

Abstract.—The growth patterns of Pacific whiting *Merluccius productus*, also known as Pacific hake, were examined for the period 1978–88 using fishery-based estimates of length-at-age. Mean length-at-age and a delta method variance estimate of mean length-at-age were computed for geographic and temporal strata in the U.S. fishery. These calculations took into account the two-phase sampling design used to sample the catch. A factorial analysis of variance of length found significant differences due to age, year, region, sex, and time-period during the fishery. Length increases with age and season. Pacific whiting found in the north are larger, and females are larger than males. The mean length-at-age began declining in 1978, and reached a minimum in 1984. From 1984 to 1986, there was a slight rebound in length-at-age, but after 1986 length-at-age again declined. To investigate the influence of population density and environmental covariates on annual growth, a generalized form of the von Bertalanffy growth model was developed. Deviations from a baseline model for sex-specific asymptotic growth were significantly correlated with changes in sea-surface temperature and adult biomass. Regression results indicate that a 0.5°C increase in mean summer sea-surface temperature would reduce annual growth by 24% at age 1 and 12% at age 4. In contrast, the effect of adult biomass on annual growth becomes greater with age. An increase of 200,000 metric tons (approximately 10% of the mean population biomass) would reduce annual growth by 5% at age 4 and by 10% at age 7. It is proposed that the effect of population density is greater for the older Pacific whiting because their diet has shifted from euphausiids, whose abundance is closely coupled with environmental processes, towards fish species with multiyear life cycles that can be affected by intense Pacific whiting predation.

Detecting environmental covariates of Pacific whiting *Merluccius productus* growth using a growth-increment regression model

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This paper describes research on the growth of Pacific whiting, also known as Pacific hake, a gadoid species that is an important component of the California Current ecosystem (Francis 1983). The coastal population of Pacific whiting is currently the target of a major fishery with an average (1977–88) annual harvest of 147,000 metric tons (t) (Dorn and Methot 1990). Adult Pacific whiting migrate north in spring and summer, feeding in the productive waters along the continental shelf and slope from northern California to Vancouver Island, British Columbia. In late autumn, Pacific whiting migrate south to spawning areas from Point Conception, California, to Baja California (Bailey et al. 1982). The U.S. fishery operates from April to November and in recent years has been conducted primarily under joint-venture arrangements, with U.S. fishing boats delivering fish to processing vessels from the Soviet Union, Poland, Japan, and other nations. The Canadian fishery for Pacific whiting is conducted in similar fashion, except that independent fishing by the foreign fleet still accounts for a significant portion of the catch.

Hollowed et al. (1988) observed that the mean length-at-age of Pacific whiting had declined in recent years, and hypothesized that the disruption of normal circulation and temperature patterns associated with the

1983 El Niño may have been the causative factor. The recruitment of strong 1980 and 1984 year-classes increased the population biomass of Pacific whiting to a maximum in 1986. The decline in the length-at-age could also have been a density-dependent growth response to this increase in population abundance. Since the Pacific whiting resource is managed by setting an annual quota in tons based on a conversion using weight-at-age from a projected yield in numbers (Dorn and Methot 1990), changes in growth must be taken into account when making management recommendations about the resource.

The objective of this paper is to examine the pattern of growth variability displayed by the coastal Pacific whiting population, and, in particular, to determine whether environmental covariates or fluctuations in population density could account for the recent changes in length-at-age. Analysis of variance, while useful as an exploratory technique to identify the sources of variability in length-at-age, is inadequate to describe changes in asymptotic growth. The nonlinear regression model presented in this paper is a simple, biologically realistic model for exploring the environmental determinants of asymptotic growth. Its potential utility is not limited to the application described in this paper, i.e., growth of Pacific whiting.

Methods

The U.S. Foreign Fisheries Observer Program at the Alaska Fisheries Science Center (AFSC) uses a two-phase sampling design to sample the catch of Pacific whiting (French et al. 1981). The first phase consists of obtaining a large initial sample of fish and recording the length and sex. For the second phase of sampling, a subsample of fixed size is selected for each combination of length category and sex. All fish in these subsamples are aged using otoliths.

Typically, each observer samples 2–3 hauls or joint-venture deliveries per day for length and sex, and 150 otoliths (5 per centimeter-length category per sex) are collected over a two-month cruise. The numbers of aged and measured fish from 1978–88 are given in Table 1. This information resides in a data base maintained by the Resource Ecology and Fisheries Management Division (REFM) at the Alaska Fisheries Science Center.

Kimura and Chikuni (1987) point out that, with a two-phase sampling design, estimates of mean length-at-age are biased when obtained simply by averaging the lengths of the aged fish. To avoid this bias, stratified length-at-age estimates were compiled from fishery data for the years 1978–88 using separate age-length keys for each stratum (see Appendix for details). Three spatial strata were defined as: (1) the area from lat. 39°00'N to lat. 43°00'N, including part of the International North Pacific Fishery Commission (INPFC) Monterey region and the Eureka INPFC region (EUR); (2) the area from lat. 43°00'N north to Cape Falcon (lat. 46°45'N) in the southern part of the Columbia INPFC region (SCOL); and (3) the area north of Cape Falcon to the U.S.–Canada border including the northern part of the Columbia INPFC region and the U.S. portion of the Vancouver INPFC region (VNC) (Fig. 1).

Table 1
Number of Pacific whiting *Merluccius productus* sampled from the midwater trawl fishery during the years 1978–88 off Washington, Oregon, and northern California.

Year	Early period April–June		Middle period July–August		Late period Sept.–Nov.		Annual total	
	Aged	Measured	Aged	Measured	Aged	Measured	Aged	Measured
1978	2060	31,819	2801	66,153	978	26,799	5839	124,771
1979	1072	37,678	1552	83,584	500	52,094	3124	173,356
1980	844	15,674	2927	43,038	1565	43,536	5336	102,248
1981	1287	26,961	1928	55,174	1053	53,605	4268	135,740
1982	1913	77,529	1463	66,683	882	27,604	4258	171,816
1983	1480	82,186	1277	70,499	475	14,173	3232	166,858
1984	1344	70,888	1304	108,272	662	64,524	3310	243,684
1985	200	23,329	1690	142,592	550	101,089	2440	267,010
1986	1203	125,542	1393	238,779	474	109,786	3070	474,107
1987	1021	102,191	1414	188,361	740	140,902	3175	431,454
1988	1192	125,714	1349	194,246	502	100,184	3043	420,144
Total	13,616	719,511	19,098	1,257,381	8381	734,296	41,095	2,711,188

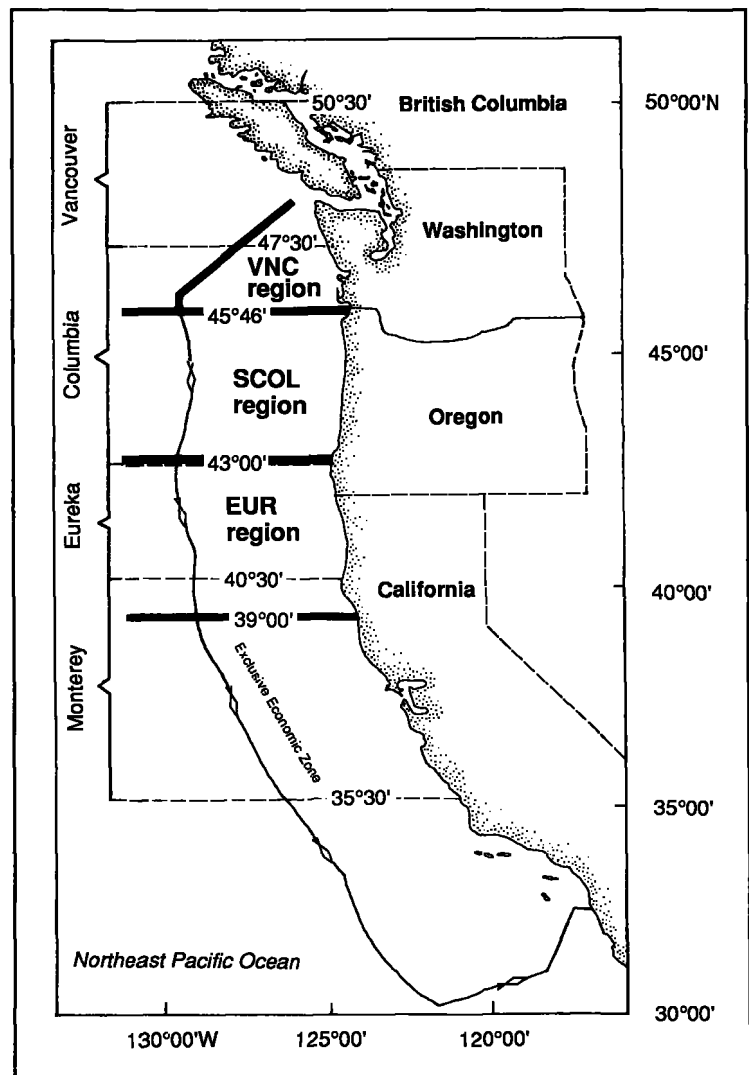


Figure 1

Spatial strata used to compile length-at-age for midwater trawl fishery samples of Pacific whiting *Merluccius productus*.

