±0.03 ml/m^3 in August and October 1999.

In summary, during the 1997-98 El Niño, juvenile salmon in the Gulf of the Farallones grew at a greater rate, maintained higher TAG reserves, and were in better condition than those during the 1999 La Niña. This profile may be attributed to somewhat higher biological productivity in the gulf in 1998, due to increased nutrient input from freshwater inflow, and the protection afforded by Pt. Reyes and the Farallon Islands, which buffered the embayment from the full impacts of oceanic processes. But, for all measures of salmon development the differences were not great. The data do support the contention, however, that the 1997-98 El Niño was not detrimental to juvenile chinook salmon development in this region during the early stage of the ocean phase of their life cycle.

References

Bradford, M.J., and Geen, G.H. 1987. Size and growth of juvenile chinook salmon back-calculated from otolith growth increments, p. 453-461. *In* R.C. Summerfeldt and G.E. Hall [eds.] The age and growth of fish. Iowa State University Press, Ames, IA.

Kaeriyama, M., Nakamura, M., Ueda, H., Anma, G., Takagi, S., Aydin, K.Y., Walker, R.V., and Myers, K.W. 2000. Feeding ecology of sockeye and pink salmon in the Gulf of Alaska. NPAFC Bulletin 2: 55-63.

Lenarz, W.H., Ventresca, D.A., Graham, W.M., Schwing, F.W., and Chavez, F. 1995. Explorations of El Niño events and associated biological population dynamics off central California. CalCOFI Report 36: 106-119.

Lynn, R.J., Baumgartner, T., Garcia, J., Collins, C.A., Hayward, T.L., Hyrenbach, K.D., Mantyla, A.W., Murphree, T., Shankle, A., Schwing, F.B., Sakuma, K.M., and Tegner, M.J. 1998. The state of the California Current, 1997-1998: transition to El Niño conditions. CalCOFI Report 39: 25-49.

MacFarlane, R.B,. and Norton, E.C. 2002. Physiological ecology of juvenile chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California. Fishery Bulletin 100 (2) (In press).

Mysak, L.A. 1986. El Niño, interannual variability and fisheries in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 43: 464-497.

Pearcy, W.G., and Schoener, A. 1987. Changes in the marine biota coincident with the 1982-1983 El Niño in the northeastern subarctic Pacific Ocean. J. Geophys. Res. 92: 14,417-14,428.

Simpson, J.J. 1992. Response of the Southern California current system to the mid-latitude North Pacific coastal warming events of 1982-1983 and 1940-1941. Fisheries Oceanogr. 1: 57-79.

Woodbury, D. 1999. Reduction of growth in otoliths of widow and yellowtail rockfish (*Sebastes entomelas* and *S. flavidus*) during the 1983 El Niño. Fishery Bulletin 97: 680-689.

Variability of the pink salmon sizes in relation with abundance of Okhotsk Sea stocks

Olga S. Temnykh[1] and Sergey L. Marchenko[2]

[1] Pacific Research Fisheries Center (TINRO-center), 4, Shevchenko Alley, Vladivostok, Russia, 690600. E-mail: tinro@tinro.ru

[2] MoTINRO, Magadan, Russia. E-mail: tinro@online.magadam.su

Beginning in the mid-1970s there was an increase in abundance of all Pacific salmon species. It was shown that global climatic factors may have caused changes in salmon abundance in the North Pacific (Beamish and Bouillon 1993, Klyashtorin and Sidorenkov 1996, Radchenko and Rassadnikov 1997, Shuntov *et al.* 1997). The rise in abundance of Asian and American stocks of salmon was accompanied by a decrease in the average size of fish, by an increase in age at maturity (due to the growth rate reduction during marine period of their life cycle), and by a reduction of the fecundity of females (Ishida *et al.* 1993, Welch and Morris 1994; Bigler *at.al.* 1996). Nevertheless, there are some exceptions to the general trend of Pacific salmon productivity in relation to stock abundance. For example, a decrease in abundance was observed for the Japan/East Sea pink salmon stocks (especially for the Primorye stock) while the average size of the Primorye pink salmon decreased during the 1970-1980s (Temnykh 1998). At the same time, abundant pink salmon from Sakhalin maintained a large size (Nagasawa 1998).

The main objectives of this research were to:

- Compare growth of pink salmon from “continental” (northern coast of the Okhotsk Sea) and “island” (Sakhalin, southern Kuril islands) regions during periods of high and low pink salmon abundance; and
- Determine those factors responsible for size differences among pink salmon stocks, particularly in the northern and southern Okhotsk Sea, during periods of low and high abundance from the 1970s-1990s.

Materials and methods

Statistical data on pink salmon catches collected by TINRO-Centre, SakhTINIRO, and MoTINRO, are used in this study. These include the average size of spawners from rivers on the Okhotsk Sea coast of Sakhalin (north and south Sakhalin as well as Terpenya and Aniva bays), from Iturup Is. (southern Kuriles), and from the mainland rivers of the northern coast of the Okhotsk Sea (Gizhiga, Kukhtuy, and Tauy rivers) (Fig. 5).

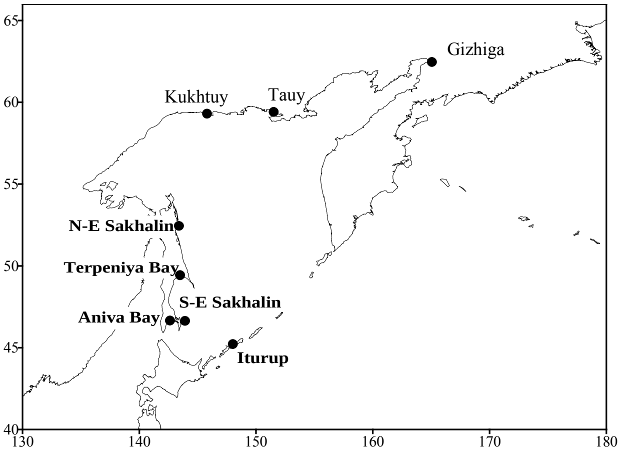


Fig. 5 Map of the location of Okhotsk Sea pink salmon regions studied.

Results

Catch dynamics for the Okhotsk Sea stocks of pink salmon

Eastern Sakhalin, western Kamchatka, southern Kurile, and northern Okhotsk Sea stocks of pink salmon are highly abundant stocks within the Okhotsk Sea. Following a period of low abundance in 1940-1960s, an increase in pink salmon number was observed in the Okhotsk Sea from the late 1970s. From the early 1990s, the total odd-year pink salmon catch increased 1.8 times when compared to the late 1970s and 1980s, and amounted to 62-133 thousand tons (Fig. 6). This was mainly due to a considerable rise of pink salmon abundance from the south-western Okhotsk Sea, particularly from eastern Sakhalin. During the last decade the share of those groups in the odd years reached 55-96% in the total number in the Okhotsk Sea.

Total even-year pink salmon catch increased 3.4 times when compared to the 1970-1980s, and amounted to 83-192 thousand tons (Fig. 6). On the Sakhalin and southern Kuriles, the number of pink salmon increased 2.2 times, while in the western Kamchatka and northern Okhotsk Sea regions it increased 4.6 and 4.3 times, respectively. Beginning in 1994, pink salmon from western Kamchatka was the most numerous among the odd-year generations (46-60% of the total number of the Okhotsk Sea stocks).

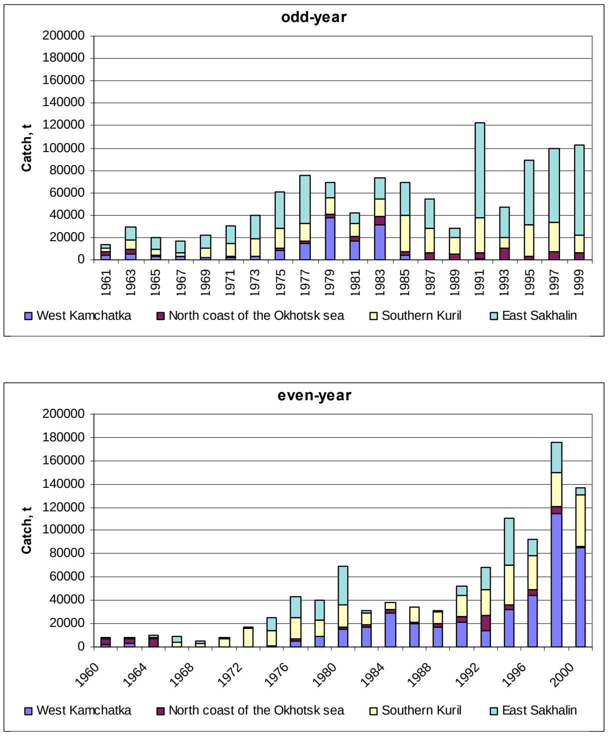


Fig. 6 Total annual catch of pink salmon in the main regions of coastal fisheries.

Changes of body weight of the Okhotsk Sea stocks of pink salmon

During the 1990s, both southern and northern pink salmon populations from the Okhotsk Sea were characterized by peculiar changes in mean size. Among the southern Okhotsk Sea stocks (eastern Sakhalin, southern Kuriles), there was a trend toward increasing body weight both in even-year, and especially in odd-year generations over the last decade (Fig. 7, Table 1).

As for the increased abundance of pink salmon from the northern Okhotsk Sea coast, the average weight was also growing in the odd-year broods, that were more abundant than even-year generations, though it was somewhat smaller in the even years. Average size changes within the "northern" and "southern" groups of pink salmon were synchronous. The increase in both abundance and average size of pink salmon from southern and northern Okhotsk Sea stocks is unequivocal evidence that favorable conditions prevailed for fish reproduction during the late 1980s - early 1990s.

Weakening of the Aleutian Low led to considerable warming of the northwestern Pacific after 1989. The carrying capacity for the Okhotsk Sea pink salmon increased. Unlike the North American pink salmon, the average size of the Okhotsk Sea pink salmon increased during a period of high abundance. We can only guess what was the main reason for that. It could be due to increased productivity as a consequence of general warming in the northwestern Pacific and/or improvements of forage reserves at the expense of significant decreases in abundance of other plankton consumers. In the 1980s, the total biomass of pelagic fishes amounted to

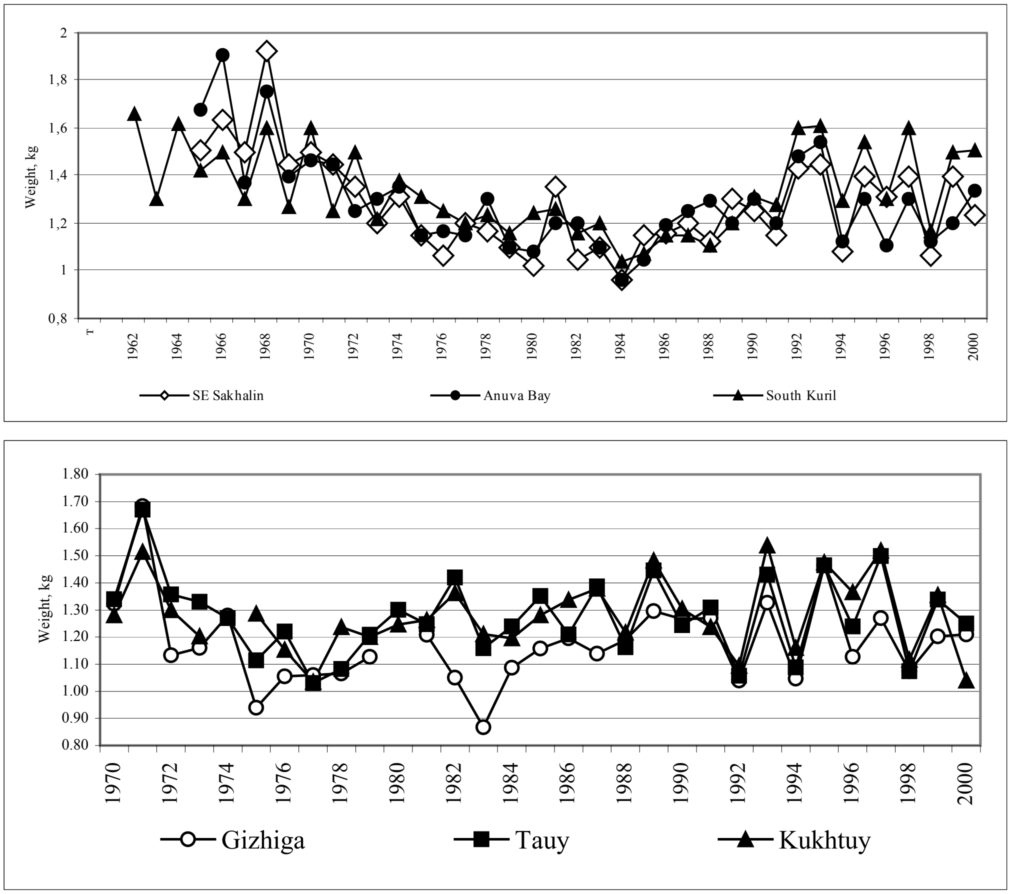


Fig. 7 Average pink salmon weight in Sakhalin-Kuril region (top panel) and northern coast of the Okhotsk Sea (bottom panel).

Table 1 Average Okhotsk Sea pink salmon catches and fish weight in the 1970-1980s and in the 1990s.

	Region		Average weight kg		Average catches ,000 t		Average total catches ,000 t	
			1978-1989	1990-2000	1978-1988	1990-2000	1978-1988	1990-2000
Even years	Northern coast of the Sea of Okhotsk	Gizhiga	1,12	1,13	1,72	5,58	43,1	123,3
		Tauy	1,12	1,13				
		Kukhtuy	1,27	1,18				
	Sakhalin Island	Aniva Bay	1,17	1,25	21,03	48,52		
		S-E Sakhalin	1,08	1,27				
		Terpeniya Bay*	1,02	1,14				
	South Kuril Islands	Iturup	1,16	1,36				
Odd years	Northern coast of the Sea of Okhotsk	Gizhiga	1,09	1,3	4,64	6,29	61,9	103,5
		Tauy	1,3	1,41				
		Kukhtuy	1,3	1,42				
	Sakhalin	Aniva Bay	1,15	1,31	39,52	85,64		
		S-E Sakhalin	1,2	1,36				
		Terpeniya Bay*	1,2	1,32				
	South Kuril Islands	Iturup	1,18	1,51				

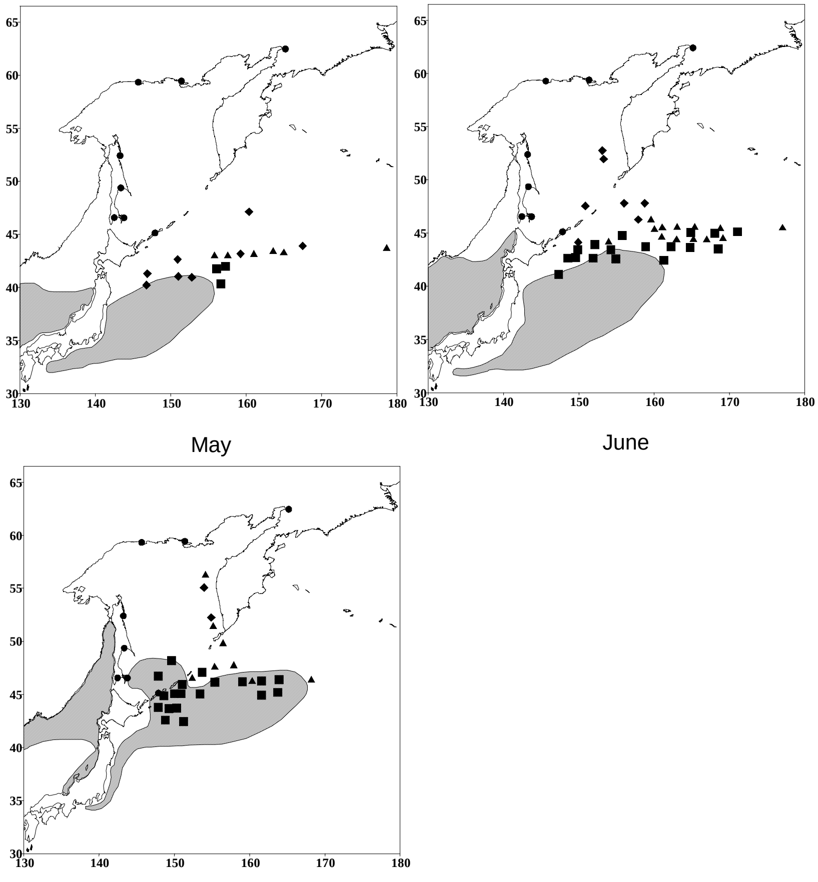
million tons in the Kuroshio Current region. In the 1990s, the abundance of these fishes decreased by 7-8 times, mainly at the expense of Japanese sardine (Belyaev 2000). During this period, total plankton consumption by pelagic fishes decreased by up to 20 times compared to the 1980s in Pacific waters of Kuril islands (Naydenko, in press).

The increase in number and size of pink salmon from the southern Okhotsk Sea population took place together with the drop in abundance of Pacific sardine after the 1990s. The low abundance and small size of pink salmon took place together with decrease in abundance of Japanese sardine after 1989. The low abundance and small size of pink salmon were observed for stocks both in the southern Okhotsk Sea, and in Japan/East Sea during high abundance of Japanese sardine (Temnykh 1998). It is unlikely that sardine are a direct competitor with pink salmon. It appears that a high abundance of the predator results in enhanced pressure on planktonic organisms. A decrease in zooplankton abundance in the western North Pacific during the 1970 - 1980s (Odate 1994) could be due to both climate and oceanological changes, and predation of abundant nektonic species.

It is interesting to note that the average weight of pink salmon was larger in the northern Okhotsk Sea during the 1980s compared to the southern Okhotsk Sea stocks, in spite of the fact that the marine life period of northern stock fishes is 30-45 days shorter than southern Okhotsk Sea stocks. In winter, pink salmon from different Okhotsk Sea stocks dwell within the same region of the northwestern Pacific but these stocks are partly separated in time and space during migrations (Fig. 8). The range of the northern Okhotsk Sea pink salmon is less connected with feeding areas of subtropical migrants in the Subarctic Front Zone, especially at the beginning and at the end of marine period of pink salmon life.

During the last decade, there is some evidence that density-dependent factors caused the decrease in average weight of highly abundant pink salmon generations within the Okhotsk Sea. In the 1990s, a permanently high weight difference was observed between even- and odd-year generations of pink salmon from rivers of the northern Okhotsk Sea coast, Sakhalin and Iturup (Fig. 7, Table 1). In the Sakhalin-Kuril region, even-year pink salmon were 100-200 g lighter than odd-year. The average weight of eastern pink salmon is lower at low stock abundance in even years, compared to fish size observed in odd years when Sakhalin population number was twice higher. Pink salmon sizes depend on the total abundance in the Okhotsk Sea, but not abundance of each stock.

We have suggested a hypothesis explaining the dynamics of fish size and stock abundance of pink salmon. To develop our knowledge in this field, it is of primary importance to look more carefully into the basic parameters of carrying capacity for pink salmon during marine period of the life cycle.



May

June

July

Fig. 8 Seasonal distribution of the Okhotsk Sea pink salmon and Japanese sardine in the northwestern Pacific. (■) pink salmon from Sakhalin-Kuril stocks, (▲) pink salmon from the northern Okhotsk Sea, (✡) pink salmon from western Kamchatka stocks (tagging data from Ogura 1994). The shaded area indicates Japanese sardine distribution during the period of high abundance in the 1970-1980s.

References

Beamish, R.J., and Bouillon, D.R. 1993. Pacific salmon production trends in relation to climate. Can. J. Fish. Aquat. Sci. 50: 1002-1016.

Bigler, B.S., Welch, D.W., and Helle, J.H. 1996. A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). Can. J. Fish. Aquat. Sci. 53: 455-465.

Ishida, Y., Ito, S., Kaeriyama, M., McKinnell, S., and Nagasawa, K. 1993. Recent changes in age and size of chum salmon (*Oncorhynchus keta*) in the North Pacific Ocean and possible causes. Can. J. Fish. Aquat. Sci. 50: 290-295.

Klyashtorin, L.B., and Sidorenkov, N.S. 1996. The long-term climatic changes and pelagic fish stock fluctuations in the Pacific. Izv. TINRO. 119: 33-54 (in Russian).

Nagasawa, K. 1998. Long-term changes in climate, zooplankton biomass in the western North Pacific, and abundance and size of the East Sakhalin pink salmon. NPAFC Technical Report, Vancouver, Canada, pp. 35-36.

Ogura, M. 1994. Migratory behavior of Pacific salmon (*Oncorhynchus* spp.) in the open sea. Bull. Nat. Res. Inst. Far Seas Fish. 31: 1-138.

Radchenko, V.I., and Rassadnikov, O.A. 1997. Long-term dynamics trends of Asian stocks of Pacific salmon and factors determing it. Izv. TINRO 122: 72-94 (in Russian).

Shuntov, V.P., Radchenko, V.I., Dulepova, E.P., and Temnykh, O.S. 1997. Biological resources of the Far Eastern Russian economic zone: structure of pelagic and bottom communities, up-to-data status, tendencies of long-term dynamics. Izv. TINRO 122: 3-15 (in Russian).

Temnykh O.S. 1998. Primorye pink salmon growth at high and low abundance. NPAFC Technical Report, Vancouver, Canada, pp. 20-22.

Welch, D.W., and Morris, J.F.T. 1994. Evidence for density-dependent marine growth in British Columbia pink salmon populations. NPAFC Doc. 97. 33 p.

The characteristic growth rate of herring in Peter the Great Bay (Japan/East Sea)

Ludmila A. Chernoivanova, Alexander N. Vdovin and D.V. Antonenko
Pacific Research Fisheries Center (TINRO-center), 4, Shevchenko Alley, Vladivostok, Russia, 690950. E-mail: tinro@tinro.ru

Pacific herring are subarctic species forming several local populations within its extensive natural habitat. The Peter the Great Bay herring form one of most southerly groups, and are typically characterized by a high growth rate. There is no uniform opinion about the hierarchical status of this group, but it has the highest biopotential among other herring groups of the Japan/East Sea (Posadova 1988, Gavrilov 1998, Rybnikova 1999).

The life cycle of Peter the Great Bay herring occurs within the Bay and in adjacent waters in the northwestern part of the Japan/East Sea. Considering its restricted distribution and spawning grounds, the potential level of biomass of this population does not exceed 150 thousand tons. From 1910 till now, three peaks of high abundance have been observed: in the mid 1920s, the mid 1950s, and the late 1970s/early 1980s. Each rise was associated with one or several dominant generations (Posadova 1988). In the 1990s, the abundance and productivity of Peter the Great Bay herring have come near to the historical minimum, and its biomass during these years varied from 5 - 10 thousand tons.

It is necessary to determine how the size-age characteristics and population structure changed in connection with the present depressed condition of Peter the Great Bay herring stocks. The biostatistical data from annual monitoring of the Peter the Great Bay herring stocks from 1971 to 2001 were analyzed. The data were collected from control catches by gill nets, seines and traps exposed directly on the spawning grounds. The data were processed using standard ichthyological techniques. The scales from a middle part of fish body under a dorsal fin were used for age interpretation. The following formula (Alimov 1989) was used for growth rate:

$$C_l = \frac{\lg(l_1) - \lg(l_0)}{0.4343(t_1 - t_0)} \times 100\%$$

where C_l is the average speed of linear growth, l_0 is length at the initial time, t_0, and l_1 is length at a later time, t_1.

The Peter the Great Bay herring are the fastest growing of all herring populations in the western Pacific (Posadova 1985). Growth is most rapid during the first and second years of life. At age

0+, herring in Peter the Great Bay have an average body length of 110 mm and weight of 9.9 g at the end of October. The average length and weight of age 1+ fish are 220 mm and 100.1 g, respectively at the end of October. After the second year of life the growth rate quickly decreases and, after the fifth year, does not exceed 10 % of the increase in the first year.

