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in Growth of
Walleye Pollock *Theragra Chalcogramma*
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Aleutian Basin with
Implications for Management**

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Regional and Temporal Differences in Growth of Walleye Pollock
(Theragra chalcogramma) in the Eastern Bering Sea and Aleutian
Basin with Implications for Management

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ABSTRACT

Regional and temporal growth patterns of walleye pollock (Theragra chalcogramma) in the eastern Bering Sea and Aleutian Basin were examined. Evidence of discrete stocks, or production units, was sought based on a statistical analysis of length-at-age data from the commercial fishery and resource surveys. Results indicate that there are two distinct production units of eastern Bering Sea walleye pollock; a slow growing unit inhabiting the Aleutian Basin and the continental slope and shelf north of the Pribilof Islands, and a fast growing unit occupying the continental slope and shelf south of the Pribilof Islands. Indirect evidence is given for a linkage between pollock of the Aleutian Basin and eastern Bering Sea continental slope and shelf.

INTRODUCTION

With an annual harvest of five to six million metric tons (t), walleye pollock (Theragra chalcogramma) (Fig. 1) is one of the world's largest single species fisheries. In the eastern Bering Sea alone, the average annual catch of pollock from 1970 to 1980 was 1.3

million t, accounting for about 90% of the catch of all fish and shellfish species (Wespestad and Terry 1984). Although there has been a steady gradual decline in the catches of eastern Bering Sea walleye pollock since the early 1970's, catch per unit effort indices indicate a significant decline in abundance beginning in the 1970's and reaching a 13-yr low in 1980 (Bakkala et al. 1985). This necessitates an examination of the relative roles of fisheries and biological and environmental conditions as factors in the apparent population decline. As a component of this analysis, the primary purpose of this paper is to examine evidence for discrete stocks, or production units, of walleye pollock in the eastern Bering Sea based on a statistical analysis of length-at-age data from the commercial fishery and resource surveys. A secondary objective is to hypothesize how oceanographic conditions may influence the distribution of eastern Bering Sea walleye pollock and to evaluate what role these conditions may play in stock mixing.

Eastern Bering Sea walleye pollock is currently managed as a single panmictic stock (Smith 1981, Bakkala et al. 1981) based largely on evidence from a cohort analysis (Chang 1974) and from studies of biochemical genetic variations (Grant and Utter 1980). Recent evaluation of Chang's analysis indicates that it was invalid since a single age-length key was used for all years, excluding the possibility of detecting variations in interannual and regional growth. Results of the genetic analysis are difficult to interpret because the samples were not all collected at the same time. On the other side of this argument, at least one study (Maeda 1972) has indicated distinct stocks of walleye pollock in the

1972) has indicated distinct stocks of walleye pollock in the eastern Bering Sea, and several others (Serobaba 1977, Yamaguchi and Takahashi 1972) have noted that concentrations of walleye pollock in different regions of the eastern Bering Sea have different morphological characteristics.

Morphological and life history differences between intraspecific populations of fish may represent only phenotypic expression of environmental differences, not necessarily indicating the existence of genetically isolated stocks. However, for fisheries management purposes, a stock should be defined as a group of fish behaving as a cohesive unit responding similarly to environmental conditions within its geographic boundary (Casselman et al. 1981). This definition includes, but is not restricted to, population units that are reproductively isolated. Distributional patterns, population parameters and morphological characteristics are sometimes relied on to distinguish stocks (Messieh and Tibbo 1971; Casselman et al. 1981; Colby and Nepsty 1981). At the level of practical fisheries management, population parameters are most useful for recognition of stocks (Ibssen et al. 1981) which may represent discrete "production units" (Larkin 1972). These population parameters include growth, mortality, and spatial and temporal characteristics of spawning. As these same parameters determine the yield of a stock to a fishery, the identity of different stocks or production units based on some or all of them is essential to successful fisheries management.

METHODS

Otoliths were collected from walleye pollock by U.S. observers aboard foreign commercial fishing vessels (Nelson et al. 1984) from 1976 through 1983, and by biologists during annual surveys conducted by the National Marine Fisheries Service during the summers of 1979-83. Otoliths were also collected aboard cooperative U.S.-Japan research surveys during 1981 and 1982. For the majority of hauls, a stratified random sample (usually 10 fish per centimeter of length interval) was chosen from the total catch. All otoliths were examined and aged at facilities of the National Marine Fisheries Service's Northwest and Alaska Fisheries Center in Seattle. Each otolith had associated with it the sex, total length, and wet weight of the animal as well as the haul location, depth of tow, vessel type, and total catch. Length frequencies from a random sample of the catch were also recorded by sex for each haul.

Haul locations were then classified into one of five regions within the eastern Bering Sea and Aleutian Basin (Fig. 2). These regions correspond with the middle shelf, outer shelf, and oceanic hydrographic domains of Schumacher (1984), with an additional north-south differentiation at a line from the Pribilof Islands to Cape Avinof. Due to the broad middle shelf frontal zone and an expected north-south gradient in water properties, we defined buffer zones to more clearly differentiate between regions. Any samples collected from these buffer zones were excluded from our analysis. Estimates of the mean and variance of the lengths at each age were then calculated separately for each year, region,

sex, and quarterly period. Stratified samples can result in biased age-length keys (Kimura 1977). To compensate, the number of observations per length strata was weighted by that strata's relative proportion of the catch (derived from random length frequency samples) before calculating the age length key. Mean lengths-at-age and associated variances were then calculated for each sex, region, year, and quarter. Since the variances of the mean length-at-age estimates were not homogeneous, we assigned weights to each estimate (i) as:

$$w_i = n_i/s_i$$

where n_i = the number of observations in the ith estimate

s_i = the variance of the estimate,

as suggested by Kimura (1979) in order to perform weighted least squares fits of various growth models.

To test for differences in growth between regions different versions of the von Bertalanffy (1938) growth model were fit to the mean length-at-age data:

Model IA. Single growth curve describing all regions

$$l_t = L_\infty (1 - e^{-k(t-t_0)}),$$

where: t = age in fractional years, as measured from the midpoint of each quarterly interval, i.e., age 4 in quarter 2 = 4.375,

L_{∞} = asymptotic maximum length,

k = von Bertalanffy growth coefficient,

t_0 = theoretical age at which length is 0, and

l_t = predicted length of age t fish.

Model IB. Region specific L_{∞} , k and t_0

$$l_{t_i} = L_{\infty} (1 - e^{-k_i(t-t_{0_i})}),$$

where: subscript i denotes the i th region.

If model IB was not rejected, the following three models were fit to test for the presence of regional differences in each of the von Bertalanffy parameters.

Model IC. Region specific L_{∞} and t_0 , common k

$$l_{t_i} = L_{\infty} (1 - e^{-k(t-t_{0_i})}).$$

Model ID. Region specific k and t_0 , common L_{∞}

$$l_{t_i} = L_{\infty} (1 - e^{-k_i(t-t_0)}).$$

Model IE. Region specific L_{∞} and k , common t_0

$$l_{t_i} = L_{\infty} (1 - e^{-k_i(t-t_0)}).$$

All models were fit using the AR derivative-free nonlinear least squares estimation procedure of the BMDP statistical package. (Dixon 1983). Since previous studies have shown differences in

length-at-age due to sexual dimorphism (Bakkala and Smith 1978), separate curves were fit for male and female pollock. The subscript for sex is implicit in the above models. Residual sum of squares, degrees of freedom, and parameter estimates were recorded for each sex and model. Since no samples were taken from the north shelf or Aleutian Basin during quarter 4, only data from quarters 1 through 3 were included in the statistical analyses.