Each of these geographic regions encloses a center of Pacific whiting abundance and a concentration of fishing activity (Dorn and Methot 1990). Three time-periods were also defined as strata: (1) early (April–June), (2) middle (July–August), and (3) late (September–November). These time-periods divide the fishing season into three roughly equal parts. Over the years 1978–88, 27.9% of the catch came from the early time-period, 47.4% came from the middle time-period, and 24.7% came from the late time-period. In compiling the length-at-age estimates for the spatial and temporal strata, all data collected within that strata were aggregated and assumed to originate from random sampling of the catch within that strata.

Some of the detrimental effects of ageing error bias and low sampling intensity of uncommon age groups—common problems in analyzing fishery length-at-age data—can be reduced if the precision of the length-at-age estimates is known. A delta-method variance estimator of length-at-age for a two-phase sampling plan was derived and implemented for the U.S. fishery samples. Details of this estimator and a procedure for combining the length-at-age from different strata are described in the Appendix.

Two general methods of analyzing the growth in length of fish have been used widely in fishery research. The first method interprets individual observations of length-at-age or mean length-at-age in the population by fitting asymptotic growth curves, most typically the von Bertalanffy (or monomolecular) growth curve (Boehlert and Kappenman 1980, Kimura 1980, Shepherd and Grimes 1983). Using this technique to study environmental effects on growth on an annual scale is difficult because growth curves summarize the growth history of a year-class or a population over the lifespan of the organism. One approach to generalizing growth curves is to include seasonal environmental effects on growth. An example of this is the work of Pauly and Gaschütz (1979); they incorporated a sine wave in the von Bertalanffy growth curve to model the seasonal growth cycle.

The second common approach to analyzing growth data is analysis of variance (ANOVA). Factorial designs have been used to investigate regional growth variability (Francis 1983, Reish et al. 1985). Multiple linear regression is often used to examine the effect of the environment or population density on growth (Kreuz et al. 1982, Ross and Almeida 1986, Peterman and Bradford 1987). A factorial ANOVA of length using age, year, region, sex, and time-period as factors is reported in the Results. It should be recognized, however, that analysis of variance does not account for changes in asymptotic growth, except by fitting interaction terms that tend to obscure the analysis. It is used in this paper only as an exploratory

technique to identify the sources of variability in length.

Because asymptotic growth is a universal feature of fish growth, a model to examine the effect of the environment on growth should account for this characteristic. At the same time, such a model must be general enough to allow for covariates to influence annual growth. To meet this objective, a simple extension of the asymptotic von Bertalanffy growth model was developed. The model has a framework similar to analysis of covariance, in that it allows for the possibility of differences in growth between constituent subgroups of the population and differences in growth due to the influence of population density or environmental covariates.

The von Bertalanffy growth model for the mean length l_a of a year-class at age a is given by

$$l_a = l_\infty (1 - e^{-k(a-a_0)}),$$

where l_∞ is the asymptotic maximum length, k is a growth coefficient, and a_0 is the hypothetical age at length zero. Subtracting the length at age $a+1$ from the length at age a gives the first difference of this equation, the annual growth increment from age a to age $a+1$,

$$l_{a+1} - l_a = l_\infty (1 - e^{-k}) e^{-k(a-a_0)}.$$

Defining $g_0 = \ln[l_\infty(1 - e^{-k})]$, and $g_1 = -k$, a simple expression for annual growth is obtained:

$$l_{a+1} - l_a = \exp(g_0 + g_1(a - a_0)).$$

As might be expected, the parameter a_0 becomes redundant in this model for annual growth, since it is confounded with the parameter g_0 . One possibility is simply to drop it from the equation. Another alternative, and the one used in this analysis, is to use a_0 to scale chronological age to some initial age for which the growth model is intended to apply. In the Pacific whiting data, there are growth increments from age 1 to age 2, so a_0 is set to 1. In this parameterization, structural growth coefficients, g_0 and g_1 , describe simple elements of asymptotic growth: $\exp(g_0)$ is the annual growth increment at age a_0 , and g_1 is the exponential decline in the annual growth increment (Fig. 2).

To assess the effect of an environmental covariate, x , this model is augmented with an additional coefficient for that environmental variable,

$$l_{a+1} - l_a = \exp\left[g_0 + \sum_i g_{0i} x_i + (g_1 + \sum_j g_{1j} x_j)(a - a_0)\right] + e_{ats},$$

where $e_{ats} \sim N(0, w_{ats}\sigma^2)$. The additional subscripts in this equation are: t for year, s for sex, and i and j to index different environmental variables (e.g., x_i and x_j). The case weights, w_{ats} , are determined by the sum of the estimation variance for the two length-at-age estimates used to calculate the growth increment.

In this regression model, environmental variables can enter as either intercept or slope terms. An intercept coefficient affects g_0 and indicates a constant percent change in the growth increment regardless of age. Slope coefficients affect g_1 and provide flexibility for a varying percent change in the growth increment with age. Together these two types of coefficients, intercept and slope, cover a wide range of different ways that environmental conditions can effect growth at different ages. Note also that in this formulation, it is possible to use indicator variables to parameterize growth differences between different constituent groups of the population; for example, sex differences or geographic differences in growth. This model resembles a linear ANOVA model proposed by Weisberg (1986) to analyze back-calculated fish lengths, though he does not use von Bertalanffy growth to scale the annual growth increments.

The general procedure for fitting a nonlinear regression model in Ratkowsky (1983) was followed using the PAR algorithm in the BMDP statistical package for estimating a nonlinear regression model using weighted least-squares (Dixon 1983). Mean-square error was estimated by fitting a full model consisting of the coefficients g_0 and g_1 , and separate intercept and slope coefficients for all environmental covariates (temperature, upwelling, biomass, recruitment strength) assessed in the analysis. Mean-square error was estimated by dividing the residual sum of squares for this model by the degrees of freedom. A full model should account for all the explainable variability, so that the residual error gives an estimate of mean-square error. A P -value of <0.05 was established as the criteria for statistical significance. Because of the presence of negatively-valued growth increments due to measurement error, it was not possible to take the logarithm of the growth increment and analyze the model using linear regression.