The relative daily linear growths of herring for the first year of life vary from 0.74 to 0.76% and appear to be constant during the periods of variable abundance (Table 2). The highest growth rate of herring during ontogenesis is 1.5% per day during the first six months of life (from May to October). The decreasing growth rate after the first year of life was associated with the process of sexual maturation.

Table 2 The relative daily linear growth (annual average, %) of Peter the Great Bay herring.

Period of observation	Age (years)							
	1	2	3	4	5	6	7	8
1999-2001	0.74	0.10	0.02	0.03	0.01	0.006	0.006	0.006
1971-1990	0.76	0.14	0.05	0.02	0.01	0.010	0.006	0.006

Table 3 Age structure (%) of herring catches in different parts of Peter the Great Bay in 1998-2001.

Period of observation	Age (years)										
	1	2	3	4	5	6	7	8	9	10	M
Amurskiy Bay											
1998			62.0	36.0		2.0					3.9
1999		6.4	68.3	19.1	3.5	2.2	0.5				3.8
2000		4.6	35.9	45.4	13.7	0.4					4.2
2001		8.3	20.5	27.1	35.8	7.1	0.7	0.5			4.2
Pos'et Bay											
1998			26.2	5.5	4.0	23.6	28.8	10.0	1.6	0.3	6.1
1999		1.8	14.1	14.3	27.6	29.0	11.1	2.1			5.6
2000		5.3	13.6	18.1	21.4	23.2	14.8	3.1	0.5		5.6
2001	0.7	13.8	24.8	6.9	37.2	8.3	1.4	3.4	1.4	2.1	4.9

A separate population of Pacific herring comprises 83% of genetic variability (Rybnikova 1999) which causes significant variability of the whole complex of its biological features.

The high interannual variability in mean body length among generations in Peter the Great Bay was connected with the annual cohort strength. In the period of high abundance during the 1970s and 1980s, high yield generations (*e.g.* 1974 and 1980) were distinguished by low growth rates (Gavrilov and Posadova 1982). That tendency was not shown during the last 15 years in Peter the Great Bay. First of all, the alternation of weak and strong cohorts was disrupted (during that period there were no strong cohorts). Secondly, all generations of herring consisted of a spawning part of the population on a background of a low reproduction level have been characterized by the low rate of growth from 1995 till now. The average body length of fish at age two and three years does not reach long-term value (Fig. 9).

Lower recruitment of Peter the Great Bay herring during the last decade has been accompanied by a reduction of the maximal age of spawners and variable age structure among sites. In the northwestern part of Peter the Great Bay (Amurskiy Bay) fish at age of 2-4 years comprised more than 80% of herring catches, whereas at the southwestern part (Pos'et Bay) the herring were from 2 to 10 years of age from 1998-2000 (Table 3).

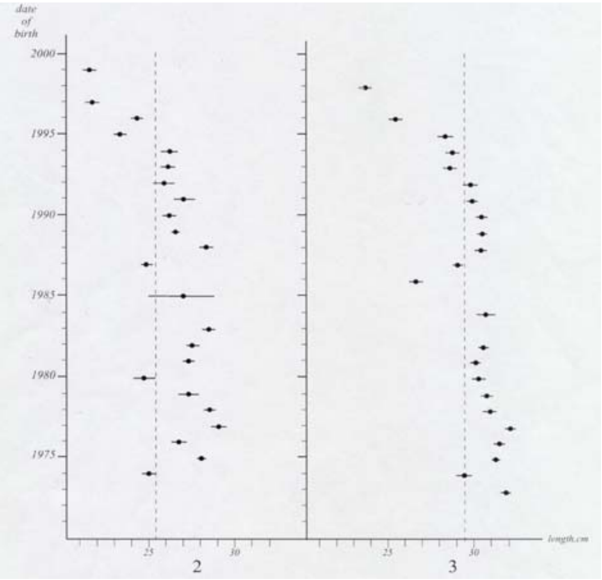


Fig. 9 Average length of Peter the Great Bay herring: generations at age 2 (left panel) and age 3 (right panel) years in 1974-1997. Dotted lines show long term average values (age 2: 25.2 cm, age 3: 29.5).

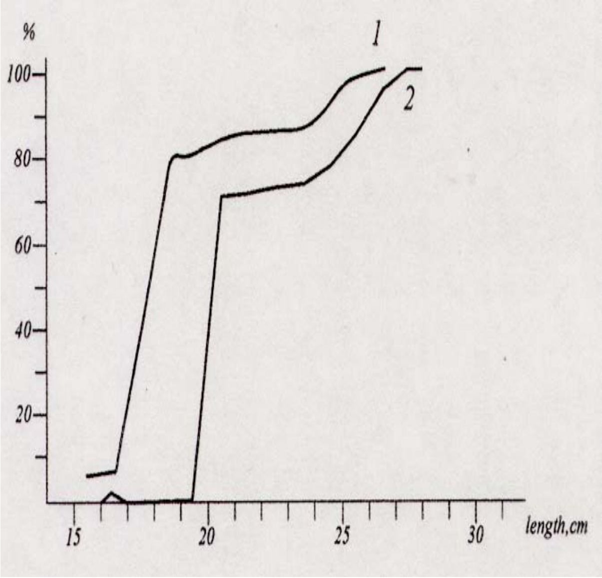


Fig. 10 The rate of maturation of herring in Peter the Great Bay in 1999-2001 (1) and 1978-1990 (2).

Evidently, the distortion of a complex age structure was consequence of the deterioration of reproduction conditions of Peter the Great Bay herring. It is quite probable that the decrease of growth rate in recent years is defined not only by any negative factors but also high rates of maturity. As was stated above, the sharp decrease of growth rate was caused by the maturation process. From 1999-2001, some herring (mainly males) began to mature at 14-17 cm body length, and 80% were mature by 18-19 cm. While in 1978-1990, the bulk of the population matured at 20-21 cm body length (Fig. 10). Accumulation of slow growing and early-maturing individuals in the spawning part of Peter the Great Bay herring population during low abundance contributes to increased reproductive potential and, probably, is one of mechanisms promoting the restoration of abundance.

References

Alimov, A.F. 1989. Introduction to the productional hydrobiology. Hydrometeoizdat, Leningrad, 152 pp.

Gavrilov, G. M. 1998. Seasonal and interannual variability of herring distribution in waters off the northern Prymorye. Izvestia TINRO-Centre 124: 758-764.

Gavrilov, G.M., and Posadova, V.P. 1982. Dynamics of Pacific herring *Clupea pallasi pallasi* Valenciennes (Clupeidae) abundance in Peter the Great Bay. J. Ichthyology 22(5): 760-772.

Posadova, V.P. 1985. Interannual variability in the spawning of herring in Peter the Great Bay. *In* Herring of the North Pacific Ocean. TINRO, Vladivostok, pp. 22-29.

Posadova, V.P. 1988. Stock assessment of herring in Peter the Great Bay. *In* Variability of ichthyofauna composition, yield year classes and forecasting techniques of fishes in the western Pacific. TINRO, Vladivostok, pp. 64-69.

Rybnikova, I.G. 1999. Population structure of Pacific herring *Clupea pallasi* (Valenciennes) in the Japan and Okhotsk seas. Abstract of the Ph.D thesis (marine biology). Vladivostok, 23 pp.

Temporal variations in size-at-age of the western Bering Sea herring

Nikolay I. Naumenko
Kamchatka Research Institute of Fisheries and Oceanography (KamchatNIRO), 18 Naberezhnaya Street., Petropavlovsk-Kamchatsky, 683600, Russia. E-mail: nnaumenko@kamniro.kamchatka.ru

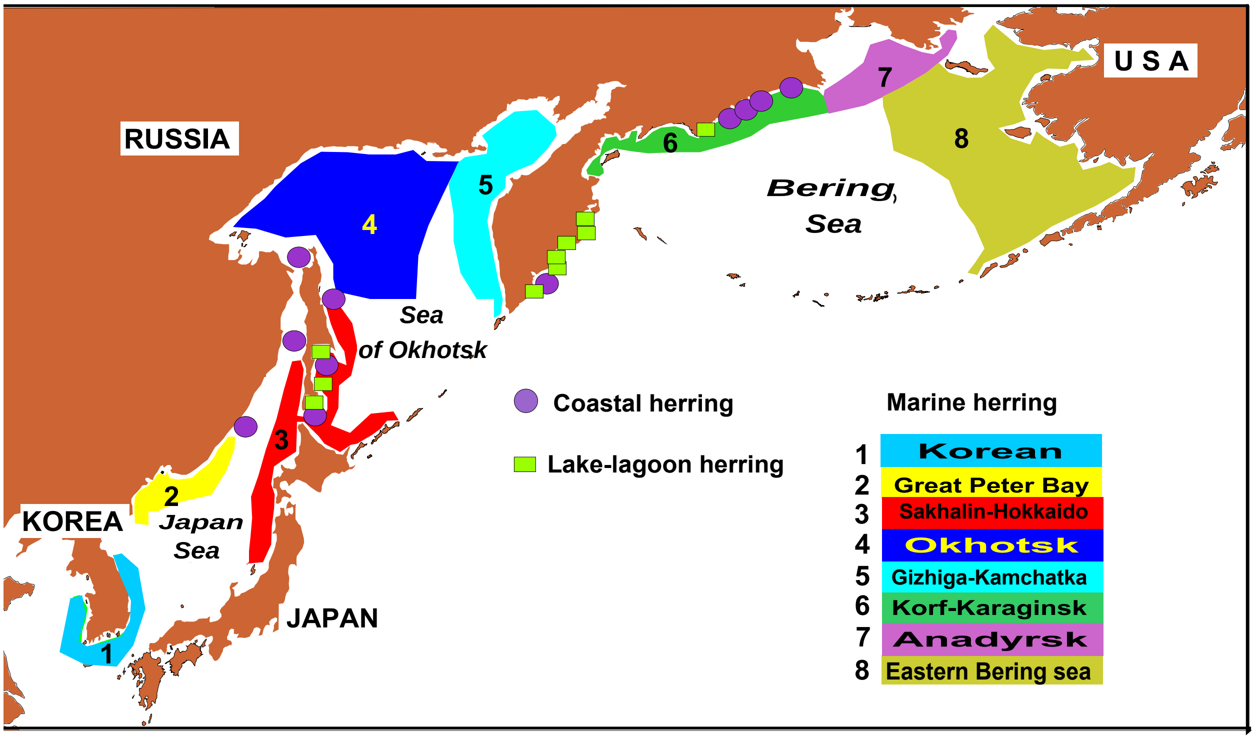


Fig. 11 Distribution of herring populations in the Far Eastern Seas.

Pacific herring inhabiting the Russian Far East Seas are represented by three ecological morphs: marine, offshore (coastal) and lagoon-lacustrine. Marine herring spend their whole life in higher salinity ocean waters where they undergo long migrations. The feeding area of this morph includes both shelf and bathypelagial waters. Off-shore herring inhabit only the shelf seas, particularly inlets and bays. This morph usually does not migrate long distances. Lagoon-lacustrine herring spend significant parts of their lives in brackish waters and migrate to feed in adjacent marine waters.

Russian waters in the northwest part of the Pacific Ocean are inhabited by 6 marine populations and by 22 off-shore and lagoon-lacustrine populations (Fig. 11). This ecological diversity provides maximum exploitation of forage resources for the species within the area and determines the extensive variability of size and growth parameters for this species.

Current information is based on many years of the author's personal observations of the growth in several herring populations inhabiting the Bering Sea and Pacific Ocean waters adjacent to Kamchatka: Korf-Karaginsky Bay, Eastern Bering Sea, Anadyr Bay, Yuzhnaya Lagoon, Nepichye Lake, Kalygyr Lake and Viluy Lake. The data on the growth of herring in the Sea of Japan and in the Sea of Okhotsk have been taken from literature. Forage base conditions are analyzed from annual standard surveys, each of them consisting of 7 stations sampled within Olyutorsky Bay in June.

The data on the size-at-age of herring taken from 19 areas within the northern part of the Pacific Ocean clearly indicate a significant difference in the growth of fish (Tables 4 and 5). Off-shore and lagoon-lacustrine herring have been classified as moderate or slow growing (Fig. 12). Marine herring are the most divergent in the growth. For example, there are extremely fast-growing (Sakhalin-Hokkaido herring inhabiting the waters adjacent to Hokkaido Island and Peter the Great Bay herring), fast-growing (Sakhalin-Hokkaido herring inhabiting the waters adjacent to Sakhalin Island, Korf-Karaginsky Bay herring, Bristol Bay herring) and moderate-growing (Okhotsk Sea herring, Gijiga-Kamchatkan herring, Anadyr Bay herring, Nunivak Island herring and Norton Bay herring) herrings. In general, the marine morph has a higher growth rate (Fig. 13).

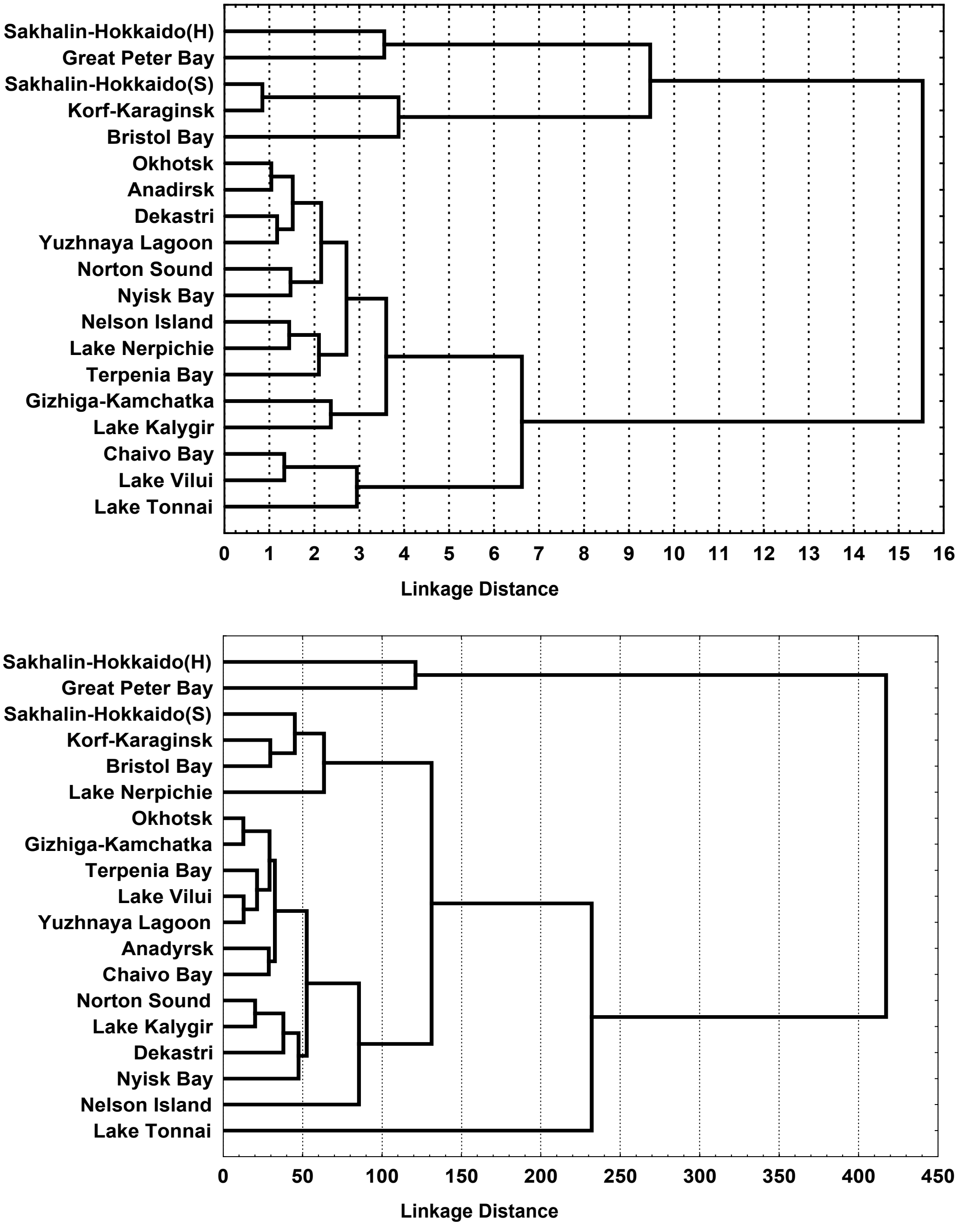


Fig. 12 Cluster analysis of length-at-age (upper panel) and weight-at-age (lower panel) of different Far East herring populations.

Table 4 Fork length-at-age (cm) of herring in different Far Eastern Seas.

Pupulation	Sea	Area	Age 1	2	3	4	5	6	7	8	9	10	11	12	13	Source
Marine herring																
Sakhalin-Hokkaido	Japan Sea	Hokkaido Island	15,0	22,0	26,0	29,0	30,5	32,0	33,0	34,0	34,5	35,0	35,3	35,6		1
Sakhalin-Hokkaido	Japan Sea	Sakhalin Island	12,3	19,4	23,8	26,1	28,3	29,7	31,0	32,0	32,5	33,0	33,3	34,0	34,5	2,3,4,5,6
The Great Piter Bay	Japan Sea	Western part	14,2	22,8	27,8	30,4	32,1	33,2	34,4	35,3	35,4	35,8	35,9	36,9	37,3	7,8,9
Okhotsk	Sea of Okhotsk	North West	7,9	15,0	20,4	23,4	25,5	27,1	28,2	29,1	29,9	30,4	31,1	31,3	31,4	6,10,11,12,13,14,15,16
Gizhiga-Kamchatka	Sea of Okhotsk	North East	7,5	13,5	19,2	22,6	24,8	26,6	27,8	27,9	29,7	29,8	30,1	30,4	31,3	6,17,18
Korf-Karaginsky	Bering Sea	Western part	12,2	19,6	24,1	26,8	28,5	30,0	31,1	32,1	32,9	33,5	34,4	35,1	35,5	19,20,21,22
Anadyrsky	Bering Sea	Gulg of Anadyr	8,2	15,6	20,7	23,3	25,0	26,6	27,9	28,9	29,7	30,8	31,4	31,8	32,2	19
Eeastern Bering Sea	Bering Sea	Norton Sound	9,8	17,2	20,5	23,0	24,7	26,4	27,9	28,8	29,6					19,23
Eeastern Bering Sea	Bering Sea	Nelson Island	9,1	16,2	20,9	23,6	25,9	27,5	28,7							19,23
Eeastern Bering Sea	Bering Sea	Bristol Bay	10,3	19,0	22,3	24,8	27,1	29,0	30,1	31,0	31,9	32,5	32,8			19,23
Coastal herring																
Dekastri	Japan Sea	Northern part	8,3	15,2	19,6	23,2	25,1	26,6	27,5	28,5	30,0	31,3	31,8	32,5		6,24,25,26
Nyisk Bay	Sea of Okhotsk	Sakhalin Island	8,9	15,7	20,2	22,5	24,5	26,6	27,9							7,27,28
Chaivo Bay	Sea of Okhotsk	Sakhalin Island	8,7	15,4	20,0	22,8	24,0	25,1	28,0							7,27
Terpenia Bay	Sea of Okhotsk	Sakhalin Island	9,0	15,6	20,6	22,5	24,4	25,3	27,1							27
Lake-lagoon herring																
Lake Vilui	N-W Pacific	Kamchatka	8,8	15	18,5	20,4	22,9	24	25,2	25,9	26,6	27	27,8	27,9	28,1	19
Lake Kalygir	N-W Pacific	Kamchatka	8,4	14,7	19,5	22,4	24,4	25,4	26,5	27,3	28,1	27,8	28,4	29,1	29,3	19
Lake Nerpichie	N-W Pacific	Kamchatka	9,1	15,4	21,4	24,5	26,3	27,3	28,2	29	29,9	30,5	31,1	31,5	32	19
Lake Tonnai	Sea of Okhotsk	Sakhalin Island	8,6	14,2	17,6	20,2	21,5	22,3	23,5							29
Yuzhnaya Lagoon	Bering Sea	North West	8,5	14,7	19,4	22,4	24,3	25,3	26,5	27,1	28,1	28,8	29,4	30,1	30,6	19,30

Sources: 1. Motoda, Hirano, 1963; 2. Kaganovsky, 1954; 3. Druzhinin, 1957; 4. Pushnikova, 1981; 5. Pushnikova, 1994; 6. Materials of Soviet-Japan Fisheries Commission, 1969-1976; 7. Ambroz, 1931; 8. Gavrilov, Posadova, 1982; 9. Posadova, 1985; 10. Kolesnik, Khmarov, 1970; 11. Labetsky, 1975; 12. Tyurnin, Yolkin, 1975; 13. Tyurnin, Yolkin, 1977; 14. Vyshegorodtsev, 1976; 15. Vyshegorodtsev, 1978; 16. Smirnov, 1994; 17. Piskunov, 1954; 18. Pravotorova, 1965; 19. Our data; 20. Kachina, 1967; 21. Kachina, 1969; 22. Kachina, 1981; 23. Wespestad, 1991; 24. Ambroz, 1930; 25. Kozlov, 1968; 26. Kozlov, Frolov, 1973; 27. Ivankova, Kozlov, 1968; 28. Gritsenko, Shilin, 1979; 29. Probatov, Frolov, 1951; 30. Prokhorov, 1965.

Table 5 Weight-at-age (g) of different populations of herring from Far Eastern Seas.

Pupulation	Sea	Area	Age 1	2	3	4	5	6	7	8	9	10	11	12	13	14
Marine herring																
Sakhalin-Hokkaido	Japan Sea	Sakhalin Island	24	72	140	191	242	279	317	360	375	398	416			
The Great Piter Bay	Japan Sea	Western part	28	135	250	308	371	399	432	465	484	525	547			
Okhotsk	Sea of Okhotsk	North West	8	30	84	119	155	186	213	237	266	285	303	315	364	
Gizhiga-Kamchatka	Sea of Okhotsk	North East	8	29	80	119	151	177	206	234	256	285	295	305	323	337
Korf-Karaginsk	Bering Sea	Western part	12	49	109	178	245	299	341	366	404	424	452	472	510	564
Anadyrsk	Bering Sea	Gulf of Anadyr	7	32	67	104	139	175	223	243	272	312				
Eeastern Bering Sea	Bering Sea	Norton Sound	8	46	79	134	166	210	234	281	313	348	357	373	391	405
Eeastern Bering Sea	Bering Sea	Nelson Island	9	38	84	129	187	227	280	306	337	376	410	429		
Eeastern Bering Sea	Bering Sea	Bristol Bay	12	62	118	174	229	283	331	376	414	445	470	492	508	523
Coastal herring																
Dekastri	Japan Sea	Northern part	8	44	102	125	153	194	215	242	274	304	305	323		
Nyisk Bay	Sea of Okhotsk	Sakhalin Island	8	42	70	100	182	198	224							
Chaivo Bay	Sea of Okhotsk	Sakhalin Island	7	39	83	121	141	160	221							
Terpenia Bay	Sea of Okhotsk	Sakhalin Island	8	40	90	117	148	164	201							
Lake-lagoon herring																
Lake Vilui	N-W Pacific	Kamchatka	8	42	80	107	145	162	184	201	218	228	248	252	255	257
Lake Kalygir	N-W Pacific	Kamchatka	8	39	90	140	179	205	232	258	274	287	295	320	328	359
Lake Nerpichie	N-W Pacific	Kamchatka	8	50	116	180	220	251	287	311	341	354	377	397	406	423
Lake Tonnai	Sea of Okhotsk	Sakhalin Island	7	30	57	85	102	114	132							
Yuzhnaya Lagoon	Bering Sea	North West	7	34	76	115	146	164	188	201	223	240	255	273	286	

Comment: sources as table 1

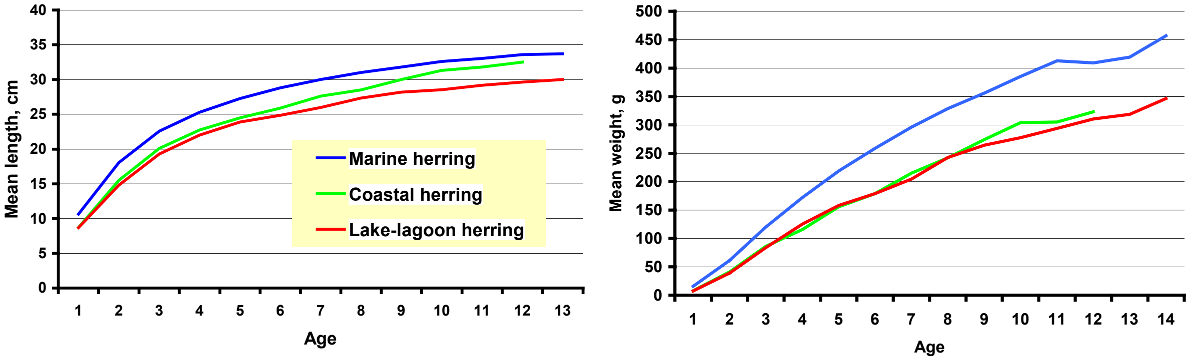


Fig. 13 Length-at-age (left) and weight-at-age (right) of different morphs of Far East herring.