Tests for Temporal Differences

To test for temporal deviations from the average growth curve for a given region and sex, consider the model:

$$\text{II. } l_{t_{ij}} = L_{\infty}(1 - e^{-k(t-t_0)}) + Y_i + Q_j + Y*Q_{ij},$$

where: subscript i denotes the ith year,

subscript j denotes the jth quarter,

Y_i = effect of year i,

Q_j = effect of quarter j,

$Y*Q_{ij}$ = year*quarter interaction term.

The subscripts for region and sex are implicit. This model assumes that the effect of year i and the effect of quarter j do not change from age to age. If in fact growth changes from year to year in response to changing environmental conditions or population levels, it is logical to test for the expression of these changes through the von Bertalanffy parameters, especially the rate parameter, k. However, the imposition of up to $i*j$ levels on any or all of the von Bertalanffy parameters results in

intractable formulations, given the inherent nonlinearity of the von Bertalanffy equation (Ratkowsky 1983) and the number of observations available. It is easier to test for an additive effect, as assumed above. Our intent was to test for the presence of a temporal effect and to estimate its sign, if it existed, rather than to estimate its magnitude.

Note that the above method is nearly equivalent to performing an analysis of variance on the residuals from the previous von Bertalanffy model (to see this subtract the von Bertalanffy model from both sides of the expression). We chose instead to fit model II so that the parameters of the von Bertalanffy growth equation could be reestimated given that there are year and quarter additive terms.

To perform the fit we linearized the model as follows:

$$Y_{t \ ij} = \mu + \beta X_t + \gamma_i + \delta_j + \gamma\delta_{ij}$$

where:

$$Y_{t \ ij} = l_{t \ ij}$$

$$\mu = L_{\infty}$$

$$\beta = -L_{\infty} e^{kt_0}$$

$$X_t = e^{-kt}$$

$$\gamma_i = \text{effect of year } i,$$

$$\delta_j = \text{effect of quarter } j,$$

$$\gamma\delta_{ij} = \text{interaction term, and}$$

$$k = \text{as estimated from the regional analysis.}$$

This approach is similar to that of Allen (1976) with the addition of the year and quarter additive and interaction terms. The model was fit using the GLIM (General Linear Interactive Modeling) statistical package (Baker and Nelder 1978).

After fitting the model with and without the year, quarter, and interaction terms, partial F (Rao 1956) tests were performed to examine the null hypothesis that the year-quarter interaction term was statistically significant. If this hypothesis was accepted, the analysis did not proceed further, since it makes little sense to test for the presence of a main effect if the first order interaction term has been found to be significant (Seber 1977). If the hypothesis was rejected, the null hypotheses that: a) the year effect was not significant, and b) the quarter effect was not significant, were tested using partial F tests.

RESULTS

Regional Differences

Table 1 presents the results of partial F tests of regional differences in von Bertalanffy growth of walleye pollock from the five regions of the Bering Sea. The first test compares the fit of a common growth curve to that of separate growth curves from each area. As can be seen from Table 1 for both female and male walleye pollock, over 67% of the residual sum of squares due to a common growth curve can be explained by region-specific growth curves. For both sexes, the hypothesis of no between-area difference in growth was strongly rejected ($p < .001$). Further tests were then performed using the residual sum of squares of the 15 parameter model IB (five regions each with three parameters) as an estimate of the error sum of squares.

The second test examined the hypothesis that regional growth differences were manifest only through the parameters L_{∞} and t_0 , and that k did not differ significantly between regions (model IC). This hypothesis was rejected for both sexes in favor of model IB. The third test examined the hypothesis that regional growth differences were manifest only through the parameters k and t_0 , not L_{∞} (model ID). Once again this hypothesis was rejected in favor of model IB. The fourth test examined the hypothesis that regional growth differences were manifest through the parameters L_{∞} and k , not t_0 (model IE). This hypothesis was rejected for females, but could not be rejected at the 5% level for males.

We conclude that there are statistically significant differences in growth between regions of the Aleutian Basin and eastern Bering Sea and that these differences are expressed through the L and k parameters of the von Bertalanffy curve for both males and females. The t_0 parameter also differs significantly between regions for females. In general, mean length-at-age increases from west to east and from north to south. Table 2 and Fig. 3 present the mean lengths-at-age averaged across years for each region, age and quarter.

To further examine the nature of regional growth differences, we performed multiple comparisons fitting two regions at a time to separate and pooled von Bertalanffy models. The results of these multiple comparisons are given in Table 3 and are presented diagrammatically in Fig. 4. Regardless of the regions being compared, separate von Bertalanffy curves always provided a significantly better fit to the data than did a pooled von Bertalanffy curve (Table 3). This underscores a problem with this type of analysis: due to the large number of observations, even apparently minor differences in mean length-at-age lead to statistically significant results. The question remains whether these results are significant from a management perspective. The answer to this question depends on whether the increased costs and effort required when managing as separate production units is offset by the gain in precision of estimates of production and allowable harvest. We suggest that an F value of 5 or 6, as in the case of Aleutian Basin versus the north slope, may be significant statistically, but has little significance from a

management perspective (see Fig. 3), whereas an F value of over 100, as in the case of the north slope vs. south slope, is significant from both management and statistical perspectives.

We therefore treated the F values in Table 4 as indices of dissimilarity which were used to produce the cluster dendrogram of Fig. 4. Note that the average partial F value is over 200 for the null hypothesis that all regions have a common growth curve, given that the alternative is two growth curves (northern and southern).

Temporal Differences

The mean lengths-at-age by sex and region are shown separately for each year in Figs. 5a-5l. After reviewing these figures, it became apparent that there was a quarterly, or seasonal, component to the variability in the length at age that could not be explained by normal von Bertalanffy growth or by yearly variation. In a number of years and regions, there appeared to be negative growth between subsequent quarters (e.g., south slope Figs. 5a-5l). It was not readily apparent whether this seasonal component to the variation was consistent from year-to-year and between regions. Thus the quarter, year, and year-quarter interaction additive terms of model II were incorporated as discussed in the methods section.

Seasonal Differences

All regions exhibited significant seasonal deviations from von Bertalanffy growth, either in the form of a significant year-quarter interaction term or a significant quarter main

effect (Table 4). However, in the north slope and the two shelf regions, the type of deviation differed between sexes. The year-quarter interaction term was found to be significant ($p < 0.05$) for Aleutian Basin (males and females), south slope (males and females), north slope (females), north shelf (females), and south shelf (males). We interpret the presence of a year-quarter interaction as an indication of seasonal deviations from Bertalanffy which are not consistent from year to year.

The quarter main effect was found to be significant in all region-sex categories not already exhibiting a significant year-quarter interaction term, indicating a seasonal effect which was constant over the years studied. However, since this is a fixed effects model, we cannot easily extrapolate to other years. This seasonal effect was most pronounced in the north slope (males) and south shelf (females) and less pronounced, although significant, in the north shelf (males).

Interannual Differences

Of those categories not already exhibiting a significant year-quarter interaction (north slope males, north shelf males, and south shelf females), only the north shelf males exhibited a significant year main effect. In this region, 1978, 1979, and 1982 were periods of lower than average growth while 1980, 1981, and 1983 were periods of high growth. The presence of the year-quarter interaction prevents such an analysis for the other regions.

DISCUSSION

Sources of Variability in Growth

Before discussing possible biological, behavioral, or environmental sources of variability, we shall examine other sources. The natural variability in growth from fish to fish is a source of pure error that is unavoidable. The effect of pure error is to reduce the power of statistical tests. In addition, this type of error may lead to bias in an unbalanced design if the within-cell variance is not constant. We have attempted to counteract any bias by assigning weights to each mean length-at-age observation as discussed in the methods section.