The analysis with this model uses the change in mean length of an age-group from the early period of the fishery (April–June) of one year to the early period of the following year. Geographic strata are not used in

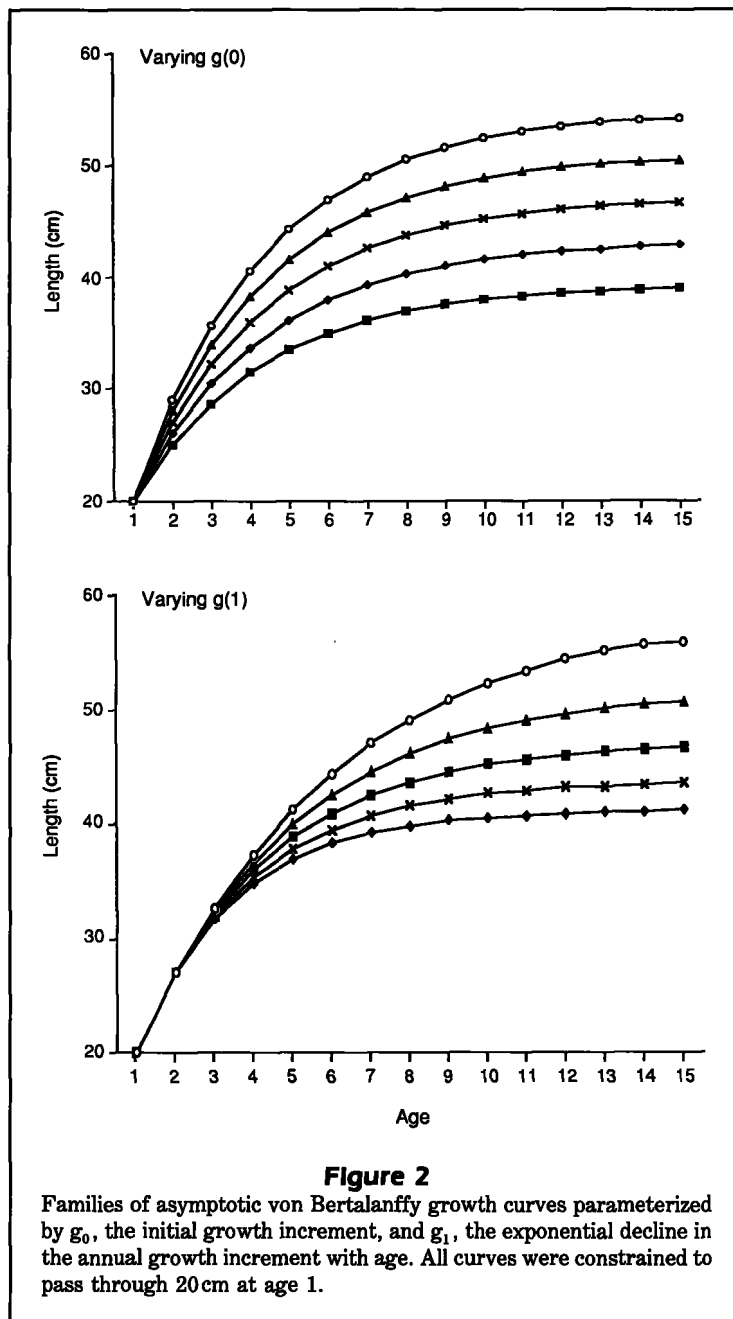


Figure 2

Families of asymptotic von Bertalanffy growth curves parameterized by g_0 , the initial growth increment, and g_1 , the exponential decline in the annual growth increment with age. All curves were constrained to pass through 20 cm at age 1.

the analysis because the migratory nature of the coastal population of Pacific whiting would make any conclusions regarding regional growth patterns impossible to defend. It is assumed that the annual increment in growth from one spring to the next is due to conditions prevalent during the summer season of active growth. Although growth increments could be studied for shorter time-periods, this was considered inappropriate for our study because of possible lags between environmental conditions and the growth response of the fish. In addition, the fishery estimates of length-at-

Table 2

Environmental and stock biomass covariates of Pacific whiting *Merluccius productus* growth, assessed using the growth-increment regression model. Mean summer (April–August) sea-surface temperature (°C) is an average over lat. 40–50°N, and from the coast, west to long. 125°W. The Bakun upwelling indices are mean summer coastal upwelling (April–August) from lat. 42–48°N. Stock biomass is measured in millions of tons of age-2 and older fish in the coastal whiting population. Anomalies of temperature, upwelling index, and biomass are calculated as the annual value minus the mean over 1978–87.

Year	Temperature ^a (°C)	Temperature anomaly	Upwelling ^b index	Upwelling anomaly	Biomass ^c	Biomass anomaly
1978	13.1	0.6	49.5	0.3	1.503	-0.268
1979	12.5	0.0	49.2	0.1	1.709	-0.062
1980	12.2	-0.3	67.1	18.0	1.640	-0.131
1981	12.5	0.0	50.0	0.9	1.384	-0.387
1982	12.1	-0.3	55.9	6.7	2.000	0.230
1983	13.4	0.9	31.5	-17.6	1.805	0.035
1984	11.9	-0.5	45.7	-3.4	1.742	-0.029
1985	12.1	-0.4	45.3	-3.8	1.685	-0.086
1986	12.6	0.1	49.6	0.5	2.225	0.455
1987	12.3	-0.2	47.6	-1.5	2.012	0.242
Average 1978–87	12.47		49.15		1.771	

^aJ.G. Norton, Pac. Fish. Environ. Group, P.O. Box 831, Monterey, CA 93942, pers. commun., Aug. 1989.

^bMason and Bakun (1986).

^cDorn and Methot (1990).

Table 3

Recruitment in billions of age-2 fish to the Pacific whiting *Merluccius productus* population for year-classes 1965–84 (modified from Dorn and Methot 1990). The recruitment anomaly is calculated as the annual number of recruits minus the average over 1965–84.

Year	Recruits	Recruit anomaly
1965	0.692	-0.331
1966	0.786	-0.237
1967	1.110	0.087
1968	0.636	-0.387
1969	0.315	-0.708
1970	3.597	2.574
1971	0.169	-0.854
1972	0.306	-0.717
1973	1.432	0.409
1974	0.139	-0.884
1975	0.220	-0.803
1976	0.094	-0.929
1977	1.716	0.693
1978	0.035	-0.988
1979	0.145	-0.878
1980	4.604	3.581
1981	0.022	-1.001
1982	0.042	-0.981
1983	0.183	-0.840
1984	4.221	3.198
Average 1965–84	1.023	

age are not point estimates in time, but averages over 2 or 3 months. As a result, relating the growth increment to the environment over a short time-period

would tend to blur environmentally-determined growth differences.

The environmental variables and stock abundance measures examined in the analysis were intentionally limited to a few variables which would characterize the environment of the population on the largest scale possible. The environmental variables are summer averages over the geographic range of the mature stock. Mean summer (April–August) sea-surface temperature (°C), provided by J.G. Norton (Pac. Fish. Environ. Group, Monterey, CA 93942, pers. commun., Aug. 1989), represents the mean value obtained from ships of opportunity between lat. 40°N and 50°N, and from the North American coast west to long. 125°W (Table 2). The Bakun upwelling indices are a mean of the monthly coastal upwelling indices during April–August from lat. 42–48°N and are in units of metric tons of water transported through the Ekman layer per second per 100 m of coastline (Mason and Bakun 1986). Stock biomass is measured in millions of tons of age-2 and older fish in the coastal whiting population, and is estimated using the stock synthesis model (Dorn and Methot 1990). The estimates of year-class strength in Table 3 come from the same source.

Results

Length analysis of variance

Annual length-at-age estimates by sex for 1978–88 were obtained using the procedures described in the

Appendix for calculating strata estimates of length-at-age, and for combining the strata estimates to produce an annual estimate (Fig. 3). The decline in length-at-age is evident in graphs of both male and female length-at-age.

The factorial analysis of mean length variance is given in Table 4. Weighted analysis of variance was used with the sampling variances as weights. The F -tests for age, year, region, sex, and time-period were all highly significant ($P < 0.0001$). Because of the large number of observations (2072), this result is not surprising. The parameter estimates in Table 4 are defined such that the intercept term represents the mean length of a 1-year-old male in the early part of the season in 1978 in the EUR region. Parameter estimates for the other factor levels can be interpreted as the difference between mean length of Pacific whiting identified by that factor level and those identified by the intercept characteristic with all other factors being held constant.

The results of the ANOVA can be summarized as follows. Length increases with age to age 10, then varies irregularly to age 15 (Table 4). Length increases 0.55 cm from the early period (April–June) to the middle period (July–August), and increases an additional 0.46 cm from the middle period to the late period (September–November). There is an increase of 1.36 cm from the EUR region in the south to the VNC region in the north, indicating that the larger Pacific whiting of an age-group migrate farther north. On average, female Pacific whiting are larger than males by 0.55 cm. Since the ANOVA model does not contain a sex-age interaction, this difference in mean length would apply to all ages. In general, these results are consistent with the previously reported findings on the growth of Pacific whiting (Dark 1975, Francis 1983). The ANOVA year coefficients show the decline in length since 1978. Mean length-at-age reached a minimum in 1984. There was a slight rebound in length-at-age from 1984 to 1986, but after 1986 length-at-age began to decline again.