The morphs differ in growth rate. By the character of the length growth the populations studied can be clearly divided into 3 types (Fig. 14A):

I. fast annual growth in the first year of life and rapid decrease of the growth in later years;
II. relatively fast annual growth in two initial years;
III slow growth in the first year of life and comparatively fast annual growth in later years.

Hokkaido Island herring have been classified to be of the first type. Most marine, all off-shore and some lagoon-lacustrine herring populations have been classified to be of second type. Most lacustrine and some marine herring populations are classified to be of the third type.

By the character of the mass growth, Far East herring populations have been divided into three types as well (Fig. 14B):

I. almost similar rich annual mass growth in second and third years of life (Sakhalin-Hokkaido herring inhabiting the waters adjacent to Hokkaido Island and Peter the Great Bay herring);
II. maximum annual mass growth in the third year of life cycle (majority of herring populations in the Sea of Japan and Okhotsk Sea);
III. maximum annual mass growth in the fourth year of life (all marine herring populations of Bering Sea).

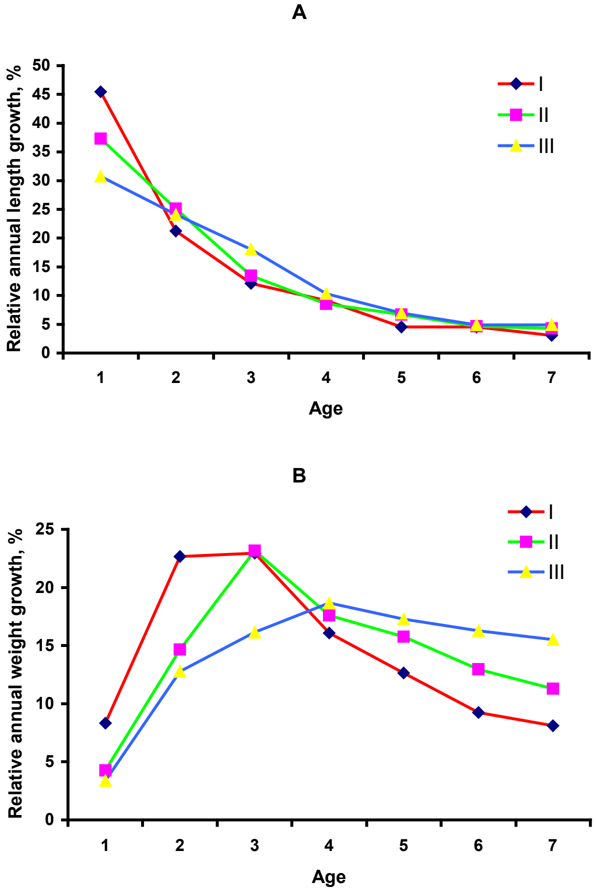


Fig. 14 Relative annual growth in length (A) and weight (B) in Far East herring morphs. See text for descriptions of each morph (I, II and III).

The most obvious trait of this species is significant year-to-year variations in size-at-age. For example, the range in the mean length of Korf-

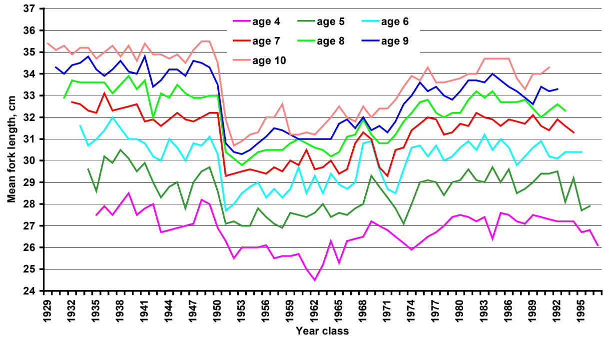


Fig. 15 Mean length-at-age of Korf-Karaginsky herring.

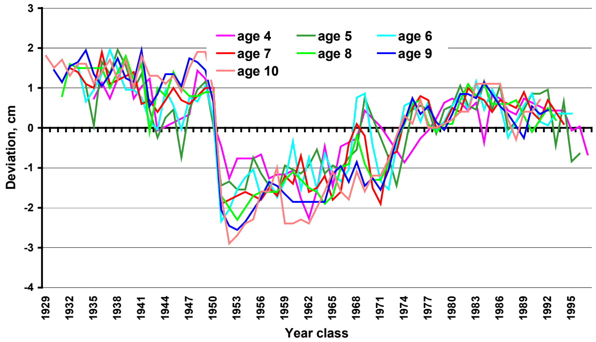


Fig. 16 Deviations from mean length-at-age.

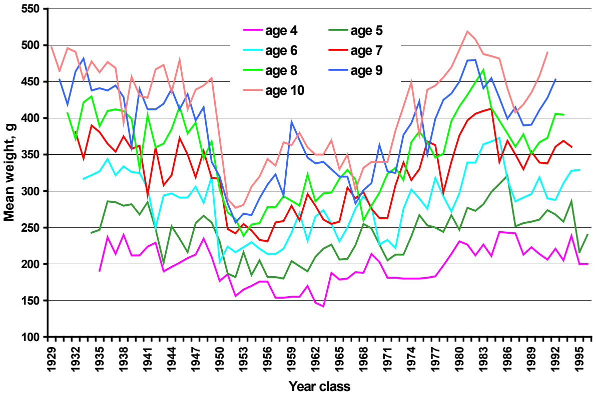


Fig. 17 Mean weight-at-age of Korf-Karaginsky herring.

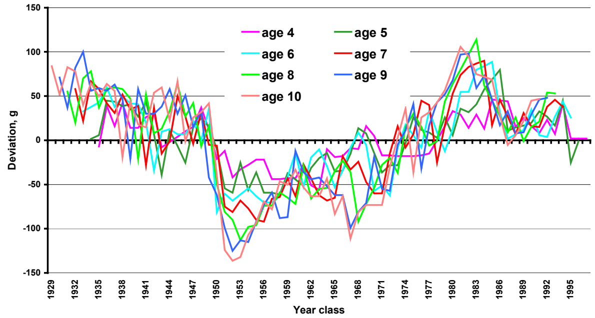


Fig. 18 Deviations in mean weight-at-age.

Karaginsky four-year-old fish is 4 cm (24.5-28.5 cm), of 10-years-old fish - 5.1 cm (30.4-35.5 cm), of 13-years-old fish - 5.9 cm (31.6-37.5 cm). The range in the mean mass of fish varies from 102 g in 4 year old fish to 227-255 g in 8-13 year old fish.

The variation in the biological patterns of Korf-Karaginsky herring demonstrates clear long-term cyclic dynamics (Figs. 15, 16, 17 and 18). The size (length and mass) of mature fish in generations for the 1930-40s was a maximum in all age groups for the whole observation period; the patterns were at a minimum for the 1950-70s and again relatively high for the 1980s. In the 1990s the size-at-age has been decreasing gradually, but being above the mean for many years, as early in the time series (Fig. 19).

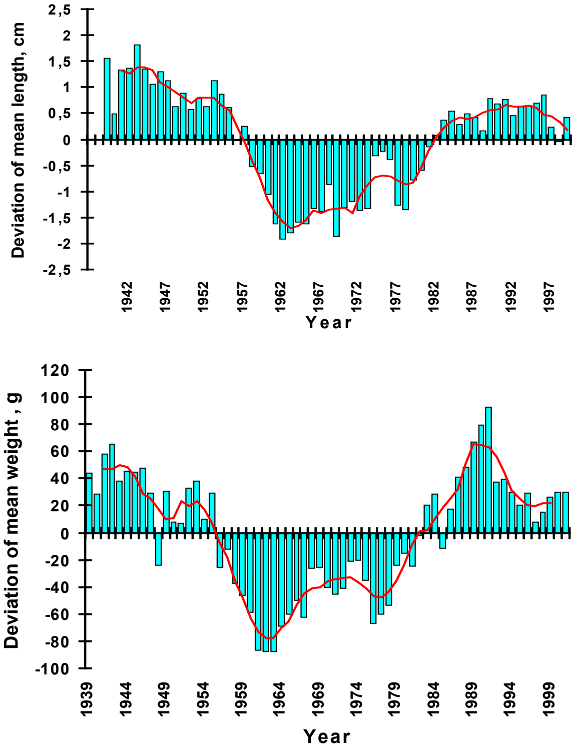


Fig. 19 Deviations of mean length (upper panel) and weight (lower panel) of age 4-10 Korf-Karaginsky herring from multi-year value.

For greater insight into the temporal pattern of the cycles of size variations in herring we used transformed data. We estimated deviations of the annual length and mass growth of 4-10-years-old fish from the mean for many years (Figs. 20 and 21). There are three periods which could be seen clearly in the curve of the dynamics of the mean for 5-year periods of annual growth of mature herring.

The first period, bounded by generations of 1930 and 1951, was generally characterized by accelerated growth; the second period (1950-1970s) was characterized by slower growth, and 1970-1990s characterized by higher growth rates. Within the three twenty-year periods of high or low growth, there are two cycles of about 10 years. Thus, the growth of Korf-Karaginsky herring has cyclic dynamics, with the cycle consisting of 10 or 22-years approximately.

The growth of mature herring in the west part of Bering Sea has been regulated by several circumstances. The length of 5-10-year-old fish depends on the length of recruits *i.e.* maturating 4-year-old fishes (Fig. 22). The more definite length of recruits is, the greater is the length of mature fish in all older ages.

Beyond doubt the growth of herring has been influenced by stock abundance or density factor. Although a reliable correlation between abundance of a certain generation and annual growth has not been observed – very abundant generations demonstrate evidently slower growth as compared to that in other generations. The growth rate is very similar in generations of moderate and low abundance, also in general it is higher compared to that in abundant and highly abundant generations (Table 6). Actually, biological characteristics are influenced much more by population condition. The highest growth rates are observed in the 1940s and the early 1950s when the abundance of mature fish has been moderate (Table 7). After several abundant generations reproduced in 1951-1956 the abundance of mature fish increased quickly. To the late 1950s the abundance of mature fish reaches its' historical maximum. The size (length and mass) of 4-6 year-old fish for this period has been minimum for the whole period of observations. Slow growth has been observed in the fish of old age groups.

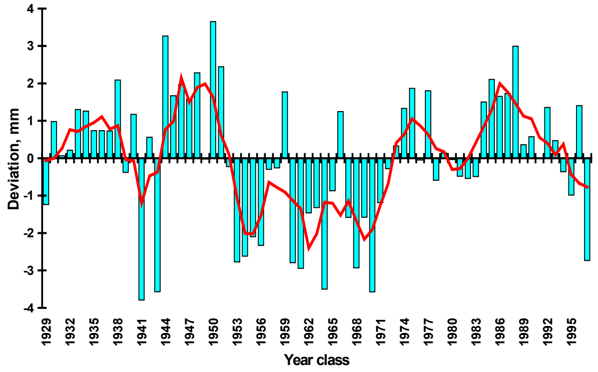


Fig. 20 Deviations of mean annual length growth of 4-10 age Korf-Karaginsky herring from multiyear value.

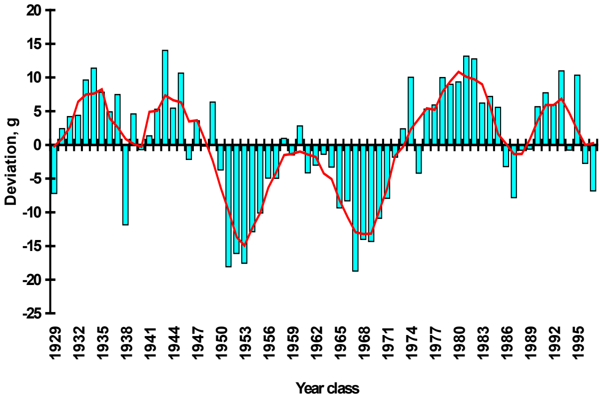


Fig. 21 Deviations of mean annual weight growth of 4-10 age Korf-Karaginsky herring from multiyear value.

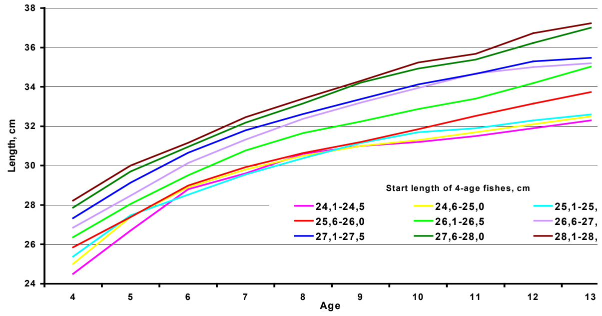


Fig. 22 Growth of Korf-Karaginsky herring in dependence on start length of 4-age fishes.

From the mid-1960s until mid-1970s the population underwent a depression. Despite the extremely low abundance of mature fish their growth stayed slow; also the individuals older than 6-years-old demonstrate the minimal growth for the whole historical period of the observations. In the late 1970s and in the 1980s the number of mature fish has increased a little, but remained

Table 6 Growth of Korf-Karaginsk herring in dependence from year-class strength.

Strength of year-class	Length/weight	Age									
		4	5	6	7	8	9	10	11	12	13
Very strong	Length, cm	26.3	27.4	28.6	29.9	30.8	31.2	31.5	31.8	32.0	32.4
	Weight, g	181	202	241	273	283	303	304	328	367	378
Strong	Length, cm	26.8	28.6	30.2	31.0	32.0	32.8	33.2	33.7	33.9	34.1
	Weight, g	192	239	273	313	355	379	401	412	414	416
Average	Length, cm	26.7	28.5	30.1	31.1	31.9	32.6	33.4	34.3	35.0	35.6
	Weight, g	198	245	284	324	348	385	414	444	475	506
Poor	Length, cm	27.0	28.8	30.2	31.6	32.6	33.4	34.2	35.1	36.0	36.2
	Weight, g	203	244	291	333	365	398	430	455	509	534

Table 7 Growth of Korf-Karaginsk herring in relation to stock abundance.

Level of stock-size	Length/weight	Age									
		4	5	6	7	8	9	10	11	12	13
High	Length, cm	25.8	27.3	28.6	30.3	31.3	32.3	33.4	33.9	34.2	-
	Weight, g	165	195	229	270	297	327	374	376	414	-
Average	Length, cm	27.3	29.1	30.7	32.0	33.0	34.0	34.6	35.3	36.1	36.4
	Weight, g	212	257	306	352	388	427	458	476	503	532
Low	Length, cm	26.9	28.8	30.2	31.3	32.1	32.7	33.1	33.7	34.4	34.9
	Weight, g	209	259	300	341	364	388	405	429	473	496
Depression	Length, cm	26.0	27.9	29.3	30.0	30.7	31.3	31.6	32.3	32.6	33.1
	Weight, g	180	220	261	277	300	335	345	352	358	365

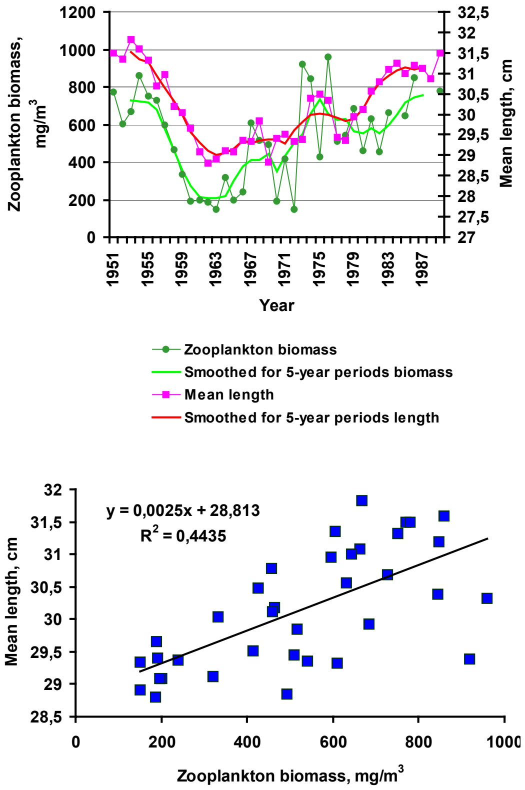


Fig. 23 Relationship between June zooplankton biomass in Olutorsk Bay and mean length of age 4-10 herring.

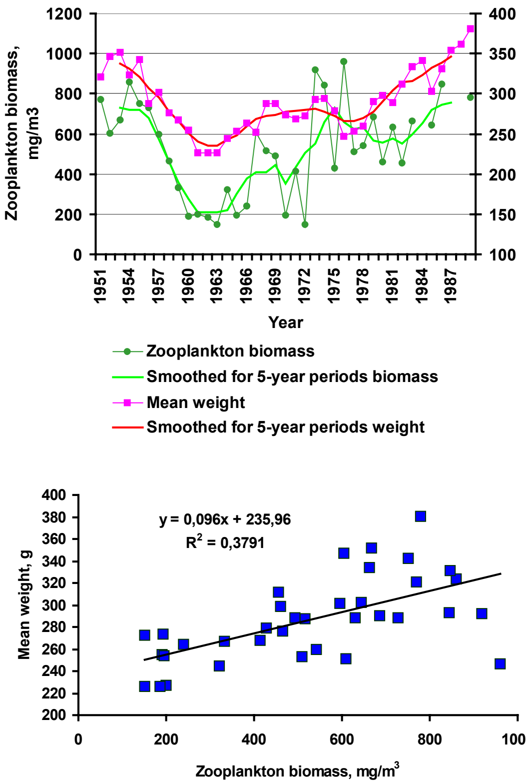


Fig. 24 Relationship between June zooplankton biomass in Olutorsk Bay and mean weight of age 4-10 herring.

low. In the 1990s the numbers have increased moderately. The size-at-age for 25 years (mid 1960s- late 1980s) has been increased gradually. To the early 1990s the size of herring has been similar to that for the 1940s. Thus, the most favorable conditions for growth of Korf-Karaginsky herring usually have been created at a moderate abundance of mature fish in the population. Under the extreme conditions (too high or too low stock abundance) individual growth has been slow.

The most important factor determining individual growth is food supply. In the 1950s - 1980s average zooplankton biomass in Olyutorsky Bay and average dimension (length and mass) of 4-10 years-old fish demonstrate synchronic variations (Fig. 23 and 24). In the periods when the biomass of zooplankton was increasing, the length and the mass of mature herring increased as well, and *vice versa*. A reliable direct correlation has been found between these patterns. The character of the correlation indicates that a zooplankton biomass increase of 100 mg/m^3 corresponds to a length increase of 2.5 mm and to the mass increase of 10 g in average in all age groups. Thus, the size-at-age variations of Korf-Karaginsky herring demonstrate cyclic dynamics. The stock abundance and forage base conditions influence the growth of fish considerably.

Effects of climate on Pacific herring, *Clupea pallasii*, in the northern Gulf of Alaska and Prince William Sound, Alaska

Evelyn D. Brown
University of Alaska Fairbanks, Institute of Marine Science, P.O. Box 757220, Fairbanks, AK 99775-7220, U.S.A. E-mail: ebrown@lms.uaf.edu

Introduction

Links between trends of North Pacific fish populations and climatic variations are well documented. One well-known example is the exceptional salmon production in the North Pacific that occurred during a period associated with an intensified Aleutian Low: high levels of salmon production are strongly correlated with the Pacific Decadal Oscillation (PDO) (Mantua *et al.* 1997), with Alaskan stocks responding positively to the positive phases of the PDO.

Pacific herring (*Clupea pallasii*) also appear to respond to climate. A negative correlation exists between southern British Columbia (BC) herring year-class strength and warm conditions; warm conditions appear to increase piscivory on herring and reduce zooplankton food resources (Ware 1992). The same negative correlation was later reported by Hollowed and Wooster (1995) with higher average recruitment for Vancouver Island herring during cool years associated with a weakened winter Aleutian Low (AL). However, the opposite effect occurred in northern BC and the Gulf of Alaska (GOA), with increased herring production during warm years associated with an intensified winter AL (Hollowed and Wooster 1995). Recruitment of Pacific herring in Southeast Alaska is positively associated with warm, wet climate conditions (Zebdi and Collie 1995). This indicates a north-south bifurcation in climate response by Pacific herring populations similar to that observed in Pacific salmon.

This study shows that the trend in abundance of northern GOA Pacific herring appears to be in phase with decadal-scale climate indices. Population parameters such as growth and spawn timing also appear to be related to climatic signals and may be in opposition to responses by Pacific herring from more southern locations.

Results

An index of GOA herring abundance was developed by combining historic fisheries catches with recent biomass estimate (Fig. 25). Herring abundances were compared to several climate indices and good, positive correlations were found for the Atmospheric Forcing Index (AFI) and Aleutian Low Pressure Index (ALPI) (Beamish and Bouillon 1993), the Pacific Inter-Decadal Oscillation (PIDO) (Enfield and Mestas-Nunez 1999) and the winter time Pacific Decadal Oscillation (PDO) (Mantua et al. 1997). The abundance of herring in Prince William Sound over the period 1973-present was well-correlated with these indices (Fig. 26), as was the composite herring time series (from 1900-present) (Fig. 27). The common result was high population levels during the positive phases of the three indices. The positive phases correspond in general to intensification of the Aleutian Low, higher sea surface temperatures, and increased storms and wind stress in the GOA. A strong Aleutian Low causes above-average water column stability in the sub-arctic Pacific, creating conditions that optimize primary and secondary production and thus may be the mechanism involved in the positive response of zooplankton and Pacific herring, as previously hypothesized for salmon.

Herring size-at-age trends exhibited oscillatory behavior with a maximum spectral density at a period of 13 years for all ages (Fig. 28). There was no evidence of density-dependence as plots of size and biomass levels were flat for each age examined. The spectral peak was strongest in ages 3-5. The raw and smoothed (using the Hamming filter) size-at-age data was significantly correlated to peak zooplankton density lagged one year ($p < 0.05$; $r \geq 0.50$; Fig. 28). Peak and average zooplankton biomass was significantly correlated to the winter PDO lagged 3 yrs (r = 0.52 and 0.65

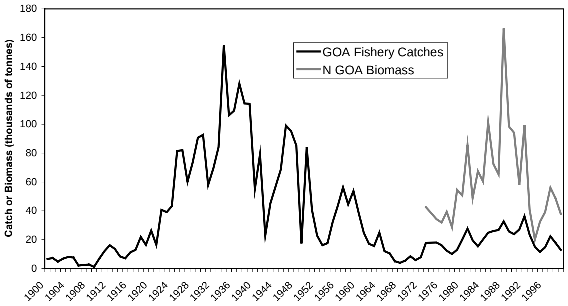


Fig. 25 The two types of fishery data used in this analysis. The solid black line is total annual Gulf of Alaska (GOA) fishery catches. The grey line represents the annual biomass estimates for Prince William Sound (see Brown and Funk for details).