Age estimation itself is another source of error, since judgment based on experience is required when reading otoliths and experience varies between readers. One possible source of seasonal variability from ageing is due to the "edge effect". As the time of year of the data collection approaches the season where an annulus is laid down (winter), the probability of misclassification of age by the reader increases. The effect of such misclassification is greater for the faster growing (younger) stages, and thus one would expect the variance in length at age due to the edge effect to decrease with increasing age. Our data showed the opposite trend: seasonal variability in length increased with age, especially in the slope regions. Neither of these sources of error account for the fact that seasonal variability is consistently higher in the slope regions than other regions.

Gear selectivity might contribute to regional or temporal differences in estimates of average length at age. Although the mechanism is not readily apparent, if walleye pollock school by size, the catch from a gear type which selects for larger fish might be biased toward faster growing fish. In the eastern Bering Sea, walleye pollock are vulnerable to a wide variety of gear types, and the predominant gear type changes from season to season and from region to region. In general, large freezer trawlers using bottom gear select for large walleye pollock, surimi fleets using off-bottom gear target all size ranges of walleye pollock, and the roe fishery using midwater gear targets on large spawning adults. Table 5 illustrates the distribution of gear by region and season. Because of the lack of overlap in time and region, we were unable to directly compare age-at-length estimates derived from the catch of different commercial gear types.

Regional Growth Differences

Possible biological and environmental sources of regional variability in growth include differences in temperature, prey abundance and composition, walleye pollock abundance, and genetic differences of stocks between regions. Kinder and Schumacher (1981) describe differences in temperature between hydrographic domains which would undoubtedly affect metabolism and growth. Bottom temperatures near 3°C are often found over the south slope region throughout the year, since this region is stratified in the summer and is moderated by the intrusion of oceanic water from the Aleutian Basin in the winter. In contrast, during the

summer growth months, the south shelf region usually experiences temperatures considerably higher than 3°C in the upper water column where most 0-age juveniles reside, and often lower than 3°C in the lower water column where most adults reside. Results of a laboratory study by Smith et al. (1984) indicate that at low to moderate food consumptions, juvenile walleye pollock grew faster at 3°C than at higher temperatures. The effect of temperature on growth of adults was not studied. It is not clear, therefore, whether the longitudinal gradients in adult growth we observed (larger in the south shelf versus south slope and larger in the north shelf versus north slope) can be explained by temperature alone. However, it seems unlikely given the results of the study of juvenile growth. We also observed latitudinal gradients in growth (smaller in the north shelf versus south shelf and smaller in the north slope versus south slope) and these may be partially explained by latitudinal temperature gradients in bottom water (colder in the north).

There is evidence of differences in prey abundance and composition in various regions of the eastern Bering Sea. The reduced growth of walleye pollock from the Aleutian Basin has been attributed to the general lack of fish in the diet of adult walleye pollock (Okada 1983, Traynor and Nelson 1985). In most regions of the eastern Bering Sea, adult walleye pollock prey heavily on young-of-the-year and juvenile walleye pollock, which are noticeably absent from the diet of Aleutian Basin fish. Dwyer (1984) examined the feeding habits of walleye pollock over the eastern Bering Sea and Aleutian Basin regions. Although data from the north slope and

north shelf were combined, cannibalism seemed to be less prevalent over the northern region than the southern region (slope and shelf) during the years of her study (1981-83). This may partially explain the reduced growth of northern fish relative to the southern regions.

Differences in walleye pollock abundance could contribute to regional differences in length at age through density-dependent growth. However, we are not aware of any studies addressing this issue for walleye pollock.

At least four studies on genetic and morphometric differences between discrete stocks of walleye pollock have been reported. Serobaba (1977) described morphometric differences between walleye pollock captured north and those captured south of the Pribilof Islands. These differences included longer gill rakers and intestines of fish from the northern regions, which may contribute to inherent differences in growth between the two areas. Meada (1972), and Yamaguchi and Takahashi (1972) have also described morphometric differences between substock of walleye pollock within the Bering Sea. In contrast, an electrophoretic study by Grant and Utter (1980) found no evidence of genetically distinct stocks within the eastern Bering Sea. None of these studies examined walleye pollock from the Aleutian Basin.

Seasonal Growth Differences

We believe seasonal deviations from normal von Bertalanffy growth are due to migration. In this scenario, fish exposed to

the feeding and growth conditions from one region migrate into or through another region to spawn or overwinter. A similar phenomenon was noted by Francis (1983) for Pacific hake (Merluccius productus) off the Washington-Oregon-California coast. During their migration from southern spawning grounds to northern feeding grounds, Pacific hake stratified by size, with the larger, faster moving fish leading the migration. Within an area, for a given age group, the average length at age tended to decrease over time as the smaller, slower moving fish moved through.

In the eastern Bering Sea, adult walleye pollock are believed to avoid water colder than about 2°C (Francis and Bailey 1983). In the winter, a cold bottom water mass (-1.5-0.0°C) usually forms in the middle shelf region. Based on catch distributions of walleye pollock during the winter, it appears that the fish aggregate along the slope regions, where bottom water temperatures are more moderate (2.0-3.0°C) due to the intrusion of warmer oceanic water from the Aleutian Basin (Shimada et al. 1983). In the summer, there is thought to be a feeding and perhaps spawning migration onto the shelf in response to warming water conditions (see Lynde 1984 for a detailed discussion). If the seasonal variability in length at age we observed is due to migration, then the areas of high variability, such as the southern slope and, to a lesser degree, northern slope, must be areas with a mixture of fish having different regional growth characteristics.

CONCLUSIONS

We believe the results of this study have bearing on a number of current management issues. First, our results indicate that there are two distinct "production units" of walleye pollock within the eastern Bering Sea and Aleutian Basin: 1) a northern, slow growing unit inhabiting the north slope, north shelf, and Aleutian Basin regions, and 2) a southern, faster growing unit inhabiting the south slope and south shelf regions (Figs. 3 and 5). This conclusion is based strictly on differences in growth rates. However, since growth rates differ significantly between regions, it is likely that other production parameters, such as fertility and natural mortality, differ as well.

Second, migration occurs between regions, as indicated by significant seasonal deviations from von Bertalanffy growth. Of particular interest is the nature of the relationship, if any, between fish from the Aleutian Basin and the two slope areas. Although we have not presented any direct evidence for a linkage between the Aleutian Basin and the eastern Bering Sea, our results can be added to a growing body of circumstantial evidence. Since walleye pollock under the age of 4 are seldom caught in the Aleutian Basin, it seems probable that adults migrate into this region from other areas. The similarity in mean length at age of fish from the north slope makes this region a likely candidate. Also of interest is the growth of north shelf walleye pollock which resembles that of the north slope and Aleutian Basin up to about age 4 and resembles the southern regions after age 4 (Fig. 3). One

possible explanation is that the walleye pollock from the Aleutian Basin reside over the north slope and shelf regions during their early life before moving into the Basin. Apparently transport mechanisms do exist which link the northern slope and Aleutian Basin regions. In 1982 a drifter buoy was deployed unintentionally in the southern Aleutian Basin. The buoy traveled eastward to Unimak Plateau then northwest with the Bering slope current to the northern slope and then back into the Aleutian Basin where it was eventually recovered (Royer and Emery 1984) (Fig. 6).

A second type of linkage between the Basin and slope may occur during spawning. Walleye pollock from the Basin are known to form spawning aggregations near the south slope (Okada 1979). It is possible that the occasionally low lengths at age exhibited by walleye pollock in the southern slope during spawning season (Figs. 7e-7h) are due to the immigration of Aleutian Basin fish.

There is a need for mark/recapture studies to determine the extent and direction of walleye pollock migration. A previous study by the Japanese was unsuccessful. In 1973, 252 walleye pollock were tagged along the northern shelf region of the western Bering Sea. As of 1977 only one fish had been recovered. Coincidentally, this fish happened to have been recovered in the Aleutian Basin (Okada 1979).