Models containing interaction terms between factors

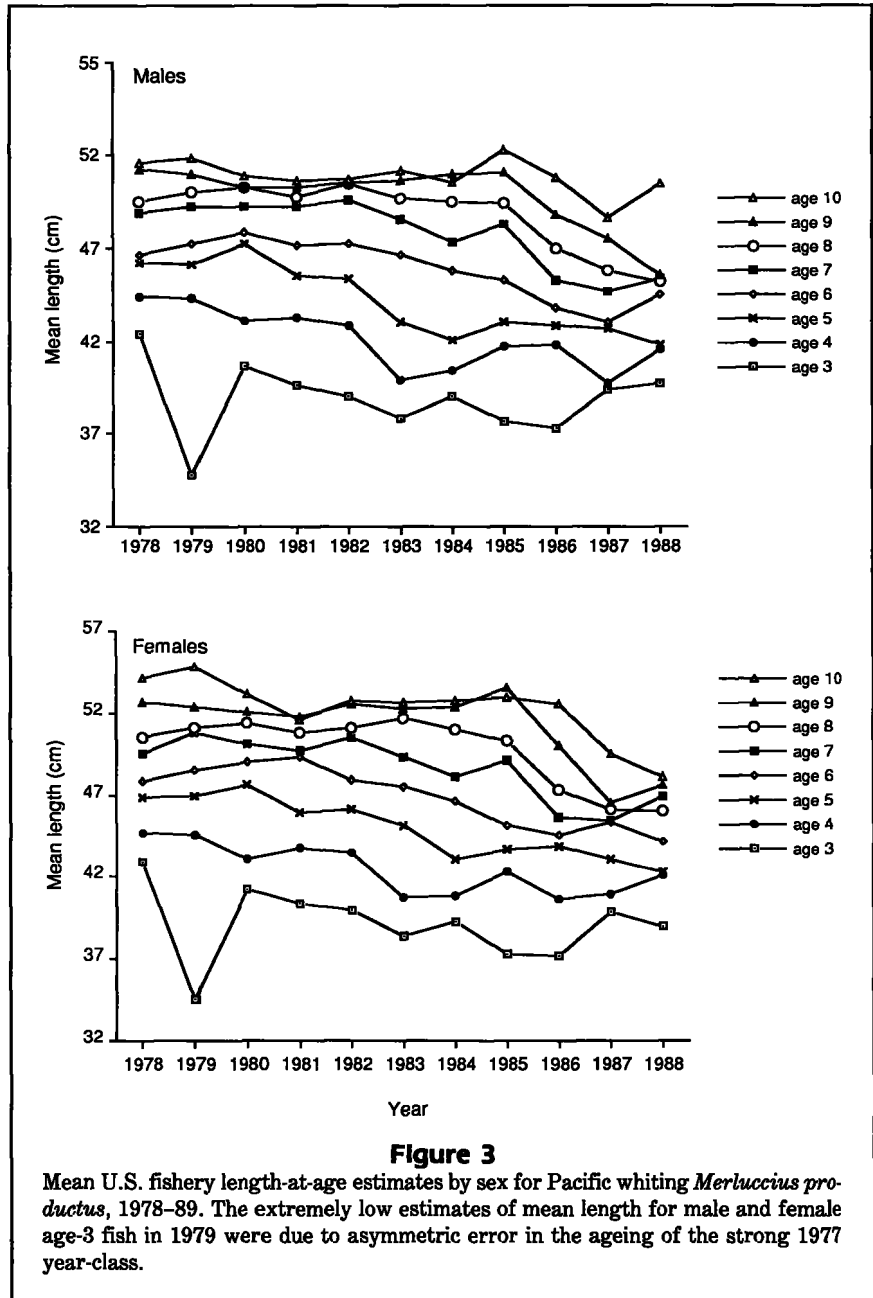


Figure 3
Mean U.S. fishery length-at-age estimates by sex for Pacific whiting *Merluccius productus*, 1978–89. The extremely low estimates of mean length for male and female age-3 fish in 1979 were due to asymmetric error in the ageing of the strong 1977 year-class.

were also analyzed. All the two-way interaction terms were statistically significant, but much less so than the main effects. The addition of more than 200 parameters to describe the two-way interactions would make interpretation difficult. Yet a model with only main effects is clearly inadequate, since it implies, for example, that both the 2-year-old and 12-year-old whiting declined in mean length by the same amount from 1983 to 1984.

Growth Increment regression

Before considering the effects of environmental co-

variates, the growth increment model was used to investigate sex differences in growth. This was done by fitting a model with only g_0 , g_1 , and indicator variables for sex. The P -value for the intercept coefficient for sex was 0.059, but the P -value for the slope term was 0.998. By the criteria established earlier, neither coefficient would be considered statistically significant, although the P -value for the intercept coefficient is close to the critical value. The estimate of the intercept coefficient for sex (0.058) indicates that the females grow approximately 6% ($e^{0.058}$) more than males on an annual basis, regardless of age. A difference of this magnitude is sufficient to account for the greater asymptotic size of the females. Figure 4 shows the fitted sex-specific curves for the annual growth increment. Despite the lack of statistical significance of the intercept term for sex, it was retained in the model while evaluating the significance of environmental covariates on growth. The larger size attained by the female Pacific whiting is compelling evidence that there are sex-specific differences in Pacific whiting growth. Including this term in the baseline model is important because it accounts for this sex-specific variability in growth.

Table 5 shows the analysis of variance using the annual growth-increment regression model. The model was built in a forward stepwise fashion, adding the environmental term to the baseline model that resulted in the largest reduction in the residual sum of squares. Temperature and population biomass were significant covariates in the model. Temperature had significant intercept ($P < 0.001$) and slope terms ($P 0.026$). For biomass, only the slope term was significant ($P 0.002$).

The parameter estimates in Table 5 indicate that a 0.5°C increase in mean summer sea-surface temperature will bring about a 24% reduction in the annual growth increment at age 1. At age 4, the same increase

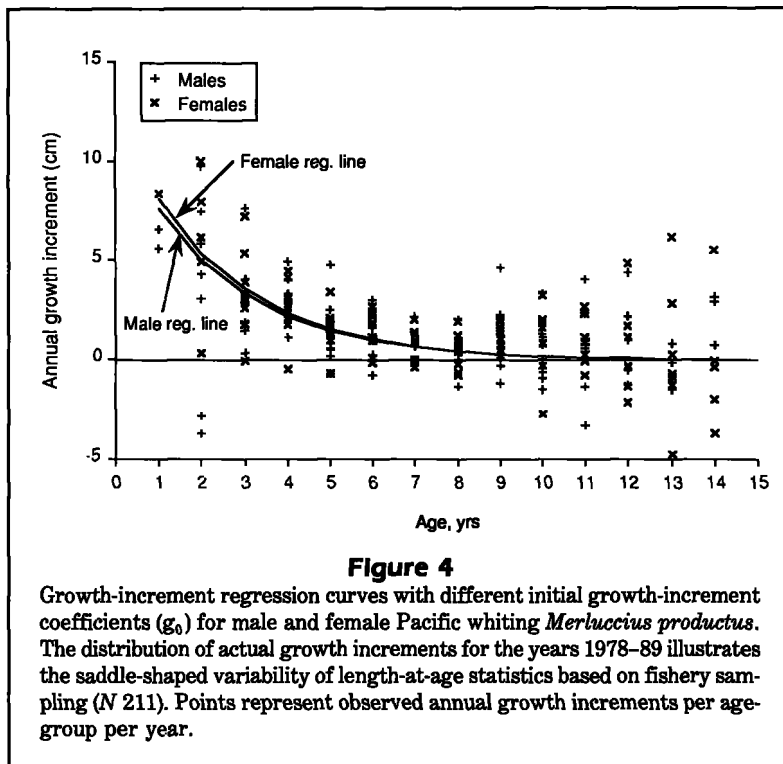
Table 4

Factorial analysis of variance of Pacific whiting *Merluccius productus* length-at-age using midwater trawl fishery samples over 1978–88. The model contains the factors age, year, geographic region, sex, and season. The intercept term estimates the mean length of a 1-year-old male in the early part of the season in 1978 in the EUR region; the other terms estimate the difference in the mean length of fish with that factor level and those with intercept characteristic.