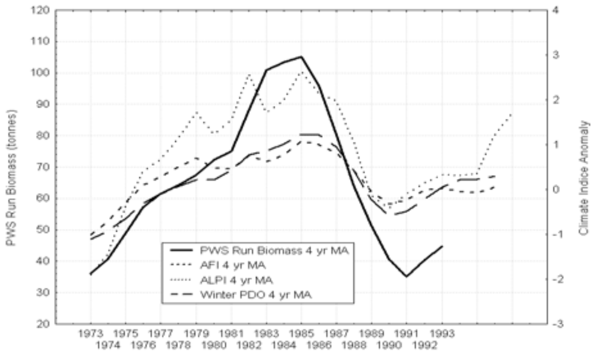


Fig. 26 A 4 year moving average (ma) transformation of the Prince William Sound (PWS) biomass index compared to the AFI, the ALPI and the winter PDO for the period of 1973 to 1993.

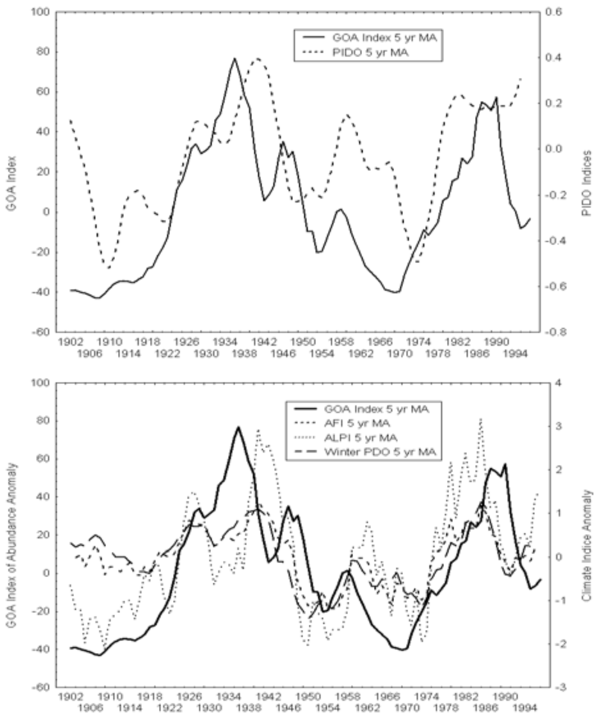


Fig. 27 A 5 year moving average (ma) transformation of the Gulf of Alaska (GOA) Index, created by combining catch and biomass, compared (upper panel) to a 5 year ma of the Pacific Inter-Decadal Oscillation and (lower panel), 5 year mas of the AFI, ALPI and winter PDO plotted for the period of 1902 to 1995.

respectively). Size-at-age for ages 7 and 8 were also significantly correlated to both the PDO lagged 3 years (r = 0.55) and the PIDO lagged 2 years (r = 0.61).

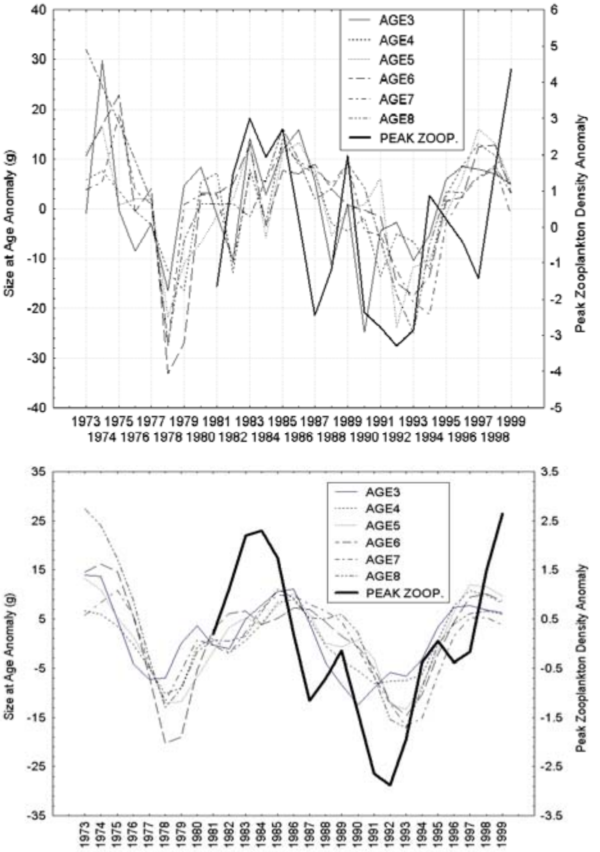


Fig. 28 Size-at-age by weight (g) of age 3-8 Pacific herring from PWS plotted with peak zooplankton density anomalies (from southwestern PWS) for the period of 1973 to 1999. The top figure are the raw values. The bottom figure shows a spectral transformation (type Hamming) of the size-at-age data plotted with a 4 year moving average transformation of the peak zooplankton anomalies.

There is an overall downward trend in spawn timing from 1973 to 1999 with mean spawn dates approximately 7 days earlier in the late 1990s than in the early 1970s (Fig. 29). Although not significantly correlated, there is a corresponding downward trend in PWS surface salinity during September and October, lagged 6 months from spawning, over the same period. There was no apparent relationship between spawn timing and either population size or climate trends. Spawn timing is affected by maturity rate that is in turn directly affected by ocean conditions, especially 6-9 months prior to spawning.

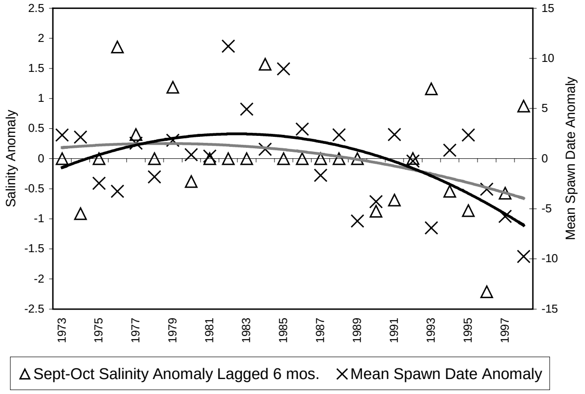


Fig. 29 Surface salinity (at 20 m) anomalies with a 6 month lag, for the combined months of September and October are plotted with the mean date of spawning anomaly for PWS for the period of 1973 to 1999. The solid lines represent 2nd order polynomial transformations of the mean spawn date (black) and salinity (grey). Note that black line is polynomial (2nd order) trend line for mean spawn date anomaly and the gray line is polynomial (2nd order) trend line for PWS Sept.-Oct. SSS anomaly

Spawning areas have also shifted over the same time period accompanied by a trend in reduced recruit per spawner rates. The implications of these observations are discussed more fully in Brown and Funk (unpublished manuscript).

References

Beamish, R.J., and Bouillon, D.R. 1993. Pacific salmon production trends in relation to climate. Can. J. Fish. Aquat. Sci. 50: 1002-1016.

Brown, E.D., and Funk, F. Effects of climate on Pacific herring, *Clupea pallasi*, in the northern Gulf of Alaska and Prince William Sound, Alaska. Unpublished manuscript available from the authors.

Enfield, D.B., and Mestas-Nuñez, A.M. 1999. Multiscale variabilities in global sea surface temperature and their relationships with tropospheric climate patterns. J. Climate 12: 2719-2733.

Hollowed, A.B., and Wooster, W.S. 1995. Decadal-scale variations in the eastern subarctic Pacific: II. Response of northeast Pacific fish stocks. Can. Spec. Publ. Fish. Aquat. Sci. 121: 373-385.

Mantua, N. J., Hare, S.R., Zhang, Y., Wallace, J.M., and Francis, R.C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. ,Bull. Am. Meteorol. Soc. 78: 1069-1079.

Ware, D. M. 1992. Climate, predators and prey: behaviour of a linked oscillating system. *In* Kawasaki T., Tanaka S., Yoahiaki T., and Taniguchi A. (eds). Long-term variability of pelagic fish populations and their environment. Pergamon Press, Sendai, Japan, pp. 279-291.

Zebdi, A., and Collie, J. S. 1995. Effect of climate on herring (*Clupea pallasi*) population dynamics in the northeast Pacific Ocean. Can. Spec. Publ. Fish. Aquat. Sci. 121: 277-290.

Herring size-at-age variation in the North Pacific

Jake Schweigert[1], Fritz Funk[2], Ken Oda and Tom Moore[3]

[1] Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, BC, Canada. V9R 5K6 E-mail: schweigertj@pac.dfo-mpo.gc.ca

[2] Alaska Department of Fish and Game, P.O. Box 25526, Juneau, AK 99802-5526, U.S.A. E-mail: fritz_funk@fishgame.state.ak.us

[3] California Department of Fish and Game, Belmont and Bodega Bay, California, U.S.A.

Introduction

Herring have been one of the more important components of the marine fisheries on the west coast of North America over the past century. Dramatic population fluctuations are common in all stocks of herring but virtually all populations from Alaska to California declined dramatically and synchronously in the late 1960s and all have subsequently recovered. Despite the impacts of a significant harvest in most of these stocks, large scale environmental forcing appears to have been a significant factor in the observed population fluctuations. However, it is unclear what mechanisms were involved in affecting survival over such a broad geographical scale. Long time series of stock abundance estimates are not available for most of these populations. Instead, we investigated the available data on fish size and growth, reviewing trends in weight-at-age, condition factor, and growth increments of Pacific herring from Alaska to California in relation to environmental conditions or food supply to assess whether these factors may have affected herring survival in the North Pacific.

Methods

Pacific herring weight-at-age data were collated for a number of stocks in the North Pacific (Fig. 30) ranging from the Bering Sea [Togiak] through the Gulf of Alaska (Kodiak], Prince William Sound [PWS]), SE Alaska [Sitka], British Columbia (Queen Charlotte Islands [QCI], Prince Rupert [PRD], Central Coast [CC], Strait of Georgia [GS], west coast of Vancouver Island [WCVI]), and California (San Francisco Bay [SFB], Tomales Bay [TB]). Unfortunately, the available data is sparse in many cases and generally available for only limited time periods restricting the type and extent of statistical analyses possible. The time period investigated for this study ranges from 1940-2000. For some populations both length and weight at age data are available and for those we examined changes in condition factor. For all populations trends in weight at age 4 were examined as well as trends in the annual growth increment at age over time.

The condition factor was also calculated annually for each age-class in each stock following Tesch (1988), as:

$$CF_t = \frac{Weight_{at}}{Length_{at}^{\ 3}}$$

Spratt (1987) has previously used similar methods to examine growth variation in San Francisco Bay herring following the strong 1982-83 El Niño.

The indices of environmental forcing that were examined included the Pacific decadal oscillation (PDO), atmospheric forcing index (AFI), the Aleutian low pressure index (ALPI), the Pacific circulation index (PCI) and the ENSO southern oscillation index (SOI). All but the last index are available from http://www.pac.dfo-mpo.gc.ca/sci/sa-mfpd/english/clm_indx1.htm. The SOI index was obtained from ftp://ftp.ncep.noaa.gov/pub/cpc/wd52dg/data/indices/soi. Information on plankton biomass is difficult to obtain since there have been few long-term efforts to collect these data. Recently, Hare and Mantua (2000) have consolidated a large number of data series for the period 1965-1997 and we have used their results in this study.

Fig. 30 Map of the study area illustrating the location of data sets for the analysis.

Results and discussion

Pacific herring generally exhibit a cline in size-at-age from south to north, with fish in the Bering Sea being far larger than fish from California. Herring also mature at later ages as one progresses from south to north. Therefore, comparison of size, condition, and growth increment becomes complicated as fish trade off growth for reproduction once they are mature. Consequently, we chose to examine trends in the average weight of fish at age 4 throughout the study area (Fig. 31). However, this is of limited utility as an index of growing conditions because it represents an integration by the fish of growing and feeding conditions over the preceding four years. Fish from the Bering Sea are much larger and demonstrate greater fluctuation in size at age 4 than herring from any of the other areas. Sitka and PWS indicate a long term decline in size since the 1940s. It should be noted that the pre-1970 data from all areas represent fall reduction fisheries whereas recent data are from spring roe fisheries and so may reflect some loss of weight by fish over the winter period. British Columbia stocks and those from Sitka show a marked increase in size at the time of the stock collapses in the early 1960s with a subsequent decline in the 1970s which may reflect a density-dependent response as the populations rebuilt. California stocks do not show evidence of any trends except for reductions in size during the 1982-83 and 1997-98 El Niño events.

The condition factor at age is presented in Figures 32 and 33. It represents an index of growing conditions for herring the previous year. However, it is possible that herring compensate for reduced food availability by growing more slowly in length while maintaining an average condition. Thus, it may not be a good indicator of growing conditions in the ocean except under extreme circumstances such as a severe El Niño which disrupted normal feeding patterns. British Columbia herring stocks do not show any marked trends in condition over time although the QCI, CC, and WCVI suggest a slight increase in condition from the 1950s through the 1990s.

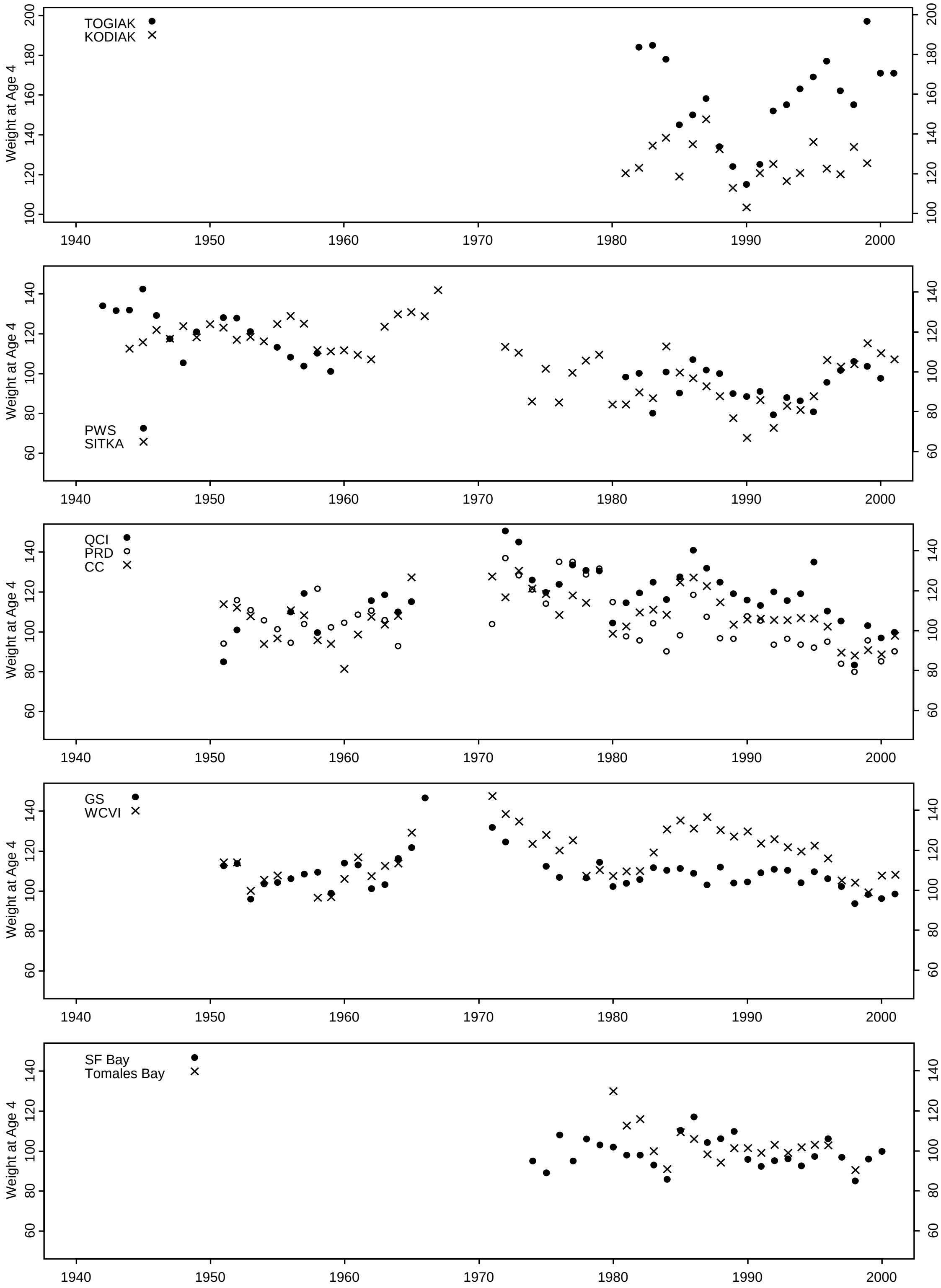


Fig. 31 Trends in weight-at-age 4 in Pacific herring from 1940-2000.

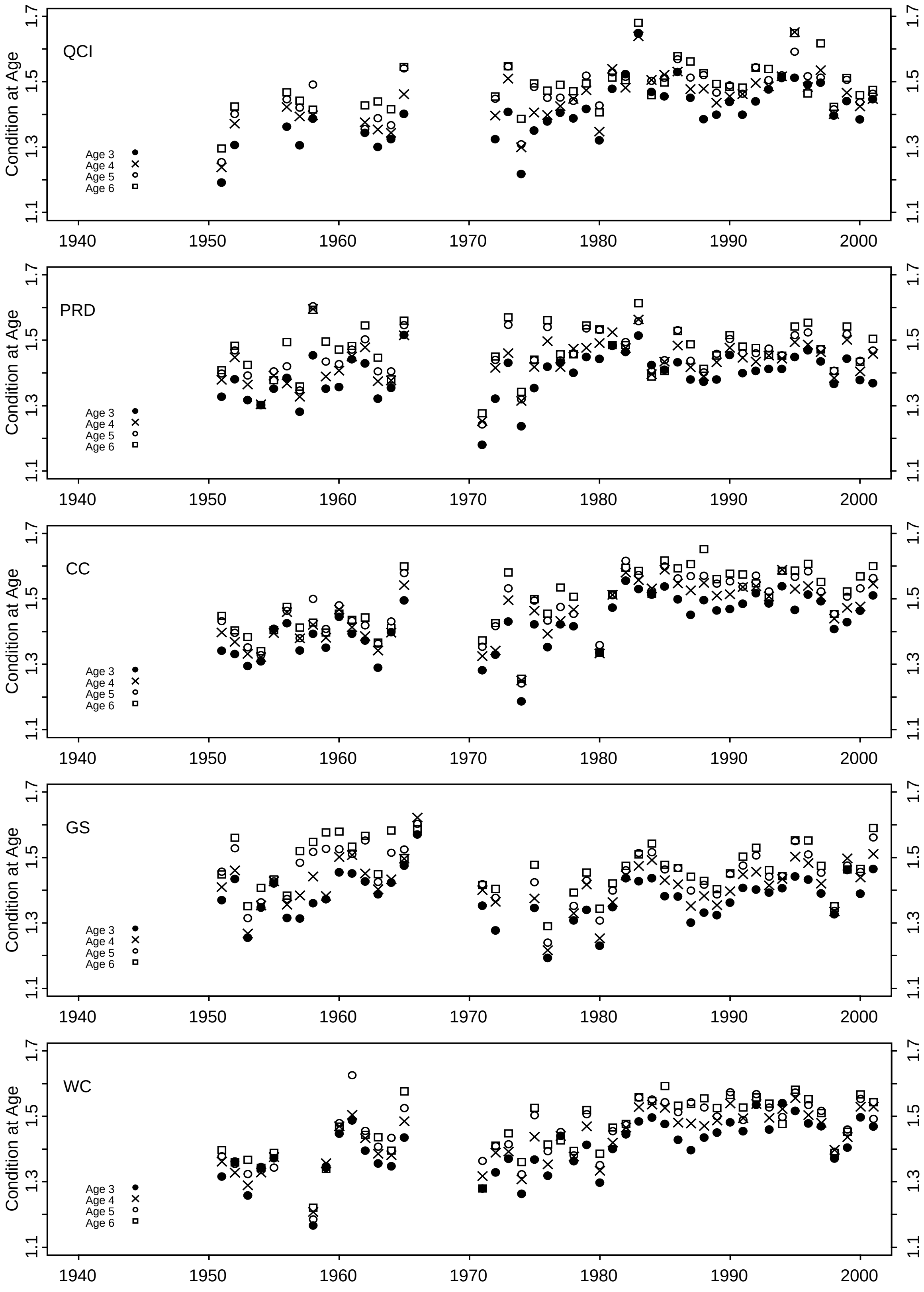


Fig. 32 Condition factor at age for British Columbia herring from 1940-2000.

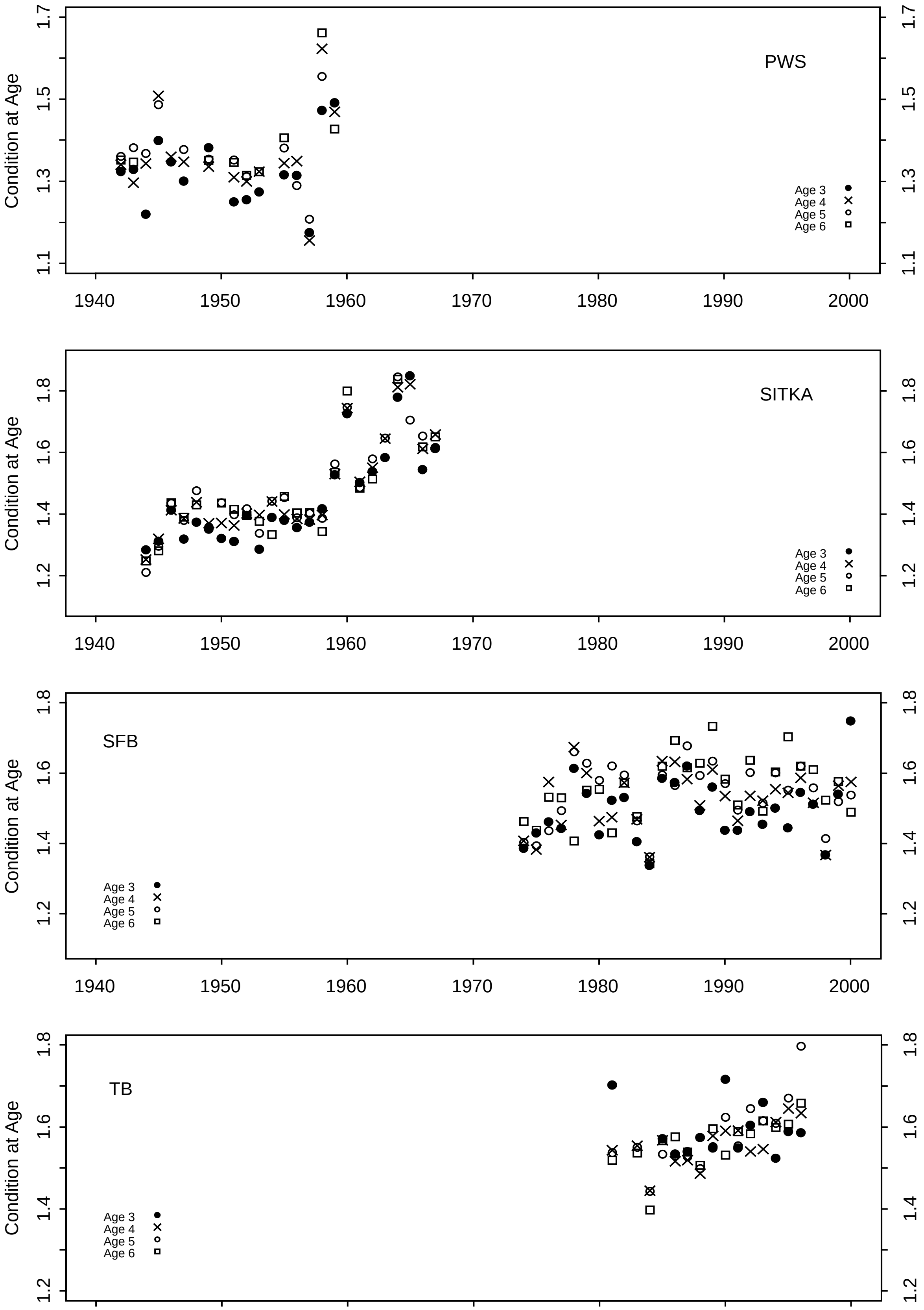


Fig. 33 Condition factor at age for Alaska and California herring from 1940-2000.