If walleye pollock from the Aleutian Basin contribute to the commercial catch from the slope or shelf regions or vice versa, then this would have serious management implications. The fishery in the Aleutian Basin has expanded dramatically in recent years. In 1984 a large portion of the catch came from an area that was

inside the U.S.-U.S.S.R. convention line but outside our fishery conservation zone (R. Nelson, 7600 Sand Point Way N.E., Bldg. 4, BIN15700, Seattle, WA 98115. Pers. comm. 1984) (see Fig. 2).

Finally, since collecting and ageing otoliths is an expensive and time-consuming process, the National Marine Fisheries Service is currently evaluating ways to reduce the number of walleye pollock otoliths to be read without significantly reducing the accuracy of stock assessment estimates. The presence of regional and temporal differences in walleye pollock growth makes it necessary to continue sampling throughout the year, over a broad area of the Bering Sea, in order to construct accurate age-length keys for future growth and catch-at-age analyses.

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Table 1. Results of analysis of regional variability in growth of walleye pollock (*Theragra chalcogramma*): partial F tests of regional differences in von Bertalanffy growth.

Hypothesis	Model number	Sex	Source	Residual		Approximate	
				S.S.	D.F.	F	Probability
Ho: no region effect	IA	F	Model IA	21673	498		
Ha: region specific L_{∞}, k, t_0	IB	F	Model IB	6578	486		
		F	Due to Ho	15095	12	92.94	<.001
		M	Model IA	17324	447		
		M	Model IB	5697	435		
		M	Due to Ho	11645	12	74.33	<.001
.....							
Ho: region specific L_{∞}, t_0 common k	IC	F	Model IC	6913	490		
		F	Model IB	6578	486		
		vs.					
Ha: region specific L_{∞}, k, t_0	IC	F	Due to Ho	335	4	6.19	<.001
		M	Model IC	6045	439		
		M	Model IB	5679	435		
		M	Due to Ho	366	4	7.01	<.001
.....							
Ho: region specific k, t_0 , common L_{∞}	ID	F	Model ID	7251	490		
		F	Model IB	6578	486		
		vs.					
Ha: region specific L_{∞}, k, t_0	ID	F	Due to Ho	673	4	12.43	<.001
		M	Model ID	6309	439		
		M	Model IB	5679	435		
		M	Due to Ho	630	4	12.06	<.001

Table 1. Continued.

Hypothesis	Model number	Sex	Source	Residual		Approximate	
				S.S.	D.F.	F	Probability
Ho: region specific L_{∞} , k, common t_0	IE	F	Model IE	6827	490		
		F	Model IB	6578	486		
vs							
Ha: region specific L_{∞} , k, t_0	IB	F	Due to Ho	249	4	4.58	<.005
		M	Model IE	5771	439		
		M	Model IB	5679	435		
		M	Due to Ho	92	4	1.76	n.s.

Table 2. Mean length at age of walleye pollock (*Theragra chalcogramma*) by area and quarter averaged for years 1978-1983.

Age	Qtr	Males					Females				
		South		North		Basin	South		North		Basin
		Shelf	Slope	Shelf	Slope		Shelf	Slope	Shelf	Slope	
1	1				20.59		19.66				
1	2	13.04					12.64	18.99			
1	3	21.39	21.87	18.64	18.52		21.04	21.37	18.25	18.77	
2	1	24.65			22.82		24.86	24.82		22.75	
2	2	27.69	27.10	23.58	23.70		28.05	27.53	23.47	24.73	
2	3	30.86	30.69	26.34	27.28		30.87	31.74	26.44	26.60	
3	1	33.98	32.84		29.08	29.29	31.89	32.64		29.57	30.10
3	2	35.52	34.96	31.47	30.36		35.08	35.60	31.62	30.69	
3	3	37.77	36.98	32.40	32.52		36.61	37.41	32.38	32.69	
4	1	40.06	38.81		33.43	34.61	37.86	39.04		33.87	34.24
4	2	39.97	39.26	36.35	35.02	34.00	40.29	40.24	37.11	35.30	
4	3	40.14	40.78	37.30	37.29	39.69	41.85	41.51	37.42	37.04	40.35
5	1	43.75	42.20		36.68	39.32	42.97	42.76		37.26	38.34
5	2	44.81	40.86	41.56	38.08	39.00	46.83	43.18	42.48	38.64	43.25
5	3	43.97	43.40	40.82	38.95	41.83	46.46	45.00	41.54	41.59	43.61
6	1	48.66	44.62		39.53	41.26	59.51	46.63		39.53	41.93
6	2	48.52	43.66	44.10	41.43	42.98	49.89	46.27	48.83	42.38	44.91
6	3	46.21	45.62	45.93	43.20	43.20	50.62	46.59	48.37	44.46	45.11
7	1	51.36	53.26		42.73	43.51	56.02	54.20		45.63	44.90
7	2	52.58	46.46	46.25	46.47	45.01	55.48	49.76	51.87	46.77	45.96
7	3	49.44	48.33	50.70	47.38	46.48	52.13	52.52	54.43	47.83	45.73
8	1	60.84			47.24	45.31	55.78	53.43		48.27	45.90
8	2	55.71	48.30	53.50	47.40	47.13	57.17	53.67	55.17	50.33	49.76
8	3	52.48	49.03	53.32	47.31	46.33	52.64	54.22	57.96	50.49	49.00
9	1	58.67			47.35	46.36	65.07	54.51		49.86	48.78
9	2	56.48	51.33	53.23	48.11	47.58	59.83	52.59	54.32	49.91	49.20
9	3	57.17	52.44	56.45	49.90	47.36	54.35	55.37	57.04	51.28	50.22
10	1	58.67			47.87	47.40	69.34	56.87		49.92	48.96
10	2	57.32	52.86		48.02	47.40	63.42	53.45	62.02	52.61	48.41
10	3		50.24	55.49		47.03		56.61	58.84	54.11	49.48

Table 3. All possible between-region comparisons of the growth of male and female walleye pollock. Approximate F values from partial F tests comparing the fit of pooled (1 curve) vs. separate (2 curves) von Bertalanffy equations.

	<u>Aleutian Basin</u>			<u>North Slope</u>			<u>North Shelf</u>			<u>South Slope</u>			<u>South Shelf</u>		
	M	F	Avg	M	F	Avg	M	F	Avg	M	F	Avg	M	F	Avg
Aleutian Basin	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
North Slope	6.50	5.54	6.02	+	+	+	+	+	+	+	+	+	+	+	+
North Shelf	20.26	55.06	37.96	22.21	46.86	34.54	+	+	+	+	+	+	+	+	+
South Slope	31.95	225.86	128.91	152.27	392.15	272.21	54.05	155.47	104.76	+	+	+	+	+	+
South Shelf	48.47	56.38	52.42	171.09	166.35	168.72	39.78	26.34	33.06	11.60	47.94	29.77	+	+	+

Table 4. Results of analysis of temporal variability in von Bertalanffy growth of walleye pollock (*Theragra chalcogramma*): partial F tests of the significance of year (Y), quarter (Q), and year*quarter (Y*Q) additive terms (V indicates von Bertalanffy growth model).