Source	df	SS	Mean square	F-value	$P > F$
Age	14	1,112,327.5	79,452.0	3611.5	<0.001
Year	10	33,126.7	3,312.7	150.6	<0.001
Region	2	5,810.9	2,905.4	132.1	<0.001
Sex	1	2,239.2	2,239.2	101.8	<0.001
Season	2	3,531.0	1,765.5	80.3	<0.001
Error	2042	44,841.1	22.0		

Parameter	Estimate (cm)	SE of estimate
Intercept	26.88	0.211
Age:		
2	7.90	0.201
3	13.22	0.189
4	17.02	0.147
5	18.44	0.182
6	19.39	0.200
7	20.76	0.205
8	22.29	0.190
9	24.04	0.262
10	29.92	0.308
11	26.51	0.361
12	26.07	0.290
13	27.56	0.528
14	27.69	0.555
15	29.94	0.453
Year:		
1979	-0.82	0.198
1980	-0.50	0.174
1981	-1.54	0.170
1982	-2.33	0.169
1983	-3.31	0.187
1984	-4.64	0.169
1985	-3.00	0.157
1986	-2.64	0.175
1987	-3.03	0.176
1988	-4.00	0.174
Region:		
SCOL	0.57	0.071
VNC	1.36	0.089
Sex:		
Females	0.55	0.052
Season:		
Middle	0.53	0.065
Late	0.99	0.079

in temperature would be expected to produce a 12% reduction in annual growth, and by age 7, the percent reduction would be close to zero. The model predicts an increase in growth due to increasing temperature above age 7, but as annual growth is very slight by this age, the consequences of this prediction are not important. One concern about the reliability of these results is that they may be overdependent on growth during the 1983 El Niño, when sea-surface temperature was the highest during the study. To investigate this possibility, a model was fit to the data excluding the

**Table 5**

Analysis of variance of annual length increments using the nonlinear regression model. The coefficient g_0 is an intercept term: $\exp(g_0)$ estimates the growth increment from age 1 to age 2. The coefficient g_1 determines the slope of the exponential decline of the annual growth increment with age under average environmental conditions. Terms relating to covariates are identified as either intercept terms (g_0) or as slope terms (g_1).

Source	df	SS	Mean square	F-value	P>F
g_1	1	4067.8	4067.8	1166.5	<0.001
g_0 (sex)	1	12.6	12.6	3.6	0.059
g_0 (temp.)	1	93.5	93.5	26.8	<0.001
g_1 (biomass)	1	36.3	36.3	10.4	0.002
g_1 (temp.)	1	17.4	17.4	5.0	0.026
Error	204	711.4	3.5		

Parameter	Estimate	SE of estimate
g_0	1.995	0.038
g_1	-0.383	0.015
g_0 (sex)	0.058	0.029
g_0 (temp.)	-0.544	0.098
g_1 (biomass)	-0.086	0.027
g_1 (temp.)	0.099	0.043

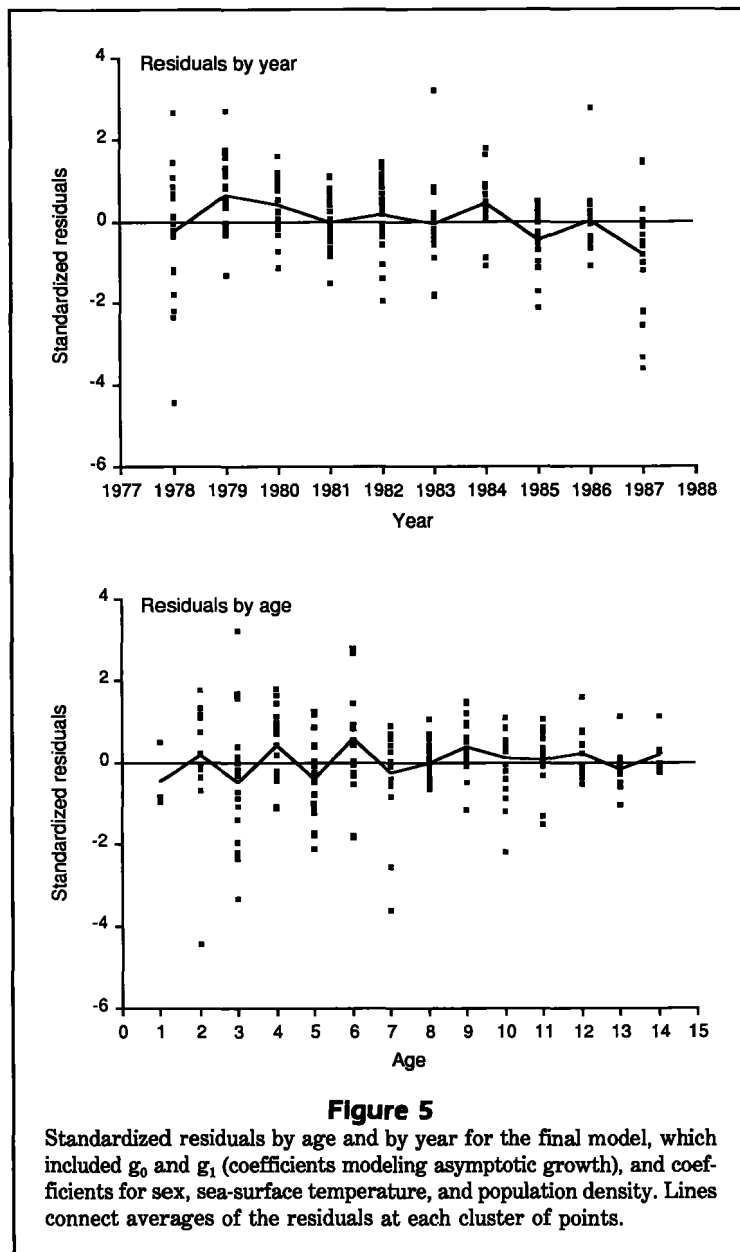
growth increments from 1983. The parameter estimates followed the same trend as the results in Table 5, with increases in sea-surface temperature associated with large reductions in growth of younger fish, and a decreasing percent reduction with age.

For population biomass, an increase of 200,000t

(~10% of the mean population biomass) would cause a 5% reduction in annual growth at age 4, and the percent reduction would increase with age, reaching a 10% reduction at age 7. Because the intercept term for biomass was not significant, growth of the age-1 fish would not be affected by changes in population biomass. During the 10 years studied, range in adult biomass was from 26% above to 22% below the mean of 1.771 million t (1978–87). This lack of contrast in adult biomass makes any interpretation very tentative, but the results do suggest that the effect of population density on growth is relatively small in comparison with the effect of temperature.

None of the other environmental covariates or measures of population density tested in the model were significant. The coefficient for upwelling was highly significant in a model without temperature, but when temperature was included in the regression, upwelling was no longer significant. Because water temperature and the upwelling index are statistically correlated off the coast of Oregon (Kruse and Huyer 1983), the parallel effects of temperature and upwelling index are not unexpected. The same parallel effect was found between year-class abundance and adult biomass. However, adult biomass accounted for more of the variability in annual growth than did year-class abundance. This suggests that the crowding that occurs when a strong year-class recruits to the population is experienced by all the adults, and not just the individuals which make up the strong year-class.

Figure 5 shows the standardized residuals from the final model, plotted against age and year. No trends are evident with respect to age. This plot also shows that the use of the estimation variances as weighting terms in the least-squares fit was successful in stabilizing the error variance with respect to age. However, there still is a noticeable trend in the standardized residuals by year, with positive residuals associated with the earlier years in the time-series (1979 and 1980), and negative residuals with the later years (1985 and 1987). This indicates that the environmental covariates examined thus far are not completely successful in accounting for the decline in mean length-at-age over the past decade.



Discussion

Although density-dependent growth has been demonstrated for many fishes (Shepherd and Grimes 1983, Reish et al. 1985, Ware 1985, Ross and Almeida 1986, Peterman and Bradford 1987, Overholtz 1989), few researchers would argue that density-dependent growth is an important characteristic of all fish populations. The age-structured yield models first developed by Beverton and Holt (1957)—currently used to manage many temperate marine fish stocks—use a fixed schedule of weight-at-age to calculate the yield, regardless of the level of population abundance. For a

stock of Atlantic mackerel, however, the historically observed variation in weight-at-age attributable to density-dependent growth had a significant effect on the projected yields from the fishery (Overholtz et al. 1991). For Pacific whiting, this potential for changes in weight-at-age to influence yield is taken into account by using the weight-at-age observed in recent years to project the yield for the upcoming year (Dorn and Methot 1990). To obtain a fishing mortality rate that gives the long-term sustainable yield, the average weight-at-age over the history of the fishery is used. This strategy tacitly assumes that the current decline in weight-at-age is not a permanent change in the population.