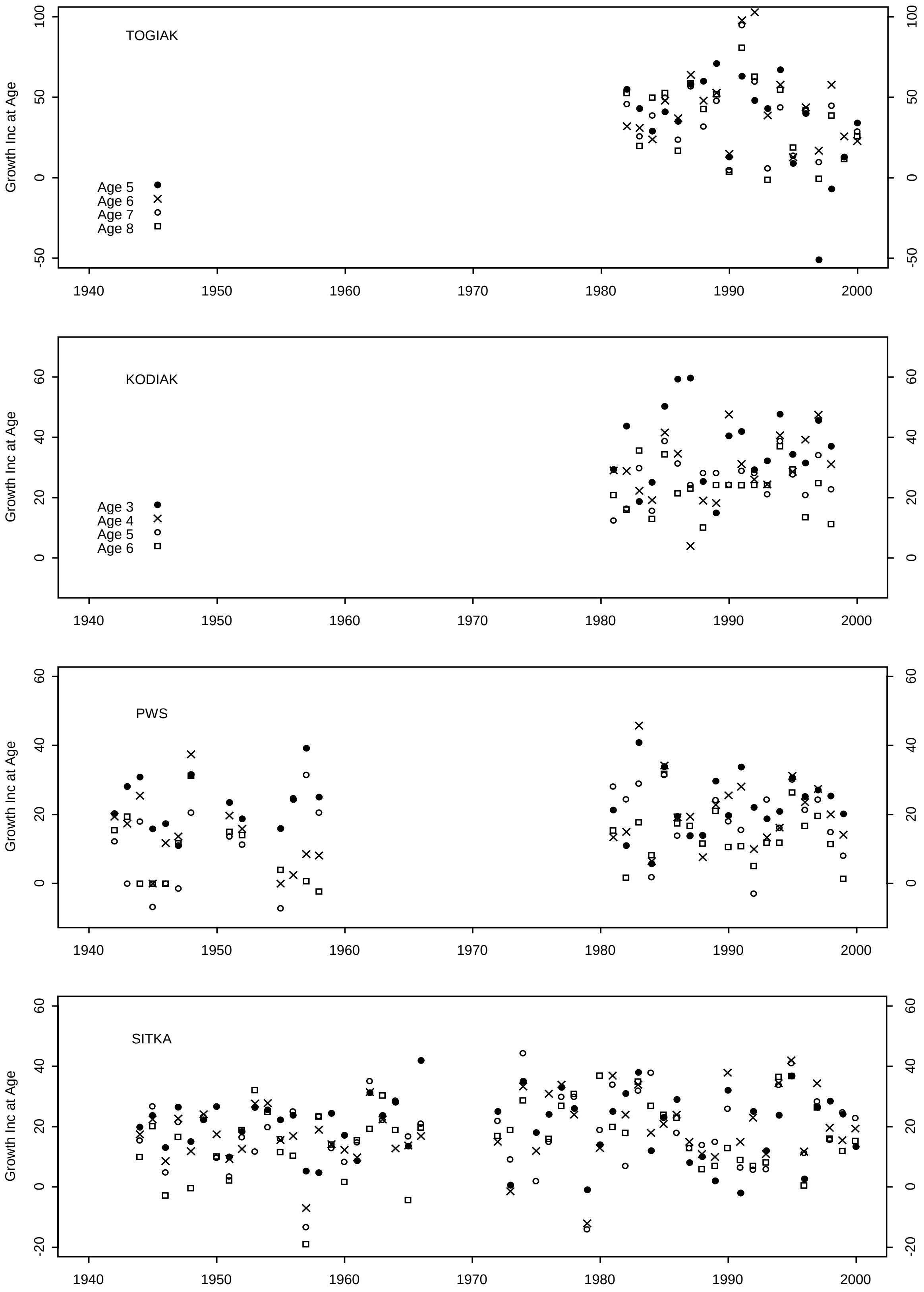


Fig. 34 Trends in the growth increment at age for Alaska herring stocks from 1940-2000.

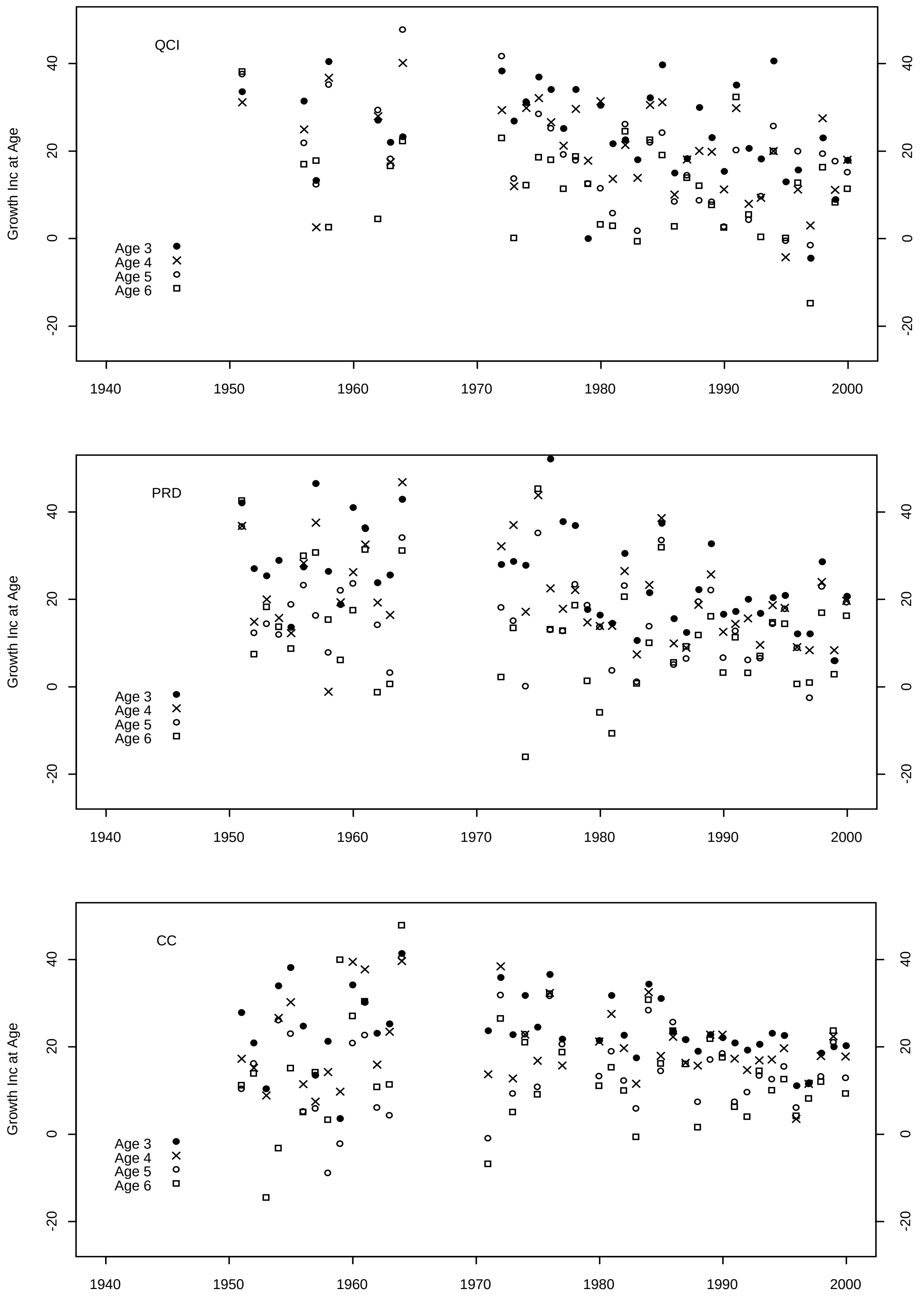


Fig. 35 Trends in growth increment at age for northern BC herring stocks from 1940-2000.

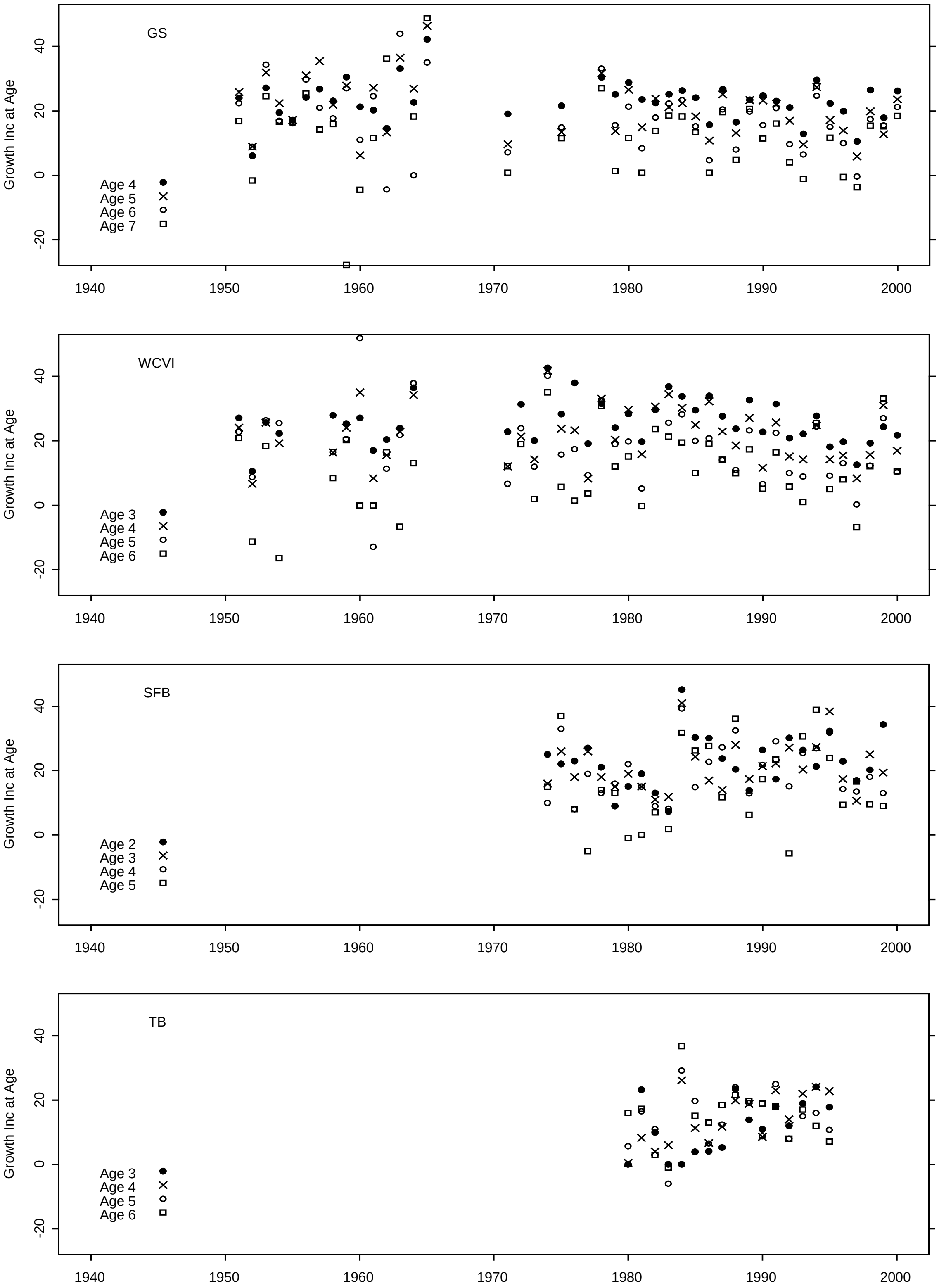


Fig. 36 Trends in the growth increment at age for southern BC and California herring stocks from 1940-2000.

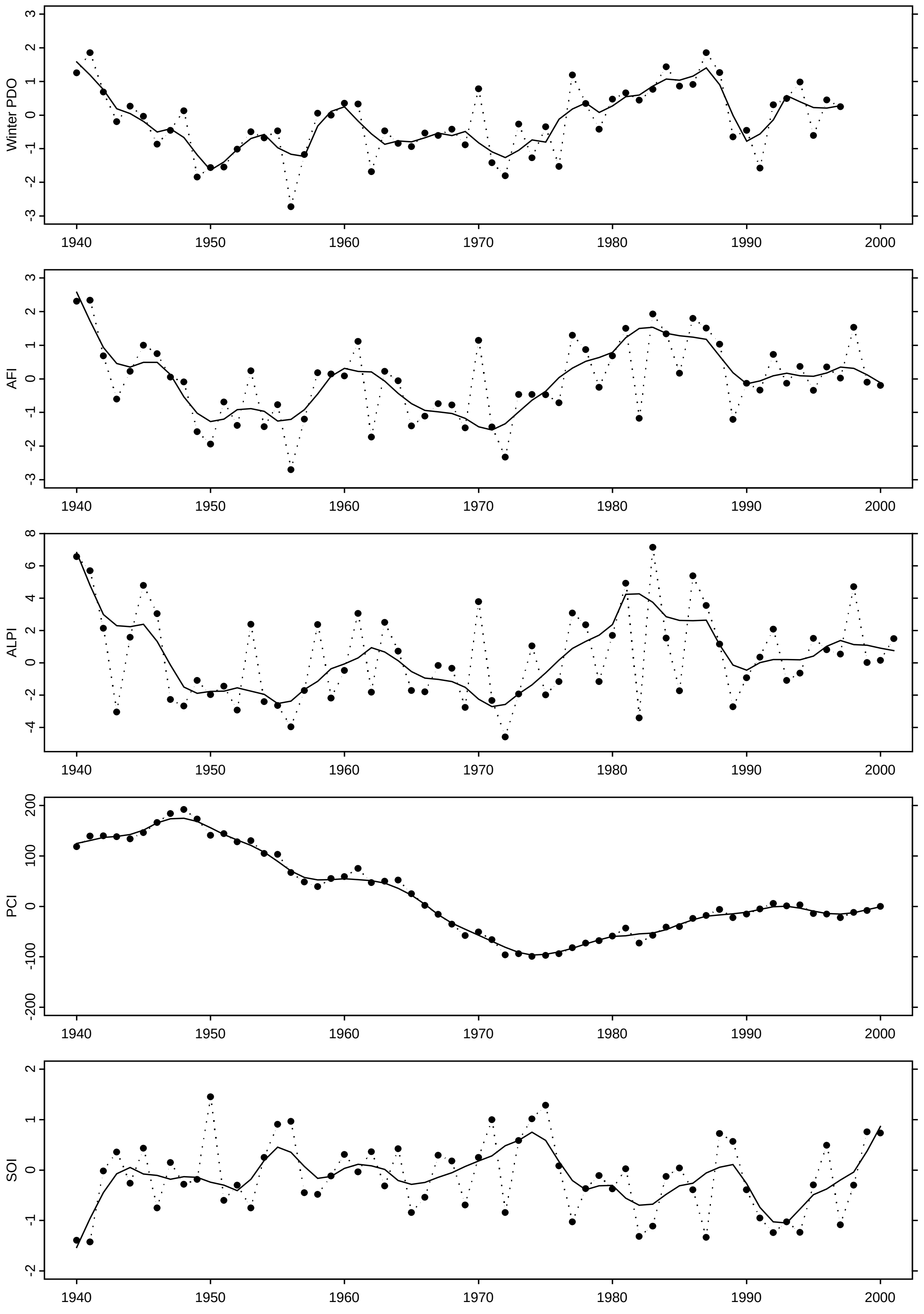


Fig. 37 Environmental indices for the North Pacific from 1940-2000.

All stocks also indicate a small decline in condition in the mid- to late 1980s and again in the late 1990s following the two strong ENSO events. Results for Alaska and California are quite variable with Sitka and PWS suggesting a marked increase in condition from the 1940s through the 1960s although this may be a function of changes in sampling locations. Both California stocks suggest a very slight increase in condition factor over time with sharp declines associated with the 1982-83 and 1997-98 ENSO events. Spratt (1987) has previously reported the strong negative effects of the 1982-83 El Niño on San Francisco Bay herring condition factor and growth.

The growth increments at age for Pacific herring stocks are presented in Figures 34-36 and are perhaps the best indicator of growing conditions in the previous year in each area. Togiak fish show the largest growth increment coastwide which includes a marked increase in the early 1990s followed by a recent decline. PWS and Sitka stocks do not demonstrate any long term trends in growth increment although there are declines in the mid-1980s and late 1990s which may correspond to El Niño effects. British Columbia stocks all show a decline in growth increment from the early 1970s through the late 1990s. They all show a marked decrease in 1997 and some in the mid-1980s. The California stocks do not indicate any clear trend in growth increment over time but both show the effects of the 1982-83 El Niño and SFB also the 1997-98 El Niño.

The environmental indices are presented in Figure 37 and demonstrate broadly similar patterns in winter PDO, AFI, and ALPI based on a lowess smoothed trend line. The PCI may be inversely related to these indices but at a different frequency since they are not quite in phase. The SOI index appears to be inversely related to the first three indices. A comparison of these indices with herring weight at age 4, condition factor, and growth increment does not indicate any strong correlation but there is the suggestion of a loose association between the trend in PDO and weight at age 4, condition, and perhaps growth increment since 1970.

Figure A9 from Hare and Mantua (2000) presents the available zooplankton data for the North Pacific and indicated a generally decreasing trend in zooplankton biomass since the 1977 regime shift (see Fig. A9 in their paper). This observation is consistent with the observed declining trend in herring growth increment in British Columbia but surprisingly not in California. It is also consistent with the trend of declining size at age 4 in British Columbia and parts of Alaska. Although not explicit in the plankton data, it is possible that changes in species composition during El Niño events are responsible for the marked decline in growth observed during these time periods so that overall plankton biomass remains relatively stable but the preferred prey items for herring decline markedly or are completely absent from the normal feeding areas.

Pacific herring populations in the eastern Pacific have experienced significant synchronous fluctuations in abundance that appear to be related to environmental forcing. We examined biological characteristics associated with changes in growth as a proxy for herring survival over the available data record. Results indicate a complex interaction between density dependent effects, food supply, and environmental variation. During the collapse of herring stocks throughout the Pacific in the late 1960s growth of herring increased dramatically, declining again as stock rebuilt. During the period from 1977 to present growth characteristics of many stocks in British Columbia and Alaska have shown a decline which is apparently a result of declining food availability. Plankton availability is most probably driven by changing environmental conditions that have at least recently not been favourable for herring growth in British Columbia and southern Alaska. Superimposed on these relationships are the recent strong ENSO episodes which have negatively impacted herring growth through the area of their effect. Overall, there appear to be threshold effects related to population density, ocean production and plankton availability, and sea surface temperature mediated by ENSO that affect the growth parameters of herring populations throughout the North Pacific. Future studies should be directed at defining the thresholds and their effects on long-term herring production.

References

Hare, S.R., and Mantua, N.J. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog. Oceanography 47: 103-145.

Spratt, J.D. 1987. Variation in the growth rate of Pacific herring from San Francisco Bay, California. Calif. Fish and Game 73: 132-138.

Tesch, F.W. 1988. Age and Growth. *In* W.E. Ricker [ed.] Methods of assessment of fish production in fresh waters'. IBP Handbook No. 3. Blackwell Scientific Publications, Oxford, pp. 93-123.

Implications of variation in euphausiid productivity for the growth, production and resilience of Pacific herring (*Clupea pallasi*) from the southwest coast of Vancouver Island

Ron W. Tanasichuk

Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, B.C. Canada. V9R 5K6. E-mail: tanasichukr@pac.dfo-mpo.gc.ca

This presentation includes the results of a number of studies which collectively suggest that the recent order of magnitude reduction in euphausiid production along the southwest coast of Vancouver Island depressed the productivity and resilience of the West Coast Vancouver Island (WCVI) herring (*Clupea pallasi*) population.

We have been studying the oceanography of the southwest coast of Vancouver Island since 1985 to learn how the ocean affects fish productivity there. Results of diet analyses show that euphausiids are the dominant prey of the more abundant pelagic fish species and that herring feed on them exclusively. We have also been monitoring the species and size composition of prey. Tanasichuk (1999) showed that Pacific hake (*Merluccius productus*), the dominant planktivore, selects larger (>17 mm) euphausiids of one species (*Thysanoessa spinifera*) regardless of how euphausiid biomass varies. WCVI herring select the same prey. Euphausiid population biology and productivity along the WCVI have been monitored since 1991 (Tanasichuk 1998). Figure 38 shows that herring and hake prey biomass has varied by an order of magnitude over the last 10 years. The same degree of prey variation has also occurred for coho salmon (*Oncorhynchus kisutch*).

The effect on herring productivity and resilience appears to operate through influencing growth. Tanasichuk (1997) examined the effect of variations in year-class strength and oceanographic conditions on the size of recruit herring and the growth rates of adult fish. At that time, data were available to 1996 only. He suggested that the 1993 year-class was an outlier because this year-class was the first to be subjected to low *T. spinifera* biomass over its first three years of life. All subsequent year-classes have been outliers, over a period when *T. spinifera* biomass remained depressed (Fig. 39). This dataset suggests that the compensatory population-

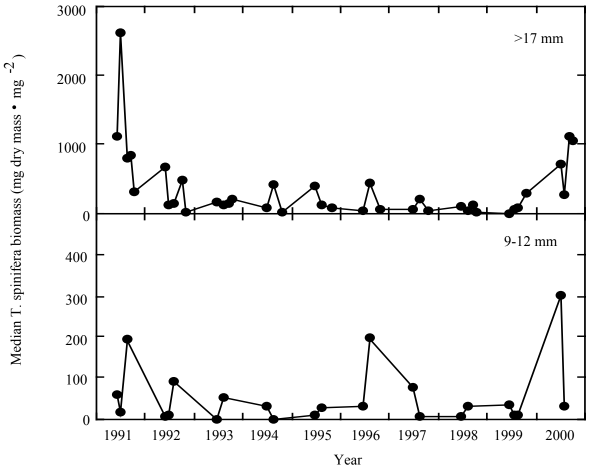


Fig. 38 Median biomass (mg dry mass/mg^2) of key prey for Pacific herring and Pacific hake (>17 mm *T. spinifera*) and coho salmon (9-12 mm *T. spinifera*) over the summer feeding period.