Area	Hypothesis	Model	Sex	Source	Residual S.S.	D.F.	Approximate F Prob.		
Basin	Ho: No YR*QTR Intxn.	2B. L=V+Y+Q	F	Model 2B	42.5	36			
		2A. L=V+Y+Q+(Y*Q)	F	Model 2A	31.8	34			
			F	Due to Ho	10.7	2	5.72	<.01	
				M	Model 2B	35.7	53		
				M	Model 2A	30.2	50		
				M	Due to Ho	5.5	3	3.04	<.05
North slope	Ho: No YR*QTR Intxn.	2B. L=V+Y+Q	F	Model 2B	778.5	123			
		2A. L=V+Y+Q+(Y*Q)	F	Model 2A	632.0	115			
			F	Due to Ho	146.5	8	3.33	<.005	
				M	Model 2B	318.1	111		
				M	Model 2A	281.2	103		
				M	Due to Ho	36.9	8	1.69	n.s.
		Ho: No YR effect	2C. L=V+Q	M	Model 2C	339.3	116		
			2B. L=V+Y+Q	M	Model 2B	318.1	111		
				M	Due to Ho	21.2	5	1.48	n.s.
	Ho: No seasonal effect	2D. L=V	M	Model 2B	375.6	118			
		2C. L=V+Q	M	Model 2C	339.3	116			
			M	Due to Ho	36.3	2	6.21	<.005	

Table 4. Continued.

Area	Hypothesis	Model	Sex	Source	Residual S.S.	D.F.	<u>Approximate</u> F Prob.		
South slope	Ho: no YR*QTR intxn.	2B. L=V+Y+Q	F	Model 2B	1211.0	125			
		2A. L=V+Y+Q+(Y*Q)	F	Model 2A	922.8	118			
			F	Due to Ho	288.2	7	5.26	<.001	
								
			M	Model 2B	581.3	100			
			M	Model 2A	420.3	94			
		M	Due to Ho	161.0	6	6.00	<.001		
.....									
South shelf	Ho: no YR*QTR intxn.	2B. L=V+Y+Q	F	Model 2B	2496.0	78			
		2A. L=V+Y+Q+(Y*Q)	F	Model 2A	2264.0	73			
			F	Due to Ho	232.0	5	1.50	n.s.	
								
	Ho: no YR effect	2C. L=V+Q	F	Model 2C	2657.0	83			
		2B. L=V+Y+Q	F	Model 2B	2496.0	78			
			F	Due to Ho	161.0	5	1.01	n.s.	
								
	Ho: no seasonal effect	2D. L=V	F	Model 2D	3256.0	85			
		2C. L=V+Q	F	Model 2C	2657.0	83			
		F	Due to Ho	599.0	2	9.36	<.001		
.....									
Ho: no YR*QTR Intxn.	2B. L=V+Y+Q	M	Model 2B	581.3	100				
		M	Model 2A	420.3	94				
		M	Due to Ho	161.0	6	6.00	<.001		

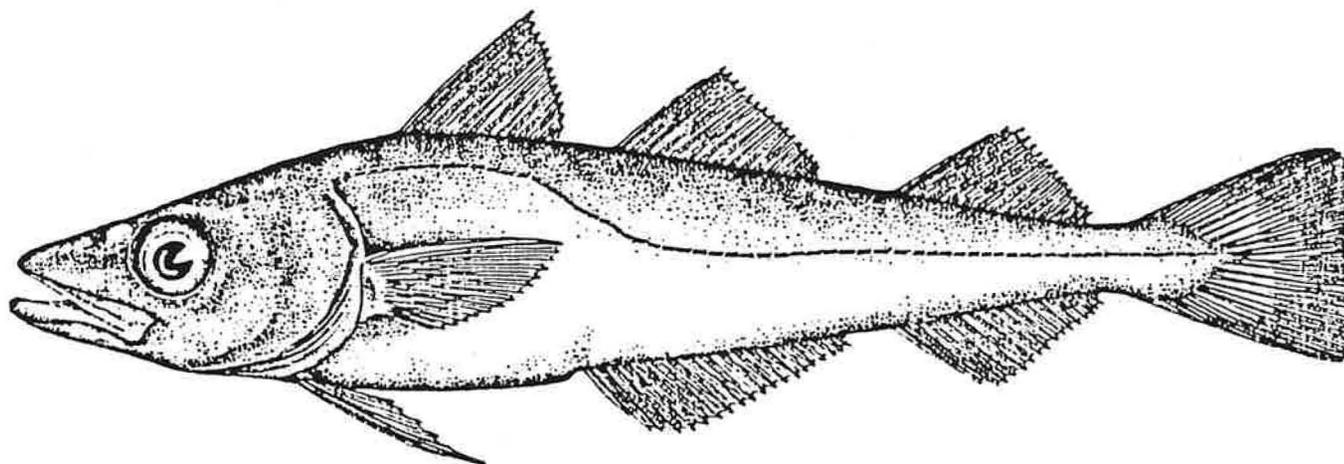
Table 4. Continued.

Area	Hypothesis	Model	Sex	Source	Residual		Approximate			
					S.S.	D.F.	F	Prob.		
North shelf	Ho: no YR*QTR intxn.	2B. L=V+Y+Q	F	Model 2B	3260.0	84				
		2A. L=V+Y+Q+(Y*Q)	F	Model 2A	2875.0	80				
			F	Due to Ho	385.0	4	2.68	<.05		
									
			M	Model 2B	961.0	64				
			M	Model 2A	921.1	61				
	Ho: no YR effect		M	Due to Ho	39.9	3	0.88	n.s.		
									
		2C. L=V+Q	M	Model 2C	1312.0	69				
		2B. L=V+Y+Q	M	Model 2B	961.0	64				
			M	Due to Ho	351.0	5	4.68	<.001		
									
Ho: no QTR effect	2E. L=V+Y	M	Model 2E	1070.0	65					
	2B. L=V+Y+Q	M	Model 2B	961.0	64					
		M	Due to Ho	109.0	1	7.26	<.01			

Table 5. Number of pollock otolith samples by gear type, area and quarter. (Males only, male:female ratio approximately 1:1).

Area	YEAR	QTR	No. by Gear Code ^{1/}					TOTAL no.	Area	YEAR	QTR	No. by Gear Code					TOTAL no.
			A	B	C	D	E					A	B	C	D	E	
North slope	1981	1	29					29	North shelf	1981	1						0
		2	9	59				68			2	38	6			44	
		3	134	22				156			3	5				5	
	1982	1		24				24		1982	1						0
		2			9		185	194			2		7	4	31	89	41
		3	401	9	26	7		443			3				328		417
	1983	1						0		1983	1						0
		2						0			2		11				11
		3	52	1	44	2		99			3				130		130
North basin	1981	1		12				12	South shelf	1981	1						0
		2	1	13				14			2	36	82	47		165	
		3	5					5			3	127		10		137	
	1982	1	7	60	1			68		1982	1						0
		2	2	19				21			2	47	191	48	107	79	472
		3					31	31			3	403	36	5			444
	1983	1		29				29		1983	1						0
		2						0			2		229	111	146		486
		3						0			3		9	36			47
South slope	1981	1	158	43				201	South shelf	1981	1						0
		2	9	42				51			2	36	82	47		165	
		3	23					23			3	127		10		137	
	1982	1	492					492		1982	1						0
		2	85	4			109	198			2	47	191	48	107	79	472
		3	96			3	15	114			3	403	36	5			444
	1983	1	153					153		1983	1						0
		2		16				16			2		229	111	146		486
		3		10				10			3		9	36			47

^{1/}
A = Surimi mothership, surimi trawler.
B = Trawlers (large, med, small, side, large freezer).
C = Joint venture mothership.
D = NMFS survey demersal trawl.
E = NMFS survey midwater trawl.



POLLOCK
Theragra chalcogramma

Fig. 1. Walleye pollock, Theragra chalcogramma.