Parrish et al. (1981) state that the principal resident species of the California Current system do not exhibit density-dependent growth. They contend that the population size of these species is controlled by environmental variability during the larval stages. As a result, the adults are seldom plentiful enough to reach a food-limited carrying capacity.

A contrasting viewpoint is found in Boehlert et al. (1989) who present evidence that the large biomass removals of *Sebastes* spp. in the years 1966–70 off the west coast of the United States resulted in increases in the annual growth of two members of this genus: canary rockfish *S. pinniger* and splitnose rockfish *S. diploproa*. They maintain that the decline in the total abundance of *Sebastes* spp. has had an effect on food availability for individual rockfish species. Although euphausiids are shared by most *Sebastes* species as the principal prey (Brodeur and Percy 1984), they are also a major link in the food chain of the California Current ecosystem, supporting numerous fish and invertebrate populations. For this reason, it is unlikely that changes in the abundance of *Sebastes* spp. alone could have had a substan-

tial impact on the overall abundance of euphausiids in the California Current ecosystem. However, since rockfish are spatially restricted to habitats with limited area, the density-dependent growth displayed by *S. pinniger* and *S. diploproa* may be due to density-dependent changes in the food availability within these habitats. The possibility that cropping by Pacific whiting and other species significantly affects the abundance of euphausiids in the California Current ecosystem at large has not yet been adequately tested, though Mullin and Conversi (1989) were unable to detect any change in the abundance of euphausiids in the California current system after the start of the

large-scale fishery for Pacific whiting *Merluccius productus* in 1966.

Environmental influence on growth has been observed for many marine fish species (Kreuz et al. 1982, Anthony and Fogarty 1985). Because it can be easily measured and is associated with widespread changes in the aquatic environment, water temperature is the covariate most often studied. Water temperature may have a direct physiological effect on the growth of fish, or it may be indirectly linked to growth. For example, decreases in water temperature occur with the onset of upwelling in many coastal marine environments. On the west coast of North America, the availability of coastal upwelling indices on monthly, weekly, and daily time scales (Mason and Bakun 1986) has made it possible to investigate the direct effect of upwelling on growth, although convincing evidence of a link has not yet been found (Kreuz et al. 1982, Francis 1983, Boehlert et al. 1989).

Results from the Pacific whiting growth-increment regression show that an environmental covariate, sea-surface temperature, and population density could explain the deviations from a simple baseline model for asymptotic growth. The effect of temperature was greatest on the youngest ages present in the fishery samples and declined as age increased. In contrast, the effect of population biomass on annual growth increased with age. Temperature was the most important covariate, both in terms of its statistical significance and its effect on growth. This association of enhanced growth and reduced sea temperature is consistent with what is known about the California Current, a major eastern boundary current system. Kreuz et al. (1982) found an identical inverse effect on the growth of English sole *Parophrys vetulus* and Dover sole *Microstomus pacificus* at two locations off the Oregon coast.

Two mechanisms are believed to contribute to the high productivity of the California Current system. Coastal upwelling, generated by wind-driven offshore transport in the surface Ekman layer, brings low temperature, low salinity, and nutrient-rich water to the surface (Bakun and Nelson 1977). A second mechanism is the southward advection of water from the Alaskan Subarctic Gyre. This water is characterized by low temperatures, high nutrient content, and a large standing stock of zooplankton (Roesler and Chelton 1987). Regardless of which mechanism is dominant during a particular year, low mean sea-surface temperature during the summer can be expected to be associated with high productivity.

The diet of Pacific whiting provides the link between primary productivity and growth. The major prey of Pacific whiting are euphausiids, primarily *Thysanoessa spinifera* and *Euphausia pacifica* (Livingston 1983,

Rexstad and Pikitch 1986). In summer, the abundance and pattern of distribution of these short-lived species (1–2 yr) are closely tied to upwelling and primary productivity (Simard and Mackas 1989). Rexstad and Pikitch (1986) found that euphausiids comprised 90% by weight of the diet of Pacific whiting 30–44 cm in length collected during a trawl survey in 1983 off the coasts of Oregon and Washington. Above 45 cm, a length which corresponds approximately to ages 5–7, this percentage drops to 20%. In the diet of the older Pacific whiting, euphausiids are largely replaced by small schooling fish and shrimp. These include northern anchovy *Engraulis mordax*, Pacific herring *Clupea harengus pallasi*, eulachon *Thaleichthys pacificus*, pink shrimp *Pandalus jordani*, and rockfish *Sebastes* spp. (Livingston 1983).

This shift in dietary preferences by Pacific whiting may help explain the effect of population biomass on growth. When the biomass of Pacific whiting is high, predation on fish species with multiyear life cycles may become intense enough to reduce their availability to the whiting population. In contrast, euphausiid abundance is closely coupled to annual variations in productivity, so whiting predation would likely have little effect on their abundance.

Some supporting evidence for density-dependent growth of Pacific whiting is found in Dark (1975), who also documented a decline in length-at-age using fishery samples from an earlier period in the fishery, 1964–69. At the time of Dark's research, estimates of population abundance were not available for Pacific whiting. It is now believed that the 1961 year-class was exceptionally strong, nearly the same size as the record 1980 year-class (Dorn and Methot 1990). Consequently, this earlier decline in length-at-age may also be partly attributable to increases in population density as the 1961 year-class moved into the population.

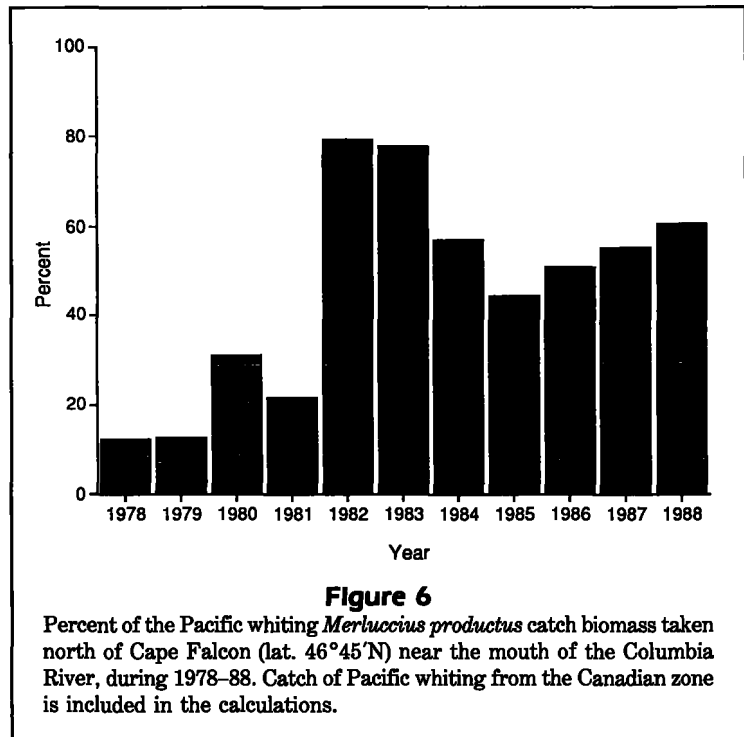
Although weight-at-age is the measure of size typically used in stock assessment models, the analysis in this paper focuses on length rather than weight. A practical reason for this strategy is that most at-sea sampling platforms are not sufficiently stable to obtain accurate individual weights of fish. Indeed, the weights-at-age used in stock assessment models for Pacific whiting are obtained by first estimating length-at-age, then converting to weight using a length-weight relationship (Dorn and Methot 1990). In addition, growth in length has several characteristics that make it amenable for analytical modeling. Except in very rare instances, changes in fish length are always positive or zero. The annual growth increment in length summarizes the growth response of the organism to environmental conditions that are prevalent throughout the year, or are short-term. In contrast, weight-at-age has a seasonal pattern of increase and decline, associated

with spawning, migration, and feeding, which would have to be accounted for in a model before analyzing environmental influences on growth.