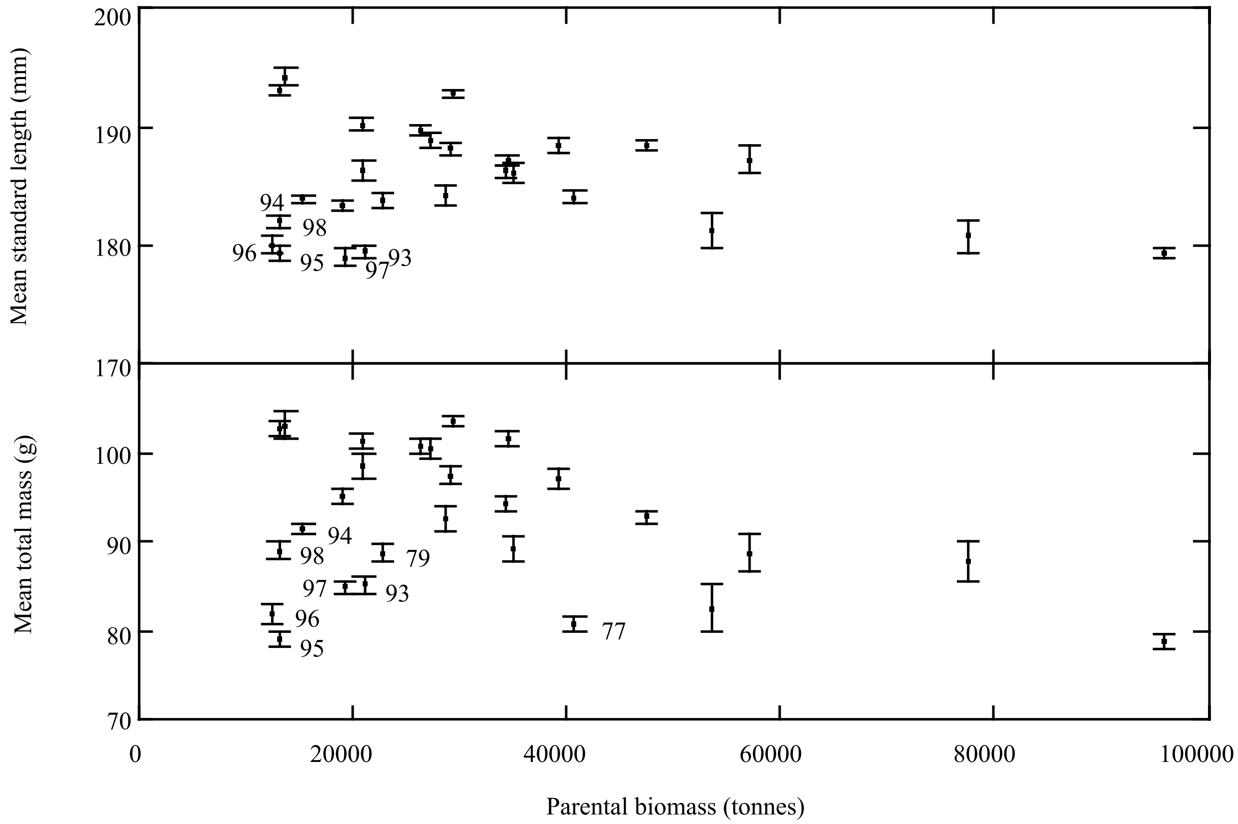


Fig. 39 Scatterplot of mean standard length- and total mass-at-age 3 for WCVI herring. Error bars are 95% confidence limits. Plot labels indicate year-class.

regulating mechanism of density-dependent recruit size has been disrupted by low euphausiid biomasses since 1993. Tanasichuk (1997) concluded that adult growth rates were influenced mainly by size at the beginning of the growth period. Because adult growth rates are affected mostly be initial size, the effect of low euphausiid biomass would persist over the entire life of the year-class. It appears that mortality and size-specific surplus energy allocation to ovarian production have not varied. Tanasichuk (2000) reported that age-specific natural mortality rates of adult herring vary as a function of age alone. Unpublished results showed that there has been no inter-annual variability in mass-specific ripe ovarian mass.

Growth suppression had a large effect on ovarian (=egg) production, and presumably resilience, that is the population's potential to increase or sustain biomass through recruitment. We calculated ovarian production for all ages for each year since 1982, when Fisheries and Oceans Canada started measuring ovarian mass. Annual estimates of observed mean mass-at-age were used to calculate ovarian production; this includes the observed mass-at-age over the time when growth appeared to be suppressed. "Non-suppressed" mass-at-age 3 was then estimated using the regression in Tanasichuk (1997) which describes recruit mass as a function of parental biomass. These estimates of recruit mass, and the regressions describing variations in adult growth rates in mass, were used to estimate what the mass of older fish of a year-class should have been in subsequent years. Figure 40 shows the effect of small recruit size on growth in subsequent years. Figure 41 demonstrates the effect on reduced growth on ovarian production. It would have been reduced by 20% as a consequence of growth suppression of recruit fish and its effect of subsequent adult size. However, after considering further that reduced egg production in 1996-98 could have reduced the number of spawners produced by these year-classes, the suppression of reproduction could have become compounded. Calculations showed that egg production would have consequently been reduced by 40%, presumably a 40% reduction in resilience, in other words a 40% reduction in potential recruitment.

These results have implications for evaluating growth in herring and the concept of the precautionary approach. Recruit size and subsequent adult growth are affected by year-class strength and food availability during the pre-recruit phase. We show an effect of food which complicates the interpretation of size-at-age trends. The precautionary approach (target- and limit reference points) implicitly assumes that fish population productivity and the ability to re-build are constant over time. These results show that assumption is invalid.

References

Tanasichuk, R. W. 1997. Influence of biomass and ocean climate on the growth of Pacific herring (*Clupea pallasi*) from the southwest coast of Vancouver Island. Can. J. Fish. Aquat. Sci. 54: 2782-2788.

Tanasichuk, R. W. 1998. Interannual variations in the population biology and productivity of the euphausiid *Thysanoessa spinifera* in Barkley Sound, Canada, with special reference to the 1992 and 1993 warm ocean years. Mar. Ecol. Prog. Ser. 173: 163-180.

Tanasichuk, R. W. 1999. Interannual variation in the availability of euphausiids as prey for Pacific hake (*Merluccius productus*) along the southwest coast of Vancouver Island. Fish. Oceanogr. 8: 150-156.

Tanasichuk, R. W. 2000. Age-specific natural mortality rates of adult Pacific herring (*Clupea pallasi*) from southern British Columbia. Can. J. Fish. Aquat. Sci. 57: 2258-2266.

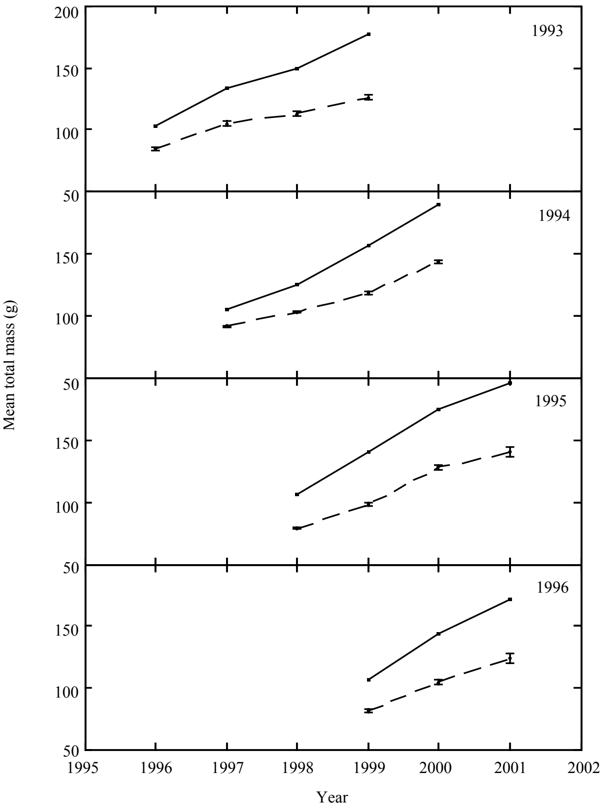


Fig. 40 Mass-at-age trajectories for WCVI herring. Dotted line – observed. Solid line - estimates from growth regressions in Tanasichuk (1997). Error bars are 95% confidence limits. Year-class is indicated in the upper right of each panel.

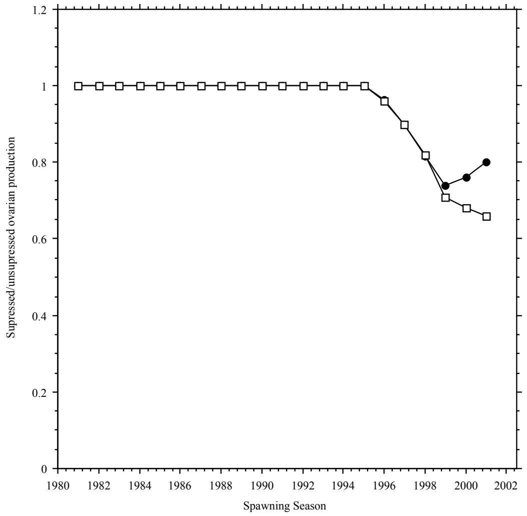


Fig. 41 Suppression of ovarian production due to growth (solid circle) and growth plus recruitment depression (open square).

Changes in growth with fluctuation of chub mackerel abundance in the Pacific waters off central Japan from 1970 to 1997

Chikako Watanabe[1], Akihiko Yatsu[1] and Yoshiro Watanabe[2]

[1] National Research Institute of Fisheries Science, 2-12-4 Fukuura, Kanazawa-ku, Yokohama, Japan 236-8648. E-mail: falconer@nrifs.affrc.go.jp; E-mail: yatsua@affrc.go.jp

[2] Ocean Research Institute, Tokyo University, 1-15-1Minamidai, Nakano-ku, Tokyo, Japan 164-8639. E-mail: ywatanab@ori.u-tokyo.ac.jp

Introduction

Changes in growth as stock size fluctuates have been found in many fish populations. Size-at-age of Japanese sardine (*Sardinops melanostictus*) has varied remarkably with the stock fluctuations from the late 1970s to the early 1990s (Wada 1989, Hiyama 1989, Wada *et al.* 1995); these have been considered to be density-dependent change in fish size.

Chub mackerel (*Scomber japonicus*) are one of the most important fish populations in Japanese waters. Two stocks are recognized, the Tsushima Current stock and the Pacific stock. The Tsushima Current stock is distributed in the East China Sea and the Sea of Japan, and the Pacific stock occurs along the Pacific coast of Japan. The biomass of the Pacific stock is larger and more variable than that of the Tsushima Current stock. Most of the catch of the Pacific stock is from the purse seine fishery in the waters off central and northern Japan. The Pacific stock spawns from March to June around the Izu islands off central Japan. Juveniles of about 6 months of age recruit to purse seine and set net fisheries from August or September in the coastal area off northeastern Japan.

The landings of the Pacific stock increased from the 1960s, to a maximum of 1.5 million tons in 1978, and then declined to 23 thousand tons in 1990 (Fig. 42). Recently, good year-classes occurred in 1992 and 1996 (Fig. 42), but most of these cohorts were exploited before first maturation, and therefore spawning stock did not recover and total biomass stayed low. With the drastic stock level fluctuations, size-at-age and maturity-at-age of the Pacific stock changed (Iizuka 1974, Chiba 1995). This study describes long-term changes in stock size and size-at-age of the Pacific chub mackerel stock and investigates the relationship between stock size and year-class abundance.

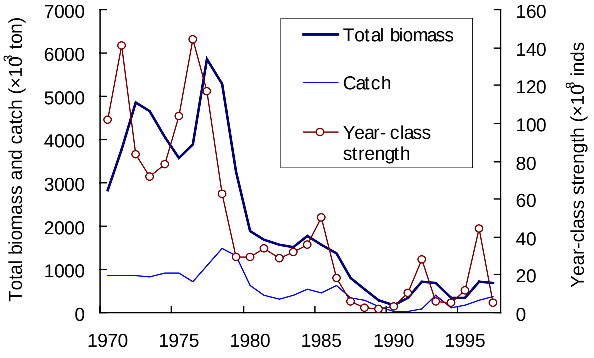


Fig. 42 Total biomass, catch and year-class strength of the Pacific stock of chub mackerel (*Scomber japonicus*). Total biomass and year-class strength were estimated by VPA.

Materials and methods

Data. Length composition and age-length keys for 1970-1997 were used to calculate mean length-at-age for each year. The length composition data of purse seine catches from September to December were used because total catches in these months were usually largest during the year. Scales were used for age determination. Length compositions of fish samples were applied to length compositions of total catches. Length compositions of total catches were divided into age groups from 0 (6 months old) to 5 years based on age-length keys. Mean fork length was calculated from length compositions of total catches for each age. Total biomass was represented by sum of VPA (virtual populations analysis) estimated biomass of chub mackerel from age 0 to age 6+. Year-class strength was represented by abundance in number at age 0.

Statistical analysis. ANOVA was used to determine if the mean length-at-ages 0 to 5 were significantly different among years. Regression analysis was applied to examine the relationships between mean length-at-age and total biomass and year-class strength.

Result and discussion

Mean length-at-age fluctuated greatly, especially at age 0 and 1, ranging from 164-259 mm at age 0 and 242-316 mm at age 1. While the biomass of chub mackerel decreased from the 1970s to the 1990s, mean lengths-at-age increased. Figure 43 shows the relationship between the total biomass and the mean length at age 0 among years. Regression analyses indicated significant negative relationships between the total biomass and the mean fork length-at-age of a year (Table 8, p<0.05). The biomass variations explained 19-36% of the inter-annual fluctuation of length-at-age.

Figure 44 demonstrates the relationship between the year-class strength and the mean length-at-age 0. Mean length-at-age of each year-class was negatively correlated with the year-class strength (Table 9, p<0.01). The variability in year-class strength explained 25-63% of the fluctuation of length-at-age.

The deviations of the mean fork length of a year-class from the mean of the 28-year time series (1970 to 1997) were calculated for several ages. Figure 45 shows the relationships between deviation at age 0 versus deviation at age 1 and the deviation at age 0 versus deviation at age 4. Regression analysis suggested significantly positive relationships between deviations at age 0 and ages 1 to 5, and between the deviations at age 1 and ages 2 to 5 (Table 10), indicating that the trend of length-at-age 0 is consistent through the life time (until 5 years old).

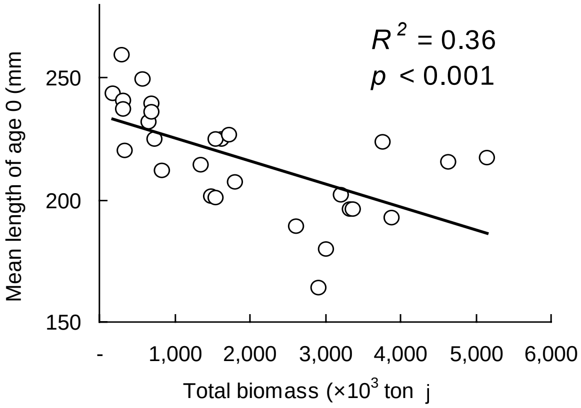


Fig. 43 Relationship between the total biomass and the length at age 0 of *Scomber japonicus*.

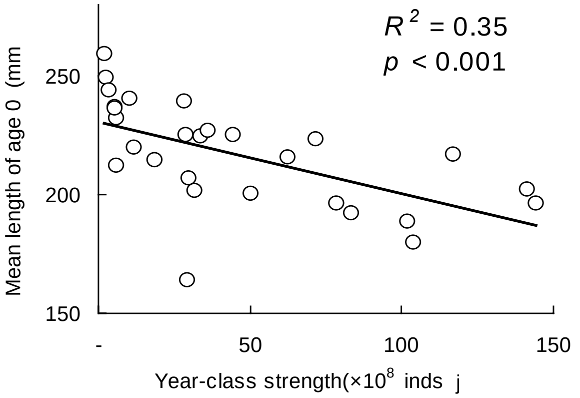


Fig. 44 Relationship between the year-class strength and the length-at-age 0 of *Scomber japonicus.*

Table 8 Statistics from regression of mean length-at-age of chub mackerel *vs*. biomass.

age	df	R	R²	p
0	27	-0.60	0.36	0.001
1	27	-0.48	0.23	0.010
2	27	-0.53	0.28	0.004
3	27	-0.44	0.19	0.019
4	26	-0.47	0.22	0.013
5	26	-0.45	0.20	0.018

Table 9 Statistics from regression of mean length-at-age of each year-class *vs*. recruitment.

age	df	R	R²	p
0	27	-0.59	0.35	0.001
1	27	-0.47	0.25	0.007
2	26	-0.60	0.34	0.001
3	25	-0.67	0.46	0.000
4	24	-0.80	0.63	0.000
5	23	-0.67	0.48	0.000

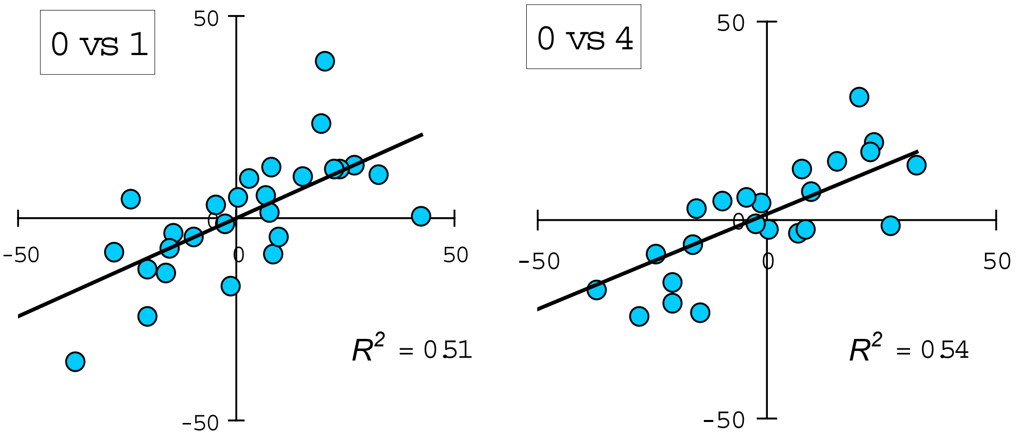


Fig. 45 Relationships between the annual mean length deviation at age 0 and age 1 (left), and between the annual mean length deviation at age 0 and age 4 (right).

Table 10 Statistics from regressions of annual mean length deviations at age 0 versus age 1 to 5 and deviations at age 1 versus age 2 to 5.

age		R	R²	p
0	1	0.71	0.52	0.001
	2	0.54	030	0.003
	3	0.54	0.29	0.005
	4	0.73	0.54	0.000
	5	0.53	0.28	0.009
1	2	0.67	0.44	0.000
	3	0.54	0.29	0.005
	4	0.71	0.50	0.000
	5	0.54	0.29	0.007

Our data confirmed that the trend in length of a year-class was determined during the first summer of life and maintained throughout the life span. These results are in agreement with Iizuka (1974), who reported on the growth of 1963-1973 year-classes of the Pacific stock of chub mackerel and found that the trend of growth at age 0 was maintained at least until age 2.

In this study, we investigated the effect of mackerel biomass and/or year-class strength on the mean length-at-age. Year-class strength significantly affected size-at-age of chub mackerel, but it only explained 25-63% of the fluctuations in the mean length-at-age. Other factors such as abiotic and/or biotic environment, sardine and spotted mackerel stocks may also influence the growth of chub mackerel.

References

Chiba. 1995. Shizuoka, Kanagawa Prefectural Fisheries Research Stations, Tokyo.

Hiyama, Y. 1998. Ecological changes in adults. 4. Migration range and growth rate in the Tsushima Current area. *In* Y. Watanabe and T. Wada [eds]. Stock fluctuations and ecological changes of the Japanese sardine. Tokyo, pp. 35-44.

Iizuka, K. 1974. The ecology of young mackerel in the north-eastern Sea of Japan: Estimation of the population size of the 0-age group and the tendencies of growth patterns on 0-age groups. Bull. Tohoku Reg. Fish. Res. Lab. 34: 1-16.

Overholts, W.J. 1989. Density-dependent growth in the Northwest Atlantic stock of Atlantic mackerel (*Scomber scomburus*). J. Northw. Atl. Fish. Sci. 9: 115-121.

Wada, T., Matsubara, Y., Matsumiya, Y., and Koizumi, N. 1995. Influence of environment on stock fluctuations of Japanese sardine, *Sardinops melanostictus*. Can. Spec. Publ. Fish. Aquat. Sci. 121: 387-394.

Wada, T. 1998. 3. Migration range and growth rate in the Oyashio area. *In* Y. Watanabe and T. Wada [eds]. Stock fluctuations and ecological changes of the Japanese sardine. Tokyo, pp. 27-34.

Inter-decadal fluctuations in length-at-age of Hokkaido-Sakhalin herring and Japanese sardine in the Sea of Japan

Yoshiro Watanabe[1], Yoshiaki Hiyama[2], Chikako Watanabe[3] and ShiroTakayana[4]
[1] Ocean Research Institute, Tokyo University, 1-15-1Minamidai, Nakano-ku, Tokyo, Japan 164-8639. E-mail: ywatanab@ori.u-tokyo.ac.jp
[2] Seikai National Fisheries Research Institute, Nagasaki 850-0951, Japan.
[3] National Research Institute of Fisheries Science, 2-12-4 Fukuura, Kanazawa-ku, Yokohama, Japan 236-8648. E-mail: falconer@nrifs.affrc.go.jp
[4] Hokkaido Prefectural Fisheries Experimental Station, Yoichi 012-3876, Japan.

Introduction

The total catch of Hokkaido spring herring (*Clupea pallasii*) in Japan peaked at 972 thousand tons in 1897 and tended to decline thereafter with steep peaks and deep troughs (Fig. 46). Spawning occurred from February to May along the coasts of northern Japan and southern Sakhalin, within the Sea of Japan and partly in the Sea of Okhotsk. With the decline of the population, spawning retreated to the north and finally disappeared from the coasts of Hokkaido in the middle 1950s (Morita 1985). After that the catches were from the local populations distributed in the coastal waters off northern Japan.

The Tsushima Current subpopulation of Japanese sardine (*Sardinops melanostictus*) in the East China Sea and the Sea of Japan experienced a peak in the late 1980s, similar to the Pacific subpopulation of these species (Watanabe *et al.* 1995). Total catch of the subpopulation first exceeded 1 million tons in 1984, maintained at this level until 1992, then rapidly declined to 33 thousand tons in 1998 (Fig. 47).

Size-at-age of these two clupeid fishes varied through the years of the large population fluctuations. In this paper we describe inter-decadal variability in size-at-age of both species and examine correlations between size-at-age and population size.

Materials and methods

Hokkaido spring herring mature at age 3 and start migrating to the spawning grounds along the west coast of Hokkaido (Hanamura 1963). Ages of about 4000 individual fishes per year caught in this area were determined from scales after 1910. Mean total length-at-age (TL) was calculated based on number of fish by ages and by 5 mm TL intervals (Kitahama, 1955). Time series of catch-at-age 3 and older fish from 1910-1960 reported by Hanamura (1963). We used this data for estimating total number of fish at age 3 and older from 1910-1950 by VPA (virtual population analysis).

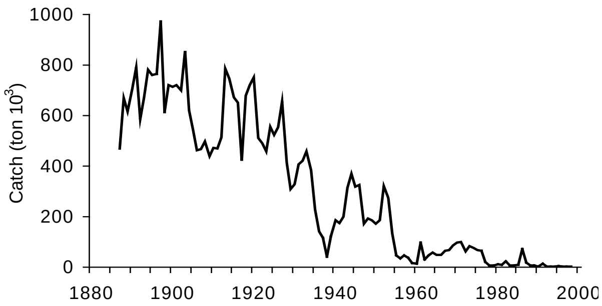


Fig. 46 Total catch of Hokkaido spring herring (*Clupea pallasii*) in Japan. Data for 1887-1911 are from Hanamura (1963); after 1911 - from Catch Statistics.

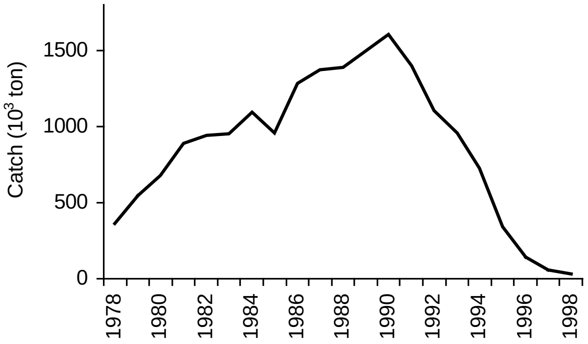


Fig. 47 Total catch of the Tsushima Current subpopulation of Japanese sardine (*Sardinops melanostictus*) from 1978-1998.

Data on catch-at-age and size-at-age of Japanese sardine caught by the Japanese purse seine fishery in the East China Sea and the Sea of Japan have been compiled since 1978. Total numbers of fish-at-age were estimated each year by VPA.

Results

Clupea pallasii. VPA estimates of spawner abundance (>3 years) of Hokkaido spring herring fluctuated greatly with a maximum of 19.6 billion fishes in 1924 and minimum of 0.4 billion in 1937. Total catch in number ranged from 3.0-0.04 billion fishes. The exploitation rate was estimated to be <30% with exceptions in the middle 1930s and the late 1940-early 1950s. Year-class population at age 4 varied greatly from 1907-1947 (Fig. 48). Dominant year-classes (>5.0 billion in number at age 4) occurred 6 times in 1909, 1911, 1915, 1921, 1926 and 1939. The maximum was 9.9 billion fishes in 1921, and minimum was 0.029 billion in 1933, about a 2.5 order of magnitude difference.