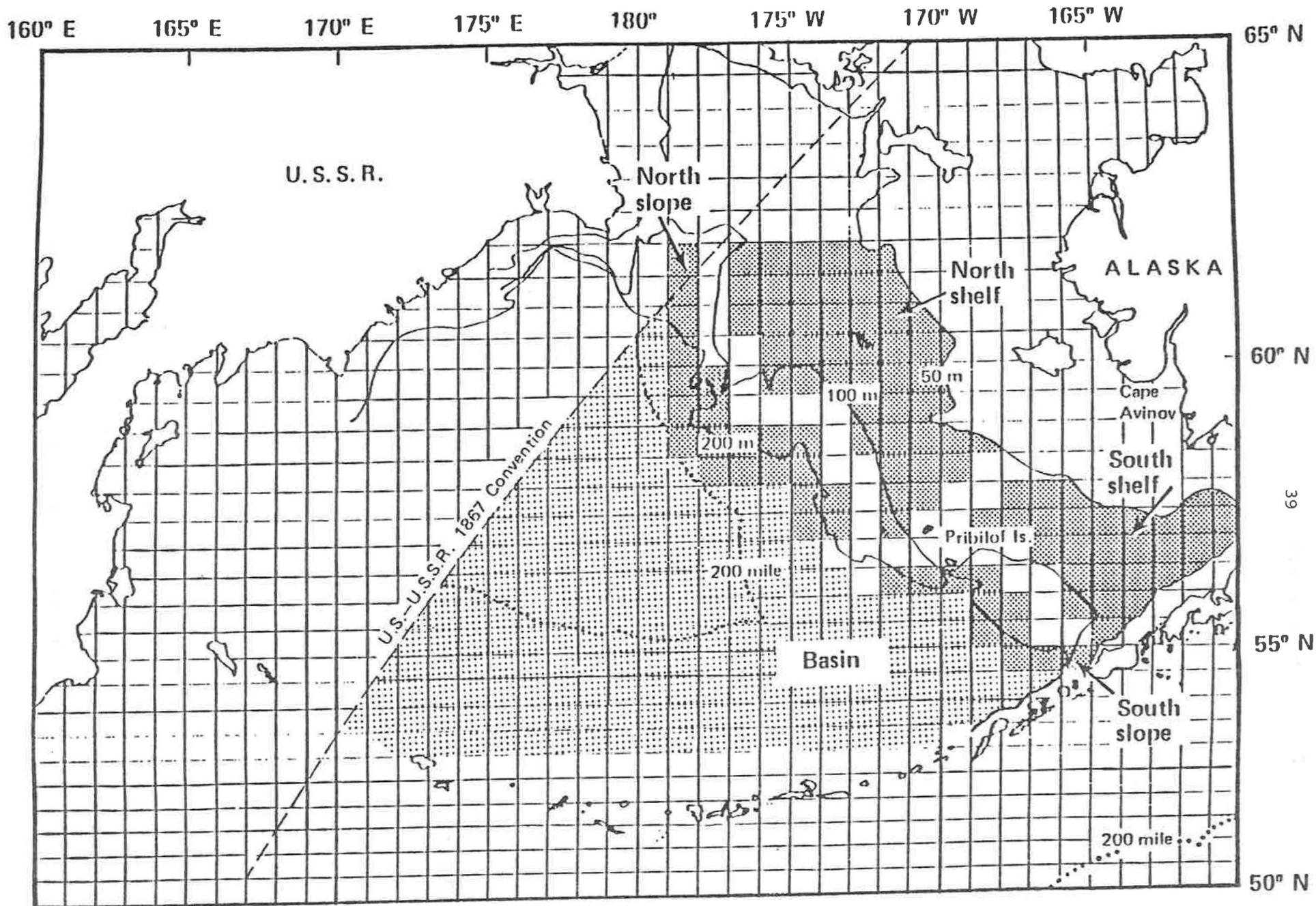
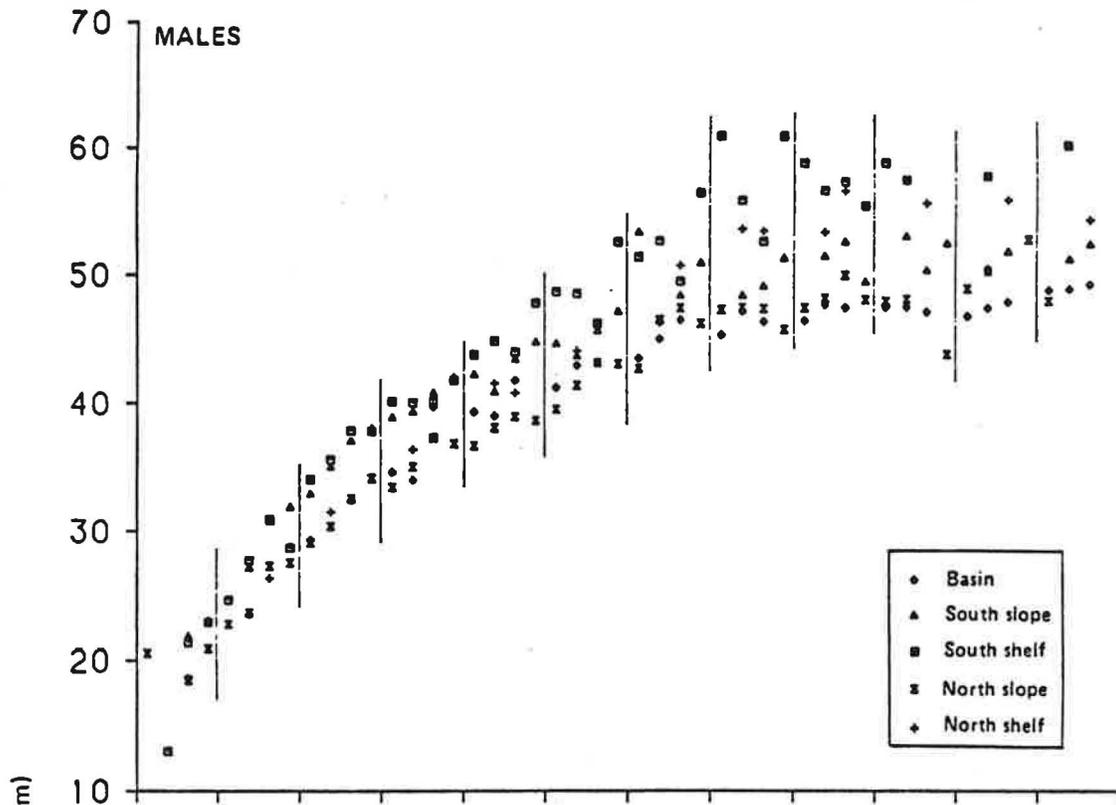


Fig. 2. Map depicting five different regions of the Bering Sea used in the analysis; north shelf, north slope, south shelf and south slope, and Aleutian Basin.