Underlying this seasonal pattern of variation in weight is the length-weight relationship characteristic to a species, determined by the overall shape of the fish. Extreme departures from the typical length-weight relationship are unlikely to persist. Fish that are heavy in relation to their length in one year would tend to grow faster in length than average, while underweight fish would tend to experience slower growth in length. Adjustments to an individual's annual reproductive effort can also dampen departures from the typical length-weight relationship (Tyler and Dunn 1976).

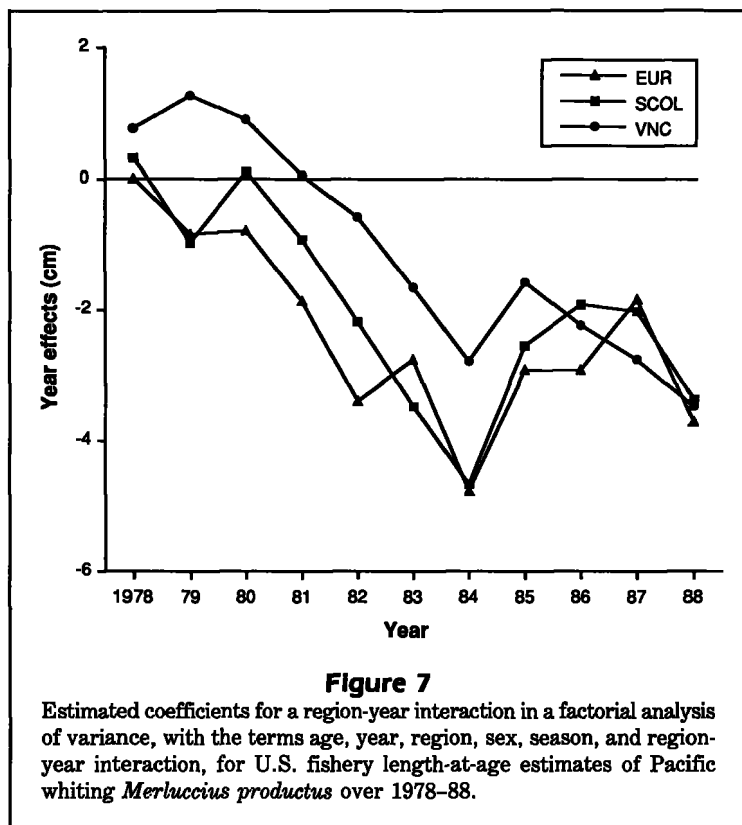
During the period covered by this analysis, the length-weight relationship of Pacific whiting has varied from year to year, most noticeably in 1983, when mean weight was extremely low at a given length (Dorn and Methot 1990). The link between anomalies in the length-weight relationship and annual growth increments is best demonstrated by the results of a trial model that used the anomaly in the estimated weight at 45 cm from the annual length-weight regression (Dorn and Methot 1990) as the only predictor variable for the annual growth increment. This variable was highly significant in the model ($P < 0.001$), indicating that the annual growth increment is low during years where the length-weight relationship is below average. This result also supports the hypothesis that variation in Pacific whiting length-at-age is caused by environmental processes that affect the availability of food.

The analysis presented in this paper is based exclusively on fishery data. It should be acknowledged that there are numerous problems associated with the use of fishery statistics to infer growth patterns of fish within a population. Incomplete, size-dependent recruitment to a fishery can make fishery data on length-at-age a biased estimate of population length-at-age. Ageing error can distort the estimates of length-at-age when the year-classes have large differences in abundance. Shifts in the geographic and temporal pattern of the fishery, or shifts in the geographic distribution of the population itself, can cause spurious changes in estimates of length-at-age. The lengths for less abundant age-groups are not estimated as precisely as those for abundant age-groups. This is particularly true of extremely young and old fish, as these age-groups may be represented in fishery samples by only one or two individuals which determine the mean length for that age-group.



The severity of some of these problems can be reduced by using the procedures described in the Appendix for compiling strata estimates of length-at-age and calculating variance estimates. Length-at-age for temporal and geographic strata can be examined separately before being combined to produce annual summary statistics. Length-at-age estimates based on only a few individuals can be discounted in the analysis by using the estimated variances of length-at-age as weights. Nevertheless, some factors affecting growth can only be addressed by modeling fisheries as both a source of information on the stock and a major influence on its dynamics. The growth-increment regression model used in this paper assumes that the fishery samples the population without bias, so it is not the appropriate framework for studying these processes. Models with size-selective fishing mortality and stochastic growth have been developed for exploited fish populations (Deriso and Parma 1988, Parma and Deriso 1990). The practical application of these models is limited by the difficulty of distinguishing between different sources of growth variability using only catch data.

Size-selective mortality may have played a role in causing variation in length-at-age of Pacific whiting over the years covered by this analysis. Since the length ANOVA found a significant increase in length from south to north, a northward shift in the fishery would tend to increase length-at-age in the catch. At the same time, however, the length-at-age of the survivors of the



fishery would decrease, and this would tend to decrease the length-at-age in the catch in the following year from what it would have been otherwise. From 1978 to 1982, the fraction of the Pacific whiting catch taken north of Cape Falcon (near the mouth of the Columbia River at lat. $46^{\circ}45'N$) increased from 10% to 80%, and was 60% in 1988 (Fig. 6). The lack of fit of the growth-increment regression model with respect to year in Figure 5 may have been a result of this northward shift in fishing mortality.

However, it is difficult to predict the long-term effects of a shift in the geographic pattern of exploitation on length-at-age, because little is known about the extent of mixing from one year to the next of fish migrating from different regions. Without mixing between regions, an increase in fishing in the northern part of the range would reduce the abundance of larger individuals of an age-group, reducing the overall population length-at-age, while length-at-age of the southern fish would be unaffected. A more likely hypothesis is that some inter-regional mixing occurs from year to year. In this case, the length-at-age in all regions would decrease, though the magnitude of the decrease should be greatest in the north where the higher fishing occurred. Ultimately, this would tend to reduce latitudinal variation in length-at-age.

To support this hypothesis, there is some evidence of a change in the degree of latitudinal segregation by size of Pacific whiting. Figure 7 shows the coefficients for a region-year interaction for a length ANOVA with main effects being age, year, region, sex, and season. The absence of interaction between year and region would be identified by parallel year effect lines for each region, and would indicate that size-specific migratory pattern has remained constant. From 1978 to 1985, the region-year interaction does not appear prominent. After 1985, however, the lengths-at-age in the three regions become much closer together; in particular, the lengths of the fish in the VNC region, instead of being 1-2 cm larger than the fish in the other regions, are the same size or smaller.

Recently, Smith et al. (1990) examined the length-at-age data from the fishery for Pacific whiting in the Canadian waters over the same years examined by this paper. They used a generalized form of the von Bertalanffy growth model that makes length-at-age a function of length-at-age in the previous year, plus environmental covariates modeled in different ways according to a hypothesized mechanism by which the environmental covariate affects growth or apparent growth. Significant covariates in their model were population biomass, a suite of oceanographic variables measuring the strength of southward advection of water from the Alaskan Subarctic Gyre, and several variables that model size-selective mortality. Since fish younger than age 5 are not common in the Canadian samples, their analysis could not examine the sources of growth variability of the younger fish. Consequently, the analysis presented here on the environmental covariates of Pacific whiting growth in U.S. waters is a necessary complement to the paper by Smith et al. (1990). For example, an inverse relationship between temperature and growth, which is most pronounced for the younger fish, was not detected by Smith et al. (1990), and can partly account for the fact that the fish currently recruiting to Canadian waters at age 5 are much smaller than those recruiting in the late 1970's.

A major contention of Smith et al. (1990) is that expansion of the Canadian fishery is largely responsible for the decline in length-at-age observed since 1976. They used the ratio of the Canadian catch (in biomass) to the total population biomass during the current year as a covariate in their nonlinear regression model, a phenomenological approach that sidesteps the need to model the population dynamics. Although the monotonically increasing Canadian catch of Pacific whiting

since 1976 (except for 1985) and the declining length-at-age over the same period guarantees a statistically significant result, the real role of the Canadian fishery in determining length-at-age can be established only in a wider context that considers the magnitude and the geographic pattern of the fishery for Pacific whiting in U.S. waters. The region-year interaction coefficients in Figure 7 show that, up until 1984, the severity of the decline in length-at-age was similar in all three geographic regions in U.S. waters, extending from California north to the U.S.-Canada border. This is difficult to reconcile with the contention that the Canadian fishery is primarily responsible for the decline in length-at-age.