We calculated deviations (%) of the mean TL at age 3 year and older for each year-class from the 40-year mean (Fig. 49). The coefficients of determination (R^2) are summarized in Table 11. The deviations-at-age are positively correlated. The coefficients between age 3 *vs* 5 and 3 *vs* 7 were small compared with those between age 4 *vs* 6 or 4 *vs* 8. Correlations of 4 year and older ages with age 3 were not statistically significant, but those of 5 year and older ages with age 4 were highly significant. This implies that the TL trends of year-classes were fixed by age 4 at the latest. The mean TL at age 3 did not represent TL trend of a year-class. Total catches in number at age 3 accounted for about 60% of those at age 4 in the 40 year-classes. Only a limited proportion of age 3 fish migrated to the coastal spawning grounds.

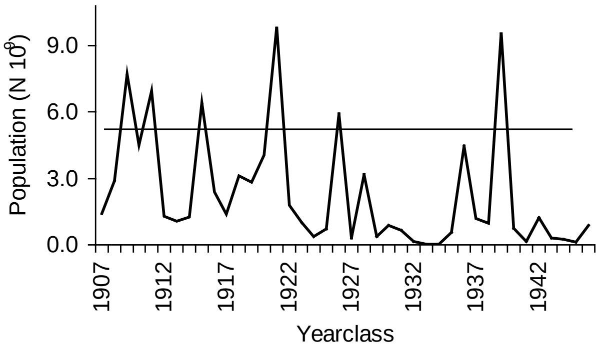


Fig. 48 Variability in year-class population at age 4 of Hokkaido spring herring.

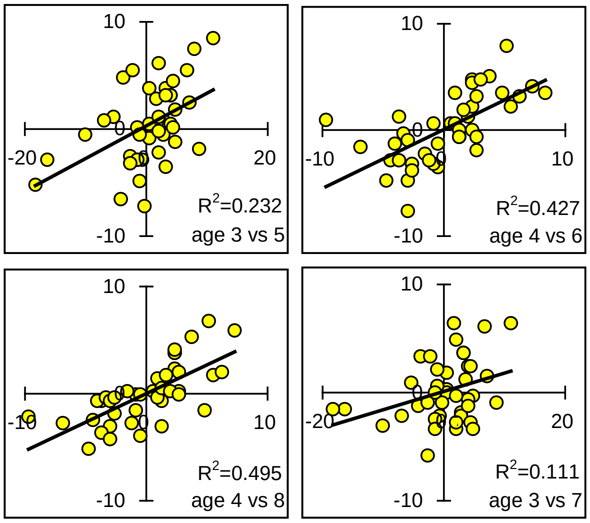


Fig. 49 Correlations of deviations (from the 40-year mean) of the mean TL-at-age in each year-class of Hokkaido spring herring.

Table 11 Coefficients of determination of TL deviations from the 40-year mean across ages (* P<0.01, ** P<0.001).

	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9
Age 3	0.323	0.232	0.127	0.111	0.103	0.068
Age 4		**0.747	**0.427	**0.465	**0.495	**0.531
Age 5			**0.573	**0.431	**0.573	**0.533
Age 6				**0.509	**0.559	*0.505
Age 7					**0.601	*0.457

TL-at-age 4 varied from 25.5 in 1925 to 30.3 in 1944 with the average of 28.2±1.0 cm (Fig. 50). TL was not necessarily smaller than the long-term mean for the 6 dominant year-classes. It tended to be larger than the mean in the early 1910s, smaller in the 1920s, and recovered in the early 1930s. A similar TL trend was found at age 5 (40 year mean was 30.0 cm).

TL-at-age 4 was not correlated with the year-class size in number at age 4. The coefficient of determination was 0.068, indicating that only a small amount of the TL variability was explained by year-class strength (Fig. 51).

TL-at-age 4 was correlated significantly ($P < 0.05$) with the mean spawning population in years when a given year-class was at age 1 to 4. About 17% of the inter-annual variability in the mean TL of year-classes at age 4 could be explained by the size of the spawning population (R^2=0.165). The variability in size-at-age of the herring inhabiting the Sea of Japan and Sea of Okhotsk is considered to be determined in a density independent manner.

Sardinops melanostictus. For Japanese sardine, year-class abundance at age 2 varied greatly during the 20 year study from 1976-1996 (Fig. 52). The population was <20 billion fishes in the 1970s. Strong year-classes (>30 billion) occurred consecutively in 1980-82 and 1984-87. Abundance reduced dramatically in 1988 year-class and further declined to 1995. The maximum and minimum year-class strengths were 77.3 and 1.4 billion in number at age 2, about a 1.7 order of magnitude difference. Strong year-classes >50 billion occurred consecutively in the 1980s. Deviations (%) of the mean TL at age 3 of year-classes from the 20-year mean were correlated with those at age 2, but not with age 1 (Fig. 53). The inter-annual trend in TL-at-age of each were fixed by age 2 at the latest in sardine. Age 1 sardines of the Tsushima Current subpopulation are not fully recruited to the Japanese purse seine fishery and do not represent size-at-age or strength of the year-classes.

Body length (BL) at age 2 of the sardine was >180 mm in the 1970s. It remarkably declined to 169 mm in 1980 and remained smaller than 170 mm until 1988. Then BL recovered to the 1970s level of around 180 mm (Fig. 54). Similar BL trend was found in size-at-age 3. The interannual fluctuation in BL corresponded inversely with the fluctuation in year-class size (Fig. 54).

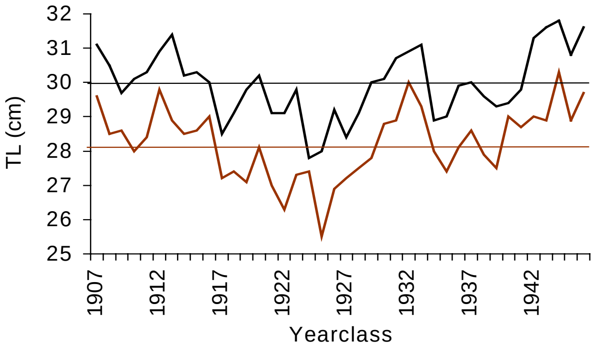


Fig. 50 Inter-decadal variations in TL-at-age 4 and age 5 of Hokkaido spring herring.

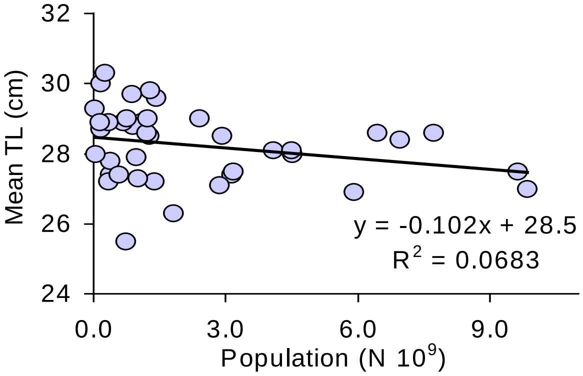


Fig. 51 Relationship between TL and year-classes size at age 4 of Hokkaido spring herring.

Fig. 52 Variability in year-class population at age 4 of Japanese sardine.

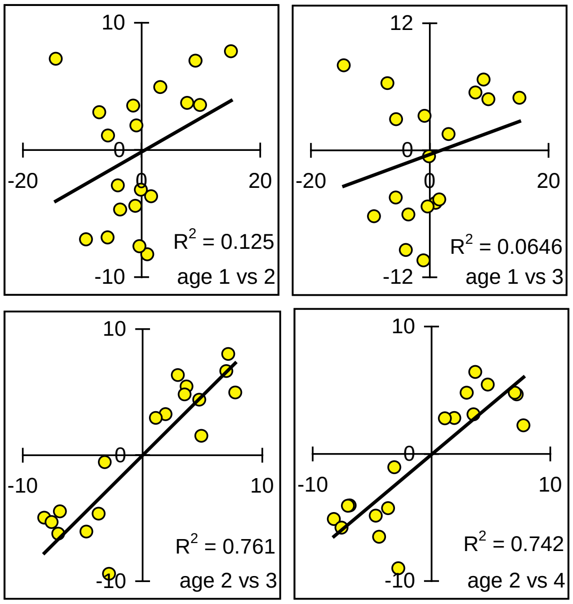


Fig. 53 Correlations of deviations from long term mean TL (20 years) among year-classes of Japanese sardine, by age.

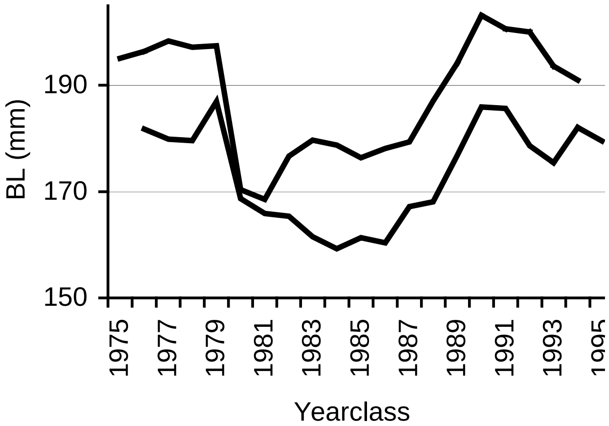


Fig. 54 Inter-decadal variations of BL-at-age 2 and 3 of Japanese sardine.

BL-at-age 2 was significantly (P<0.001) correlated with the year-class size in number at age 2 (Fig. 55). The coefficient of determination indicated that 60% of the BL variability can be explained by year-class strength. BL-at-age 2 was significantly (P<0.001) correlated with the total population at age 2. The coefficient of determination was 0.587. The variability in BL-at-age of the sardine inhabiting in the temperate Sea of Japan and the East China Sea is considered to be determined in a density-dependent manner.

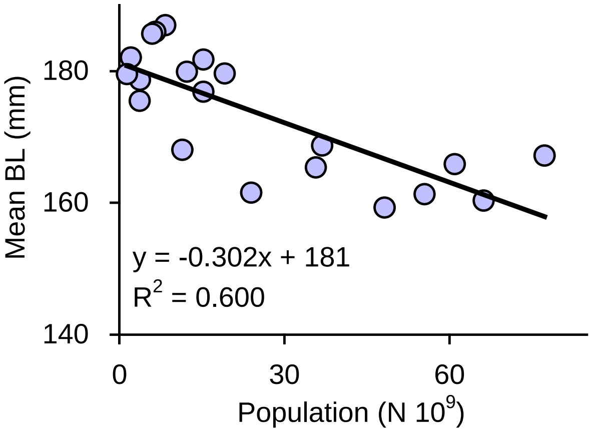


Fig. 55 Correlation of the mean BL with population of year-classes at age 2 of Japanese sardine.

Discussion

The fluctuations in year-class strengths were greater in the herring (2.5 orders) than in the sardine (1.7 orders) during the years studied. This may be related to the differences in the magnitude of inter-annual variability of ocean environment between the subarctic and temperate waters.

Size-at-age of herring and sardine varied about ±4 or 5% in the years studied. Growth of sardine up to 2 years old is considered to be largely determined through density-dependent processes such as competition for food, while that of the herring up to 4 years old was independent from the density of the population. Two factors may be responsible for the difference in the growth determining processes in herring and sardine.

The maximum year-class strength of the Tsushima Current subpopulation of the sardine was as large as 77.3 billion in 1987. The total population reached 370 billion in 1987. In the Hokkaido spring herring, the maximum year-class was 9.8 billion in 1921 and the total spawning population reached 19.6 billion in 1924. The population size of sardine was more than 10 times larger than herring. Comparison in migration ranges of sardine in the East China Sea and the Sea of Japan and of herring in the Sea of Japan and the Sea of Okhotsk are required, but the large population size of sardine seems to be a potential factor of density-dependent determination of size-at-age.

Another potential factor is the difference in biological productivity between the temperate and subarctic waters in the Sea of Japan and the Sea of Okhotsk. The Tsushima Current is derived from the warm Kuroshio Current and its productivity is considered to be lower than subarctic waters inhabited by the herring. Carrying capacity of the subarctic waters in the Sea of Japan and the Sea of Okhotsk may be sufficiently greater than the total food requirement of the herring population and competition for food may not be realized in these waters.

References

Hanamura, N. 1963. A study on the method of prediction of the Hokkaido spring herring resources. Bull Hokkaido Reg. Fish. Res. Lab. 26: 1-66.

Kitahama, H. 1955. Data on the total length compositions of Hokkaido spring herring. Hokkaido Pref. Fish. Exp. Stn., Yoichi, pp 46.

Morita, S. 1985. History of the herring fishery and review of artificial propagation techniques for herring in Japan. Can. J. Fish. Aquat. Sci. 42 (Suppl 1): 222-229.

Watanabe, Y., Zenitani, H., and Kimura, R. 1995. Population decline of the Japanese sardine *Sardinops melanostictus* owing to recruitment failures. Can. J. Fish. Aquat. Sci. 52: 1609-1616.

Long-term variability in length of walleye pollock in the western Bering Sea and east Kamchatka

Pavel A. Balykin and Alexander V. Buslov

Kamchatka Fisheries and Oceanography Research Institute (KamchatNIRO), 18 Naberezhnaya Street, Petropavlovsk-Kamchatsky, Russia 683600. E-mail: kamniro@mail.kamchatka.ru

The mean body length of walleye pollock yearlings from the western Bering Sea increases when the area of the ice cover is reduced. The average length of 2 to 6-year-old walleye pollock varies in relation to the dynamics of total stock biomass and environment. The biomass of walleye pollock is lower when the area of ice cover in the Bering Sea exceeds 700,000 km^2. When the area of ice cover is reduced, the total stock abundance of walleye pollock increases and the average length of 2 to 6-year-old fish decreases. A reliable relationship has been observed between condition factor and the growth of fish, indicating that the growth of walleye pollock is dependent on the forage base. Currently the biomass of walleye pollock in the western Bering Sea is very poor, therefore the growth in length is not dependent on the environment and total stock biomass.

The average length of 2 to 6-year-old walleye pollock in the Pacific Ocean waters adjacent to Kamchatka has changed in relation to the biomass of total stock and the abundance of generations. When the biomass has been high, the growth has been slow and *vice versa*. The environmental factors do not affect the growth of walleye pollock to the east of Kamchatka.

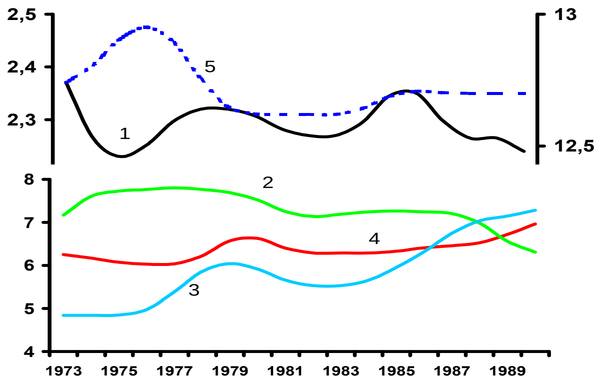


Fig. 56 Variation of natural logarithms of average length of walleye pollock yearlings (1), walleye pollock (2), Pacific herring (3), mesoplankton biomass (4), and area of ice cover (5) in the western Bering Sea.

Figure 56 shows changes in the length of walleye pollock yearlings, the biomass of mesoplankton and ice cover in the Bering Sea for the period from 1973-1990. The reduction of the ice cover area in the Bering Sea leads to the growth of total stock and an increase in average length of fish (Fig. 57).

Comparison of 2 to 6-year-old walleye pollock from the western Bering Sea and eastern Kamchatka waters indicates that variability in

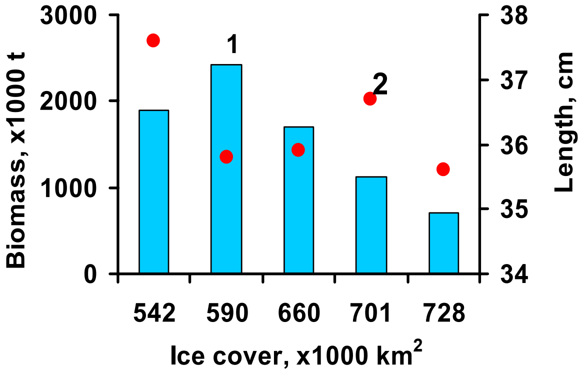


Fig. 57 Relationship between total biomass of walleye pollock (bars) and length of 4-year-old fish (dots) and ice conditions.

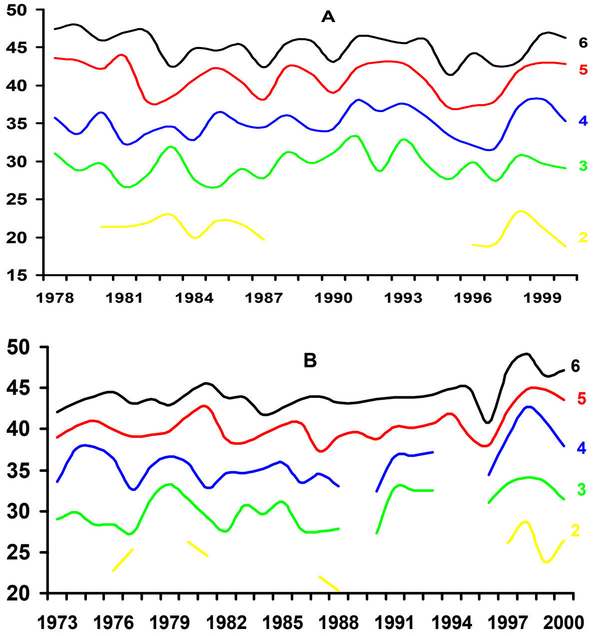


Fig. 58 Long-term dynamics of average length of 2 to 6-year-old walleye pollock: (A) western Bering Sea and (B) eastern Kamchatka.

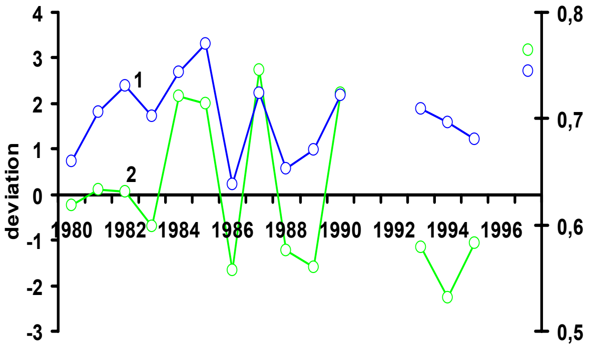


Fig. 59 Long-term dynamics of (1) average condition factor in 3 to 6-year-old walleye pollock and (2) averaged deviations in length from the long-term mean of these age groups.

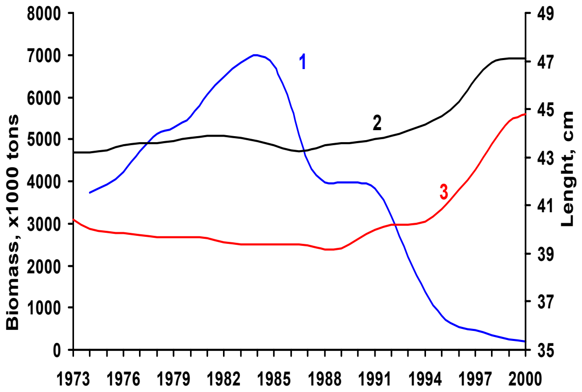


Fig. 60 Long-term dynamics of total biomass of east Kamchatka walleye pollock (1), average length of 6-year-old fish (2) and average length of 5-year-old fish (3).

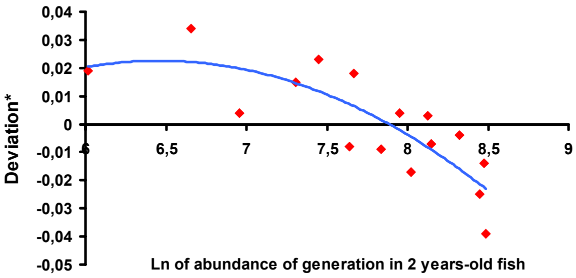


Fig. 61 Relationship between generation growth rate and abundance in the periods of high and intermediate stock abundance of the east Kamchatka walleye pollock, shown as the deviation from the average specific growth rate.

body length among nearby age groups is similar (Fig. 58). For the period 1980-1997, the condition factor is related to linear growth of fish (Fig. 59). For the east Kamchatka stock, changes in growth of 5-6-year-old walleye pollock are inversely related to the total biomass of species (Fig. 60). For the periods of high and intermediate stocks the growth rate of the east Kamchatka walleye pollock depends inversely on cohort abundance (Fig. 61).

Effect of population abundance increase on herring distribution in the western Bering Sea

Alexander A. Bonk
Kamchatka Fisheries and Oceanography Research Institute (KamchatNIRO), 18 Naberezhnaya Street, Petropavlovsk-Kamchatsky, Russia. 683600. E-mail: kamniro@mail.kamchatka.ru

The last two decades have been important for the development of the Korf-Karaginsky Pacific herring population. After a long period of low abundance in the 1980s, the population has been growing dynamically since 1990, reaching a maximum in 1997, and then started to decline again (Fig. 62).

The annual distribution and migratory behavior of the Pacific herring during are determined by hydrology and the stock abundance fluctuations. The time period and the distance of the Pacific herring feeding migration are now significantly different from those when stock abundance was low.

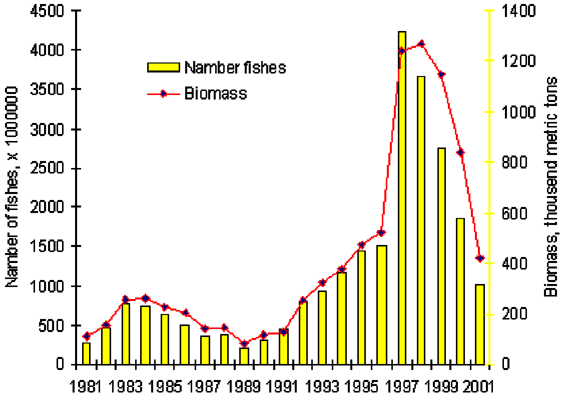


Fig. 62 The stock abundance dynamics of the Korf-Karaginsky herring in the western Bering Sea.

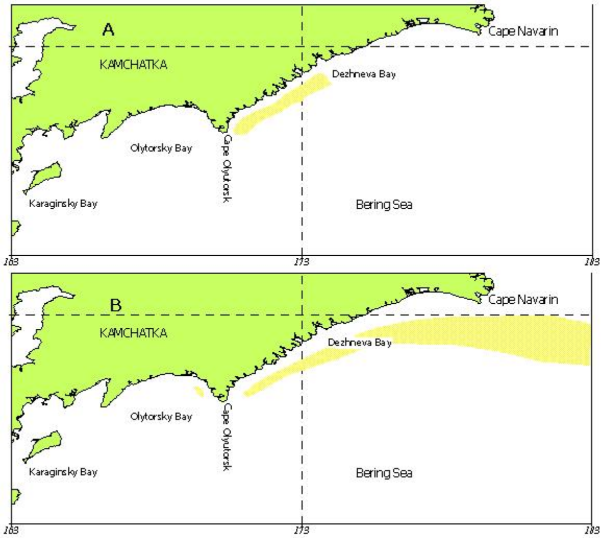


Fig. 63 The Korf-Kagarinsky herring distribution during the feeding migration: (A) low stock abundance and (B) high abundance.

During periods of low abundance, the feeding migration of the mature part of the stock occurred in Anastasiya and Dezhneva bays (Fig. 63A). Herring returned to Olytorsky Bay for winter before October 10th. This period was characterized by relatively stable conditions providing sufficient feeding for the Korf-Karaginsky herring. From the 1980s until the mid-1990s positive changes were observed in the Bering Sea. These included: 1) warming of the upper 200 m which resulted in an increase of the forage zooplankton abundance, and 2) decrease in the stock abundance of walleye pollock, the nearest competitor of herring for food. Thus during the 1980s and early 1990s, when the herring abundance was low, the feeding conditions for the Pacific herring became favorable. In 1993, conditions were optimal for the production of an abundant generation (Fig. 64). In 1997, the

4+ generation was the only one that recruited to the commercial fishery; in the last 40 years, it had the highest abundance and biomass, $4{,}230 \times 10^6$ fishes or $1{,}240 \times 10^3$ tons, respectively (Fig. 62).