POLLOCK (all years averaged)

3A



3B

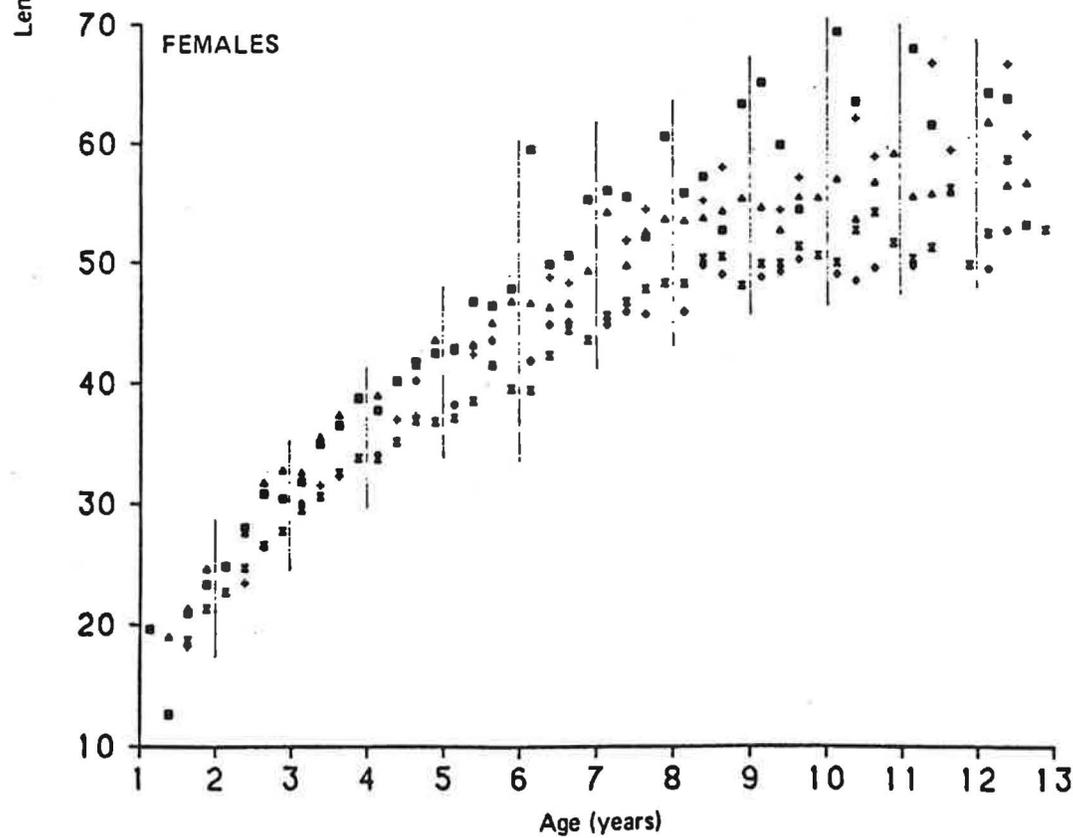


Fig. 3. Mean lengths-at-age of walleye pollock males (3A) and females (3B) averaged across years for each region, age, and quarter.

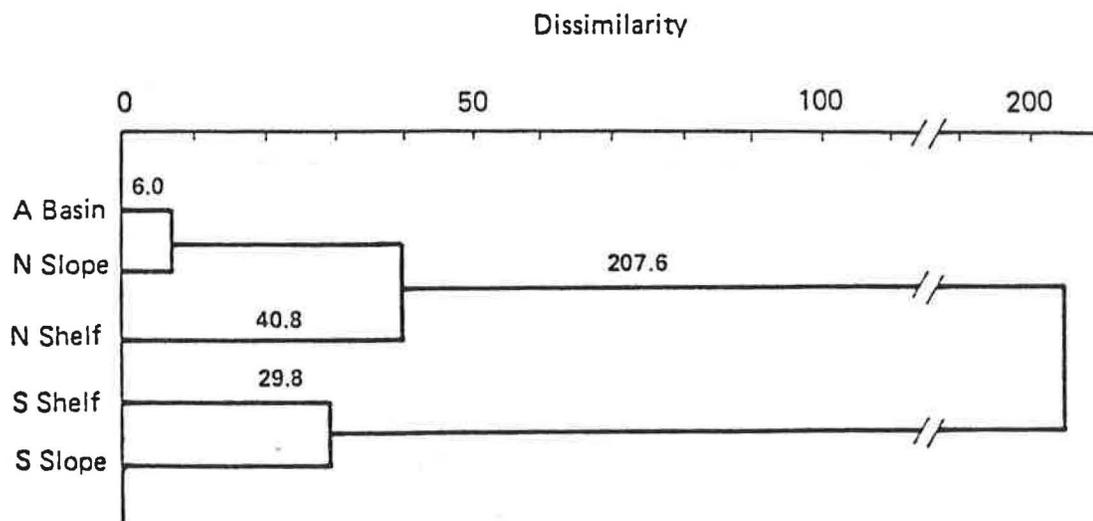
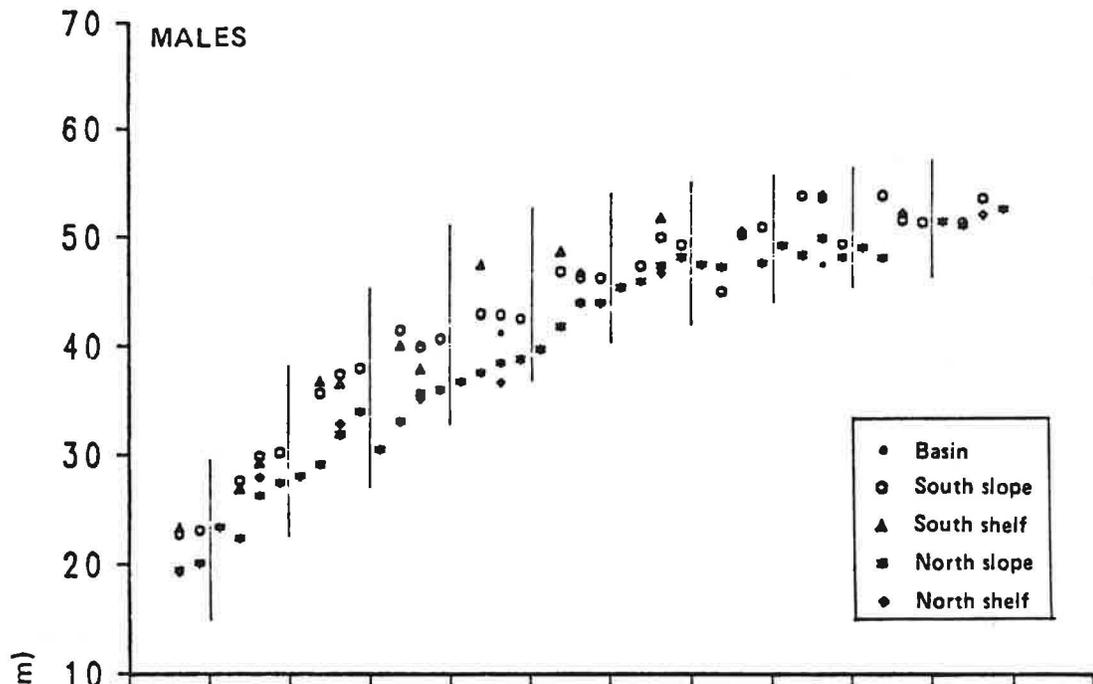


Fig. 4. Cluster dendrogram representing the degree of dissimilarity in growth of walleye pollock between regions in the eastern Bering Sea and Aleutian Basin. Dissimilarity indices are based on approximate F values from multiple comparison partial F tests (Table 3.).

POLLOCK 1978

5A



5B

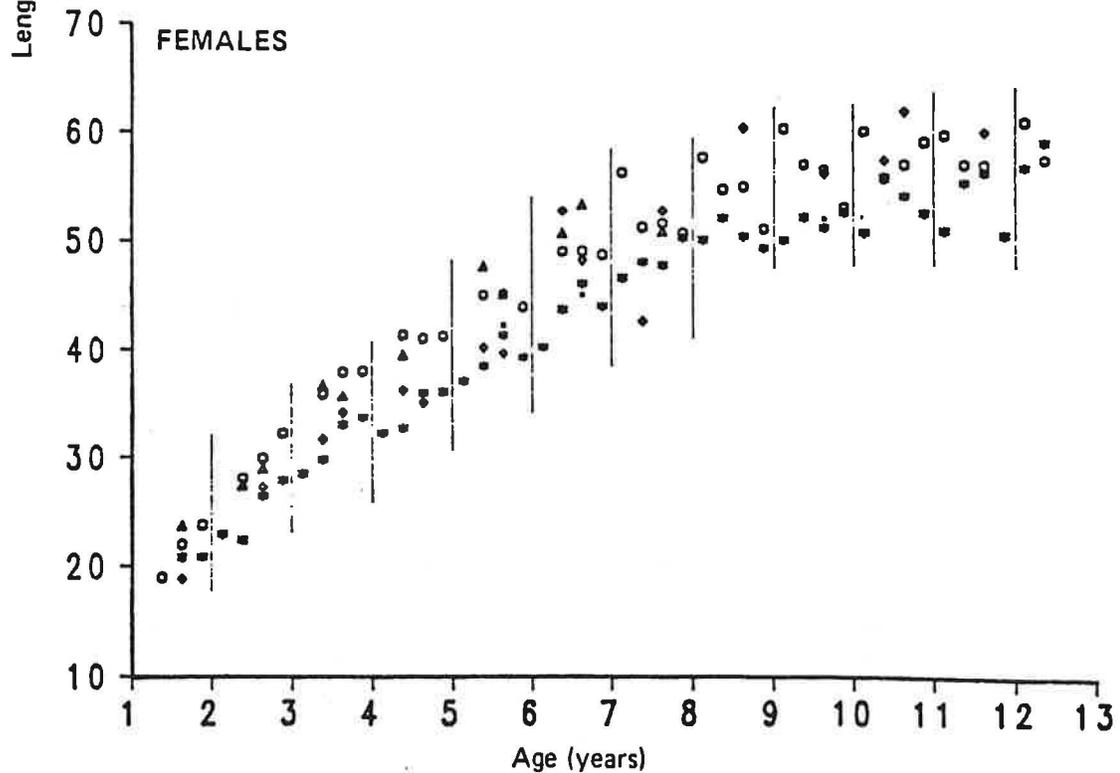
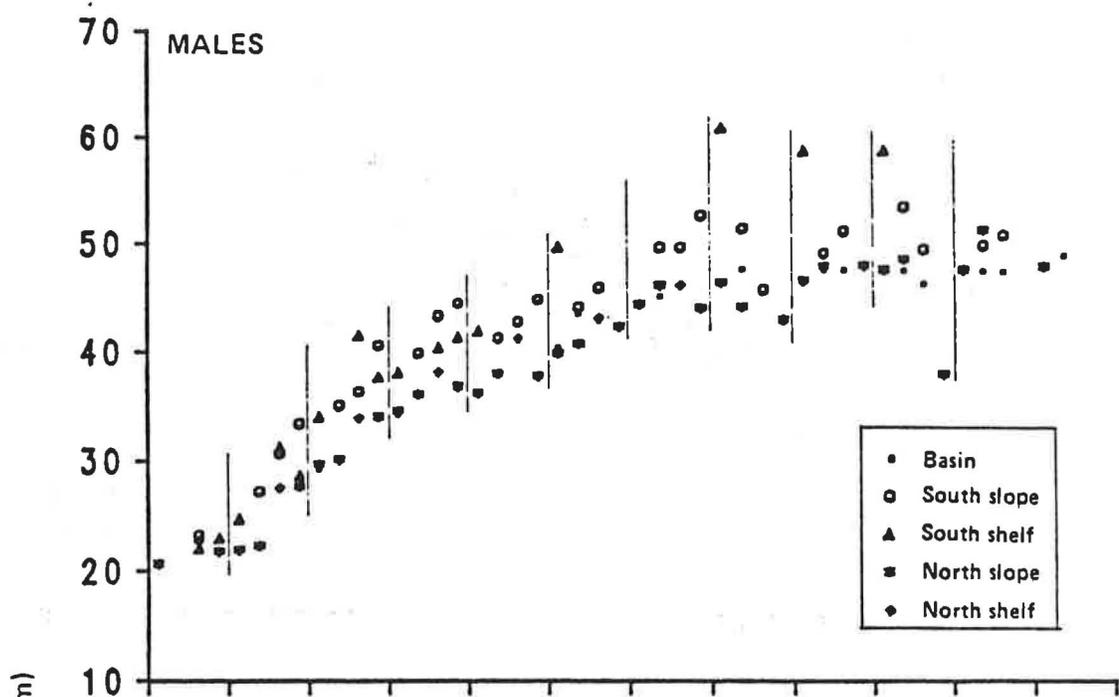


Fig. 5. Mean lengths-at-age for walleye pollock males 1978 (5A), females 1978 (5B), males 1979 (5C), females 1979 (5D), males 1980 (5E), females 1980 (5F), males 1981 (5G), females 1981 (5H), males 1982 (5I), females 1982 (5J), males 1983 (5K), females 1983 (5L).

POLLOCK 1979

5C



5D

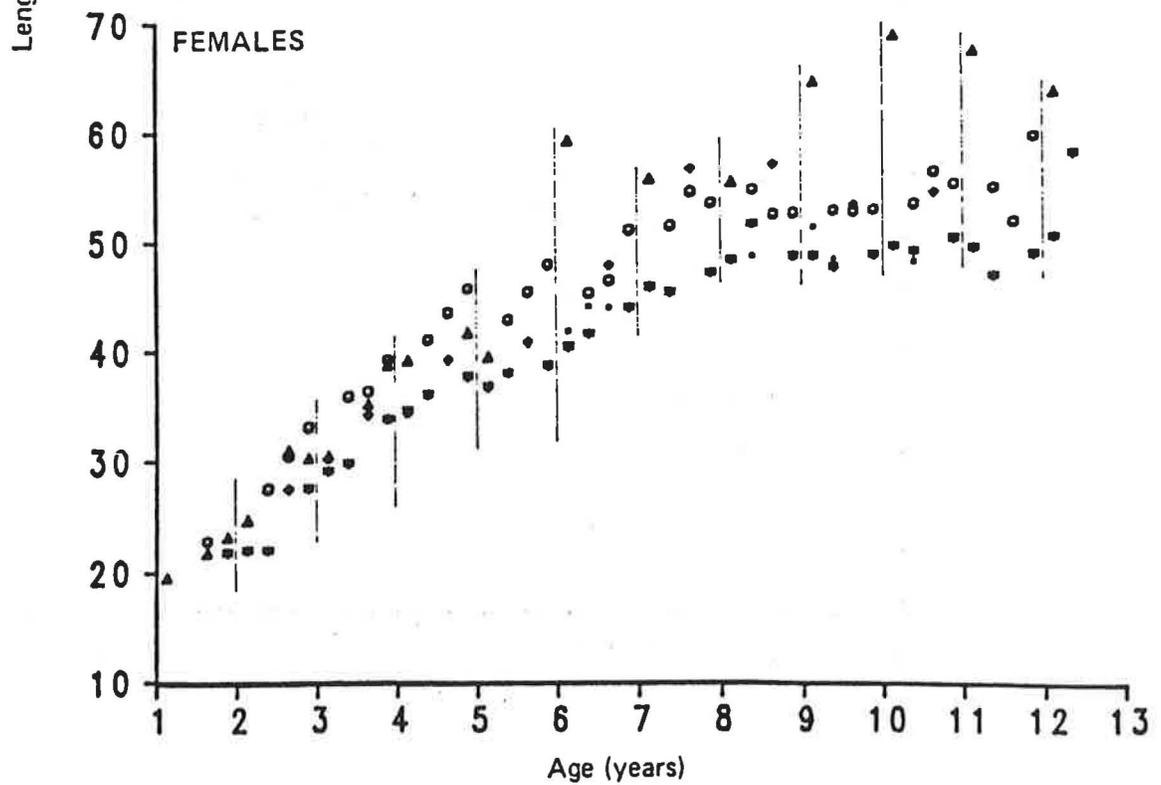