Both Smith et al. (1990) and this study used growth models that do not take into account the dynamics of the population, and as a consequence both have shortcomings which limit the growth-related phenomena to which they can be applied. An important direction for further research is the development of models for Pacific whiting that simultaneously model the growth and the population dynamics of the stock, including size-specific migratory behavior.

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Appendix: Variance estimates of mean length-at-age using a two-phase sampling procedure

The length and age samples collected by observers in the Pacific whiting fishery are recorded by haul or joint-venture delivery. The position and date of each sampled haul and joint-venture delivery are also recorded. In compiling the length-at-age estimates for spatial and temporal strata, all the data collected within that strata are aggregated and assumed to originate from random sampling from the catch within that strata.

Sampling design

A large initial random sample is obtained from the catch, and the length and sex of each fish is recorded. For the second phase of sampling, a subsample of fixed size is selected for each combination of length category and sex. All fish in these subsamples are aged using otoliths or other ageing structures.

Notation

- $i = 1, \dots, I$ length categories
 $j = 1, \dots, J$ age categories
 n' = first-phase sample size
 n'_i = number of fish of n' in length category i
 q_i = probability that a fish is in length category i
 n_i = subsample sizes
 n_{ij} = number of the subsample taken from length category i of age j
 q'_{ij} = $\text{pr}(j|i)$, probability of age j given length i
 q_{ij} = $\text{pr}(i|j)$, probability of length category i given age j
 p_j = $\text{pr}(j)$, probability of age j
 l_i = midpoint of i th length category
 \bar{l}_j = mean length of age j fish

To simplify notation, subscripts for males and females are not defined. The variance estimator obtained here is conditional on the first- and second-phase sample sizes. Separate estimates for males and females can be obtained by separating the samples by sex and conditioning on the number of each sex in the first- and second-phase samples. The same variance estimator is appropriate for separate sex estimates.

Sampling distributions

Assuming that the first-phase sample size n' is much smaller than the size of the population being sampled, the distribution of n'_i can be modeled by the multinomial distribution,

$$f(\{n'_i\} | n', \{q_i\}) = \left(\frac{n'!}{\prod_i n'_i!} \right) \prod_i q_i^{n'_i},$$

where $\sum_i q_i = 1$. Estimators for $\{q_i\}$ and the elements of the variance-covariance matrix of $\{q_i\}$ are

$$\hat{q}_i = \frac{n'_i}{n'},$$

$$\text{V\`ar}(\hat{q}_i) = \frac{\hat{q}_i(1-\hat{q}_i)}{n'},$$

$$\text{C\`ov}(\hat{q}_i, \hat{q}_h) = -\frac{\hat{q}_i \hat{q}_h}{n'}.$$

To obtain a distribution for $\{n_{ij}\}$, it is convenient to condition on the fixed subsamples n_i . As in the case of the first phase of sampling, it is assumed that n_i is much less than the number in the population of that length category, so that a product of multinomial distributions is obtained for the second phase of sampling,

$$f(\{n_{ij}\} | \{n_i\}, \{q'_{ij}\}) = \prod_i \left[\left(\frac{n_i!}{\prod_j n_{ij}!} \right) \prod_j q'_{ij}{}^{n_{ij}} \right],$$

where $\sum_j q'_{ij} = 1$ for all i . Estimators for $\{q'_{ij}\}$ and the elements of the variance-covariance matrix of $\{q'_{ij}\}$ are

$$\hat{q}'_{ij} = \frac{n_{ij}}{n_i},$$

$$\text{V\`ar}(\hat{q}'_{ij}) = \frac{\hat{q}'_{ij}(1-\hat{q}'_{ij})}{n_i},$$

$$\text{C\`ov}(\hat{q}'_{ij}, \hat{q}'_{hk}) = -\frac{\hat{q}'_{ij} \hat{q}'_{hk}}{n_i},$$

for $i=h$ and zero otherwise.

A troublesome inconsistency with this approach is that the n_i are assumed to be predetermined quantities. In fact, n_i is necessarily less than or equal to n'_i , the number in the i th length category from the first-phase sampling, and n'_i is a random variable that can take values between zero and the $\min(n', N_i)$ where N_i is the number of fish of length category i in the total catch. Singh and Singh (1965) address this issue while developing variance estimators for what in this fisheries application would correspond to mean age.

While they were able to obtain estimators which correctly modeled the sampling procedures, they also found that their exercise in theoretical rigor did not result in any appreciable difference in practice.

Estimation of mean length-at-age

An unbiased estimate of \bar{l}_j is given by

$$\bar{l}_j = \sum_i l_i q_{ij},$$

where q_{ij} is the probability of length i given age j . An expression for q_{ij} is obtained using Bayes theorem,

$$q_{ij} = \frac{q_i q'_{ij}}{\sum_i q_i q'_{ij}}.$$

A variance approximation for mean length-at-age

Because the above expression for mean length-at-age is nonlinear in the observations $\{n'_i\}$ and $\{n_{ij}\}$, a delta-method approximation is derived. Delta-method estimators can be algebraically complex but all have the same simple structure. For mean length-at-age, a delta-method approximation is given by

$$\text{Var}(\bar{l}_j) \approx \mathbf{d}_j^T \mathbf{V} \mathbf{d}_j,$$

where \mathbf{d}_j is the vector of partial derivatives of \bar{l}_j with respect to $\{q_i\}$ and $\{q'_{ij}\}$, and \mathbf{V} is the variance-covariance matrix of $\{q_i\}$ and $\{q'_{ij}\}$. Defining

$$A_j = \sum_i l_i \hat{q}_i \hat{q}'_{ij},$$

and

$$\hat{p}_j = \sum_i \hat{q}_i \hat{q}'_{ij},$$

the elements of the vector of partial derivatives are given by

$$\frac{\partial \bar{l}_j}{\partial q_i} = \frac{\hat{q}'_{ij}(l_i \hat{p}_j - A_j)}{\hat{p}_j^2}$$

and

$$\frac{\partial \bar{l}_j}{\partial q'_{ij}} = \frac{\hat{q}_i(l_i \hat{p}_j - A_j)}{\hat{p}_j^2}.$$

Combining these expressions with the estimators for the variance-covariance matrix of q_i and q'_{ij} given earlier,

$$\text{Var}(\bar{l}_j) = \left[\frac{1}{\hat{p}_j} \right]^4 \left\{ \sum_i (l_i \hat{p}_j - A_j)^2 \left(\frac{\hat{q}_i(1-\hat{q}_i)\hat{q}'_{ij}{}^2}{n'} + \frac{\hat{q}'_{ij}(1-\hat{q}'_{ij})\hat{q}_i{}^2}{n_i} \right) - \sum_{i \neq h} \hat{q}_i \hat{q}_h \hat{q}'_{ij} \hat{q}'_{hj} (l_i \hat{p}_j - A_j) \frac{(l_h \hat{p}_j - A_j)}{n'} \right\}.$$

Combining length-at-age from different strata

An estimate of combined mean length-at-age is

$$\bar{l}_j = \sum_h \left(\frac{c_{jh}}{c_j} \right) \bar{l}_{jh},$$

where l_{jh} is the length-at-age in the h th stratum, and c_{jh} is the catch-at-age for the same stratum.

Again using a delta-method approximation,

$$\text{Var}(\bar{l}_j) = \sum_h \text{Var}(c_{jh}) \left[\frac{(\bar{l}_{jh} c_j - \sum_h c_{jh} \bar{l}_{jh})}{c_j^2} \right]^2 + \sum_h \text{Var}(\bar{l}_{jh}) \left[\frac{c_{jh}}{c_j} \right]^2.$$

The complete expression should include a term involving $\text{Cov}(c_{jh}, \bar{l}_{jh})$. This term was always negligible compared with the other two terms, and depended on the method used to calculate the catch-at-age. Consequently, it is not included here. The variance estimator for combined length-at-age for several strata requires an estimate of the variance of catch-at-age. A method for obtaining this is given in Kimura (1989).