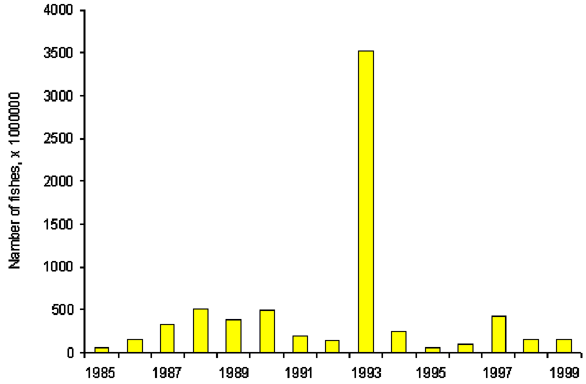


Fig. 64 Year-class abundance of age 4+ generations of the Korf-Kagarinsky herring in the western Bering Sea by brood year.

The increase in abundance of the fishery-size individuals in the Korf-Karaginsky herring population took place simultaneously with water cooling in the region. The indicators of that were: (1) a general decrease in the mixed water layer thermal capacity, and (2) extension of the ice cover in the Bering Sea since 1998. Cold water masses dominated on the shelf, providing poor conditions for the forage base. High abundance of the Korf-Karaginsky herring and poor food supply caused intensification of intra-specific competition for food. Unable to completely fulfil their food requirements, herring had to enlarge the area of feeding.

In 1998-2000, herring used marine bathypelagial in the Olytorsky-Navarinsky zone instead of the shelf zone for feeding until mid-October. In August and September, the echosounder tracks of herring shoals were discovered at the depth of 340-400 m. At the same time, local shoals of feeding herring were found in the eastern part of Olytorsky Bay (Fig. 63B). From the second half of October, fish shoals were distributed at depths of 80-150 m, on both sides of Olytorsky Cape (Fig. 65), however, these shoals were not stable. Herring migrated actively westward in small shoals, along the edge of the warmer and more saline Pacific waters, where trophic activity was high. During the daytime fish were distributed near the bottom, and at night they created thick shoals in the water column.

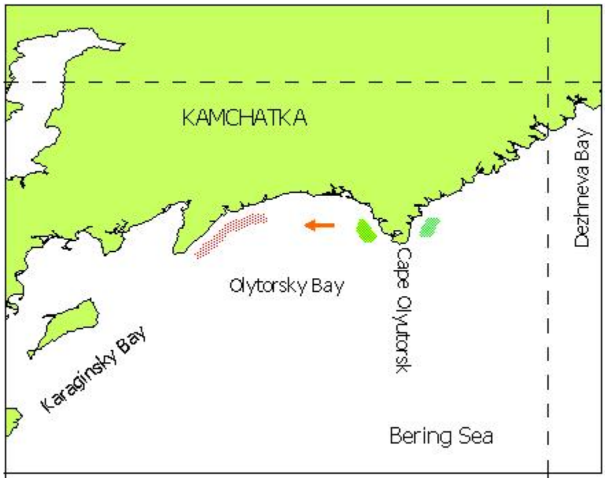


Fig. 65 Distribution of the Korf-Kagarinsky herring in the western Bering Sea, in October-November.

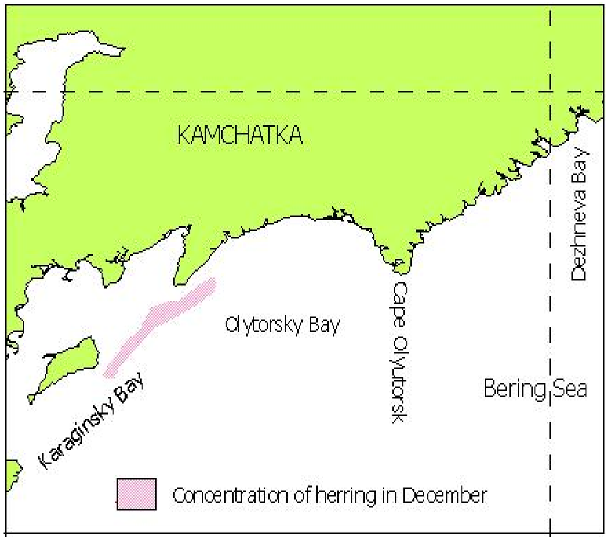


Fig. 66 The area of wintering of the the Korf-Kagarinsky herring in the western Bering Sea.

The transformation from summer to winter conditions in Olyorsky Bay has been normally completed in November. This transformation results in the quick cooling of the offshore waters. In 1998-2000, stable, favorable temperature conditions in November occurred at depths of 150-200 m, in the central and western parts of the bay. Therefore, the herring stocks formed at these depths. Their behavior at that time was similar to their behavior in October. Following the arrival of cold water, herring migrated westward, forming non-mobile stocks at the depth of 180-250 m between the Cape of Goven and the Cape of Golenischev in December (Fig. 66).

Since 1993, there has been no single abundant cohort produced by the population. Due to natural mortality, and fishing, the stock abundance of the Korf-Karaginsky herring has decreased. Moreover, at the present time, hydrological conditions can hardly provide the required biomass of forage zooplankton. This should prolong the feeding period until mid October and expand the feeding area.

Survival of yellowfin sole (*Limanda aspera* Pallas) in the northern part of the Tatar Strait (Sea of Japan) during the second half of the 20th century

Sergey N. Tarasyuk
Sakhalin Research Institute of Fisheries and Oceanography, 196 Komsomolskaya Street, Yuzhno-Sakhalinsk, Russia 693023. E-mail: taras@sakhniro.ru

The northern part of the Tatar Strait is one of the traditional areas where yellowfin sole (*Limanda aspera* Pallas) dominate, averaging 60% of flounder abundance. The commercial fishery of flounder stocks began in 1943. In 1944, their catch reached the historical maximum – 10.1 thousand tons, but during the following year it reduced up to 7.4 thousand tons, and a catch per unit of effort (CPUE) decreased almost 2 times. Since 1945, the fishery ceased and until the beginning of the 1950s, the flounder catch did not exceed 0.1 – 1.0 thousand tons a year. Regular scientific research on this species was not conducted until 1956. Nevertheless, the data collected on the size composition of flounder catches during 1946, and some similar data since 1956, indicated overfishing in the mid-1940s (Tarasyuk, 1994A). After the 1950s, catch varied from 5.45 thousand tons in 1955 to 0.35 thousand tons in 1979. In the last ten years of the century, the catch constituted 0.4 – 2.0 thousand tons per year.

Age structure of the yellowfin sole population is characterized by an extended age distribution. Fish at age 4 to 18 occur in catches. Age-7 yellowfin sole are usually a modal age group, as their average long-term age value is 8.8. Body weights of yellowfin sole change according to the equation of allometric growth. A coefficient of allometry exponent in the equation is 3.1315, and the scale coefficient is 0.0073 when body weight is measured in grams and length (AC) in cm. Yellowfin sole from the shelf zone of western Sakhalin cease annual increments at age 8-9+. The instantaneous natural mortality rates vary by age decreasing from 0.22 to 0.12 beginning in age-4 to age-6-8 individuals, respectively, and then gradually increasing to 0.60 at age 15. The broods become fully available to the fishery beginning at age 8.

Methods

Data on the age structure of catches, annual catches, catch per unit of effort, natural mortality by age, rate of maturation, and average body weight by age during the period of 1956-2000 were processed using a method of virtual populations (VPA), with the help of program developed at the Fishery Laboratory Lowestoft (Darby and Flatman 1994). The Louric-Shepherd method was used for adjusting fishing mortality coefficients (Pope and Shepherd 1985).

Further processing of VPA results was done to reveal the causes determining brood year abundances. The abundance estimates of broods at age 4 were used as the index of recruitment. A cohort survival rate at age 4 was estimated as a quotient between the number of age 4 fish obtained from the VPA method, and the number at age 0. The spawning stock was calculated as the total number of the age groups taking into account the rate of maturation, less a year catch, since the fishery in this region is the most intensive before the beginning of spawning. The number at age 0, or a start number of generation was determined from the number of spawners in the year of reproduction, considering the fecundity and age, and assuming under equal sex ratio from the catches.

Results

The biomass of the commercial part of the stock calculated by VPA changed significantly during the period of observation. In 1956, it constituted 13.9 thousand tons, reduced to the minimum 2.8 – 3.1 thousand tons in 1971 – 1975, and then began to increase to the maximum 19.2 thousand tons in 1991 – 1992. At the end of the century yellowfin sole stock reduced a little (Fig. 67). The commercial stock varied by 6.9 from 1956-2000. Spawning stock also varied within the wide limits: from the minimum 11.7 million fish in 1970 to 68.8 million fish in 1996, a factor of 5.8. The cohort size at age 4 varied from 6.09 million to 30.62 million fish in the 1962 and 1989 brood years, respectively, a factor of 5.0.

A potential population fecundity or cohort strength at age 0 varied from 4.0 to 25.4 trillion eggs according to changes in spawning stock and its age structure. Survival from age 0 to 4 averaged one individual from 3,000 eggs. This index ranged widely, up to 7.5.

Figure 68 shows the stock recruitment relationship and the estimated Ricker's model. A correlation coefficient with the amount of spawning stock was significant (0.79, $p<0.05$) for abundance of broods. The portion of the explained dispersion after calculating the coefficients of non-linear regression for the Ricker's model was 63.08%.

The survival rate for generations was well-correlated with the numbers of age group 0; the correlation coefficient was 0.61 ($p < 0.05$). Use of the equation of exponential growth approximated the relationship between those indices, with 37.16% dispersion explained. Based on the estimated curve, survival practically does not change at the initial number of brood more than 7 million individuals, and keeps at a stable level providing a minimum survival for population. Reduction in the number of eggs laid brings about a sharp increase in survival, varying about twofold (Fig. 69). This suggests a density dependent mortality.

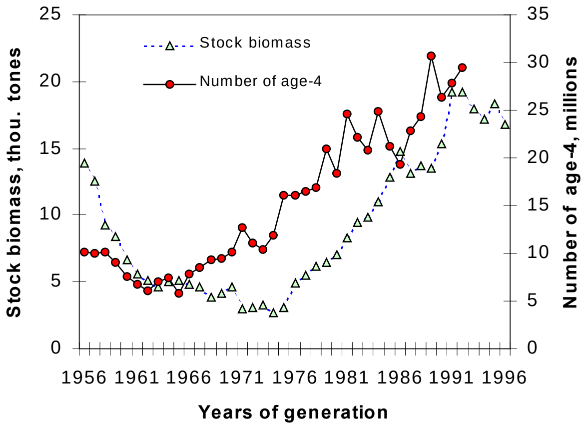


Fig. 67 Dynamics of biomass of the spawning stock and number of broods at age 4 from this stock generation for the Tatar Strait yellowfin sole population.

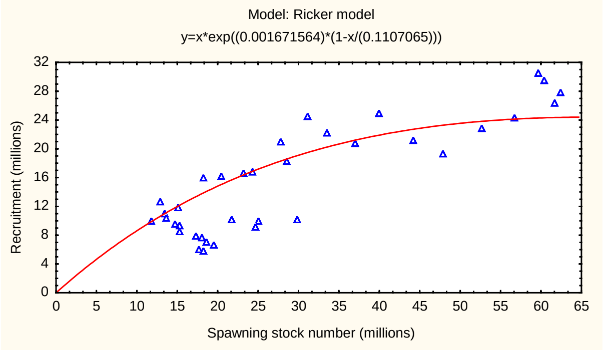


Fig. 68 Ricker's "stock-recruitment" model fit to the 1956-1992 observed data.

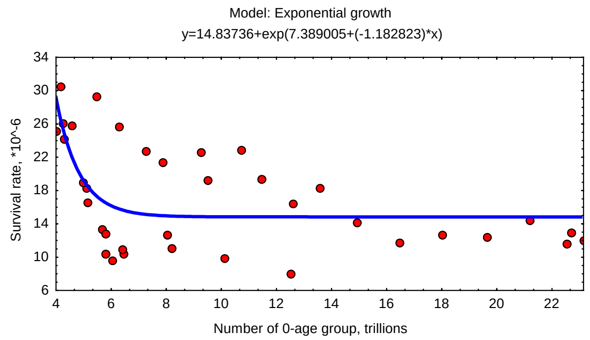


Fig. 69 Exponential model of the relation between survival rate and number of broods at age 0.

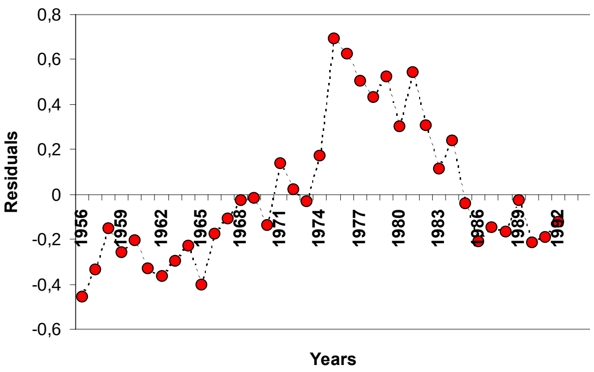


Fig. 70 Dynamics of standardized residuals of the survival rate regression by the birth years of broods.

The observed deviations from the exponential growth curve have causes other than the initial density of a population. The standardized residuals indicated a maximum of survival appears from 1974 to 1984, and low survival from the mid-1950s through the mid-1960s, 1985 through 1992 is characterized as slightly less than average.

A temporal series of the regression residuals on fish density demonstrates the potential climatic causes affecting a survival. According to the data of coastal hydrometeorological stations (Kholmsk GMS), a maximum heating of the surface water in the northern part of the Sea of Japan occurred in the early to mid 1970s, whereas the 1980s were characterized as cold years. Nevertheless, temperature conditions in the coastal zone may non-adequately characterize biota during early stages of the yellowfin sole ontogenesis when a brood abundance is formed. The longest oceanographic time-series observations in Tatar Strait are standard transects: Antonovsky and Cape Slepikovsky. The temperature regime in this region strongly depends upon the Tsushima Current. Its strengthening during the autumn in a warm year forms a stable water column until the beginning of winter. This is evident in the dynamics of May temperature in the layer 50-100 m (Kantakov 2000; Fig. 71). The layer temperature, smoothed by a 5 point moving averages, has decreased from the mid-1970s to the late 1980s, whereas the mid-1950s to the mid-1970s was characterized by higher temperatures. A correlation of initial estimates of the layer temperature with the regression residuals, the index of survival, appeared to be significant with a correlation coefficient of -0.48. A reconstructed zooplankton biomass time series for the southwestern Sakhalin coast has shown that maximum zooplankton biomass observed in cold years, and low plankton biomass occurred in warm years (Kantakov 2000; Fig. 71).

Maximum of atmospheric activity also occurred in the 1950s, when the greatest number of tropical typhoons moved through the region, whereas in the 1970s, the number of typhoons was minimum (Fig. 72). The correlation coefficient was -0.50 (Tarasyuk 1994 B).

Discussion

The noted relationships demonstrate the influence of climatic factors on the abundance of yellowfin sole generations. To understand the mechanism of these relationships, we review the ecology of yellowfin sole spawning. They spawn in the northern part of the Sea of Japan in July-August, at the depths less than 50 m. Eggs are spawned in batches (Fadeev 1957, Ivankov *et al*. 1972). Spawned eggs are relatively small, their diameter is 0.8 – 0.9 mm. Embryos and larvae develop in the upper 50-m of water column at temperatures from 8 to 19ºC (Pertseva- Ostroumova 1961). At the length of 16 - 27 mm, larvae settle on the bottom (Nikolotova 1975). The planktonic stage is about a one month, and on the whole, taking into account the duration of spawning, may continue up to 4 months (Tarasyuk 1994B). The peculiarity of yellowfin sole reproduction is the timing of their aggregations at plankton stages of development to small areas with circulation that prevents the larvae from flowing out of favorable sites (Moiseev 1952). Plankton and nektobenthic crustaceans at juvenile stages of development form the basic food for planktotrophic larvae (Nikolotova 1975). Evidently, a long stay in the upper water column, their peculiarities of feeding, and concentration in a limited area create a special vulnerability of yellowfin sole at early stages of ontogenesis to the negative affects of environment, and also a high mortality as a result of intra-population competition.

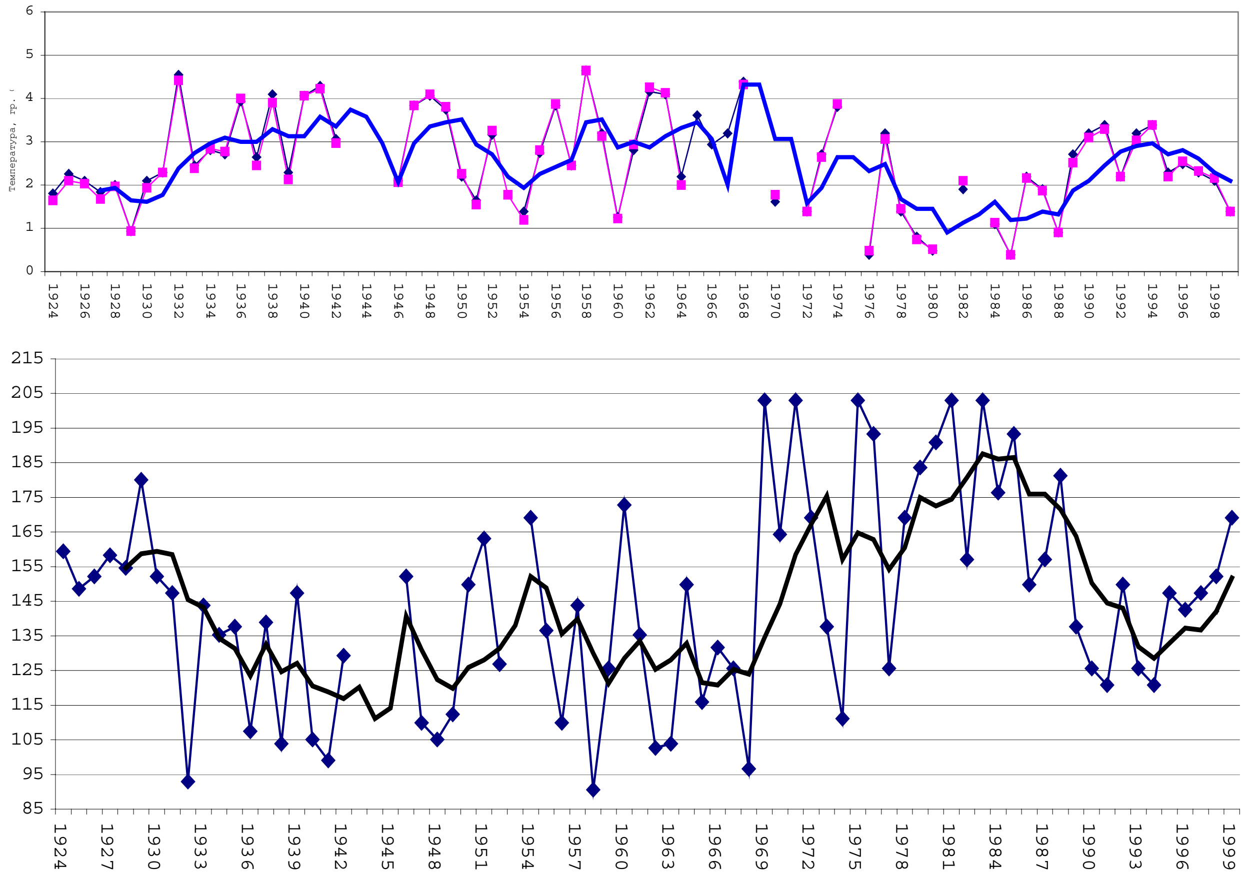


Fig. 71 Dynamics of the May temperature in the 50-100 m layer along the transects Antonovsky and Cape Slepikovsky (top panel) and autumn biomass of the net zooplankton (bottom panel). Zooplankton biomass is in units of mg wet weight per cubic meter. (Source: Kantakov 2000).

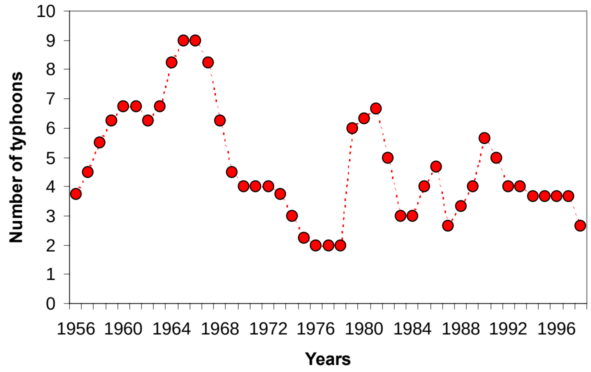


Fig. 72 Frequency of tropic typhoons moving through the area of Sakhalin Island.

Comparing these relationships with the peculiarities of reproduction of yellowfin sole, we conclude that the negative influence of the initial cohort abundance upon their survival is realized through the deterioration of feeding conditions under the increased density of larval aggregations, diet selectivity, and limited resources of food fields. The influence of tropical typhoons (more than 80 % of them occur in June-August) (Eremin and Tretyakova 1980) may result both in the negative impact of hydrodynamic wave on the embryos survival at the sensitive stages of development, and in their impact on the small-scale circulation systems, causing the appearance of cold deep water masses on the surface and carrying eggs and larvae out of zones favorable for inhabitation. In the cold year periods, zooplankton biomass in the northern Sea of Japan increases, and that reduces the level of intra-population competition for food. In turn, this favorably affects the larval survival.

References

Darby, C.D. and Flatman, S. 1994. Virtual Population Analysis: Version 3.1 (Windows/DOS) User Guide. Info. Tech. Ser., MAFF Direct, Fish. Res., Lowestoft, (1): 85 pp.

Eremin, P.G. and Tretyakova, E.I. 1980. To a question about the cyclicity of typhoons above Sakhalin Region. Information Letter No. 1/90. Yuzhno-Sakhalinsk, SakhUGCS, pp. 31– 45 (in Russian).

Fadeev, N.S. 1957. On the type of spawning and fecundity for some commercial Sakhalin flounders. Zoological Journal 36(12): 18-41 (in Russian).

Ivankov, V.I., Ivankova, Z.G., and Volkova, T.D. 1972. Types and terms of spawning for flounders from Peter the Great Bay. Scientific Notes of DVGU 60: 49-61 (in Russian).

Kantakov, G.A. 2000. Oceanographic Retrospective Analysis of the Zooplankton Population Inhabitation Conditions at the Southwest Sakhalin in 20th Century. *In* 15th International Symposium on Okhotsk Sea & Sea Ice. Okhotsk Sea & Cold Ocean Research, pp. 384-390.

Moiseev, P.A. 1952. Some specific features of the bottom and near-bottom fish distribution in the Far East seas. Izv. TINRO 27: 129 – 137 (in Russian).

Nikolotova, L.A. 1975. Larval feeding of the west Kamchatka flounders. Izv. TINRO 97: 51-61 (in Russian).

Pertseva-Ostroumova, T.A. 1961. A spawning and developing patterns of the Far East flounders. M.: AS USSR Publishers. 484 pp. (in Russian).

Pope, J.G. and Shepherd, J.G. 1985. A comparison of the performance of various methods for tuning VPA's using effort data. J. Cons. Int. Explor. Mer. 42: 129-151.

Tarasyuk, S.N. 1994A. Results of modeling biological indices of the yellowfin flounder from the western Sakhalin waters during the initial period of fishery. *In* "Fishery researches in Sakhalin-Kuril region and adjoining areas". Yuzhno-Sakhalinsk, Sakhalin Region Book Publishers, pp. 33-38 (in Russian).

Tarasyuk S.N. 1994B. On the possible causes providing the abundant broods of yllowfin flounder. *In* "Fishery researches in Sakhalin-Kuril region and adjoining areas". Yuzhno-Sakhalinsk, Sakhalin Region Book Publishers, pp. 23-32 (in Russian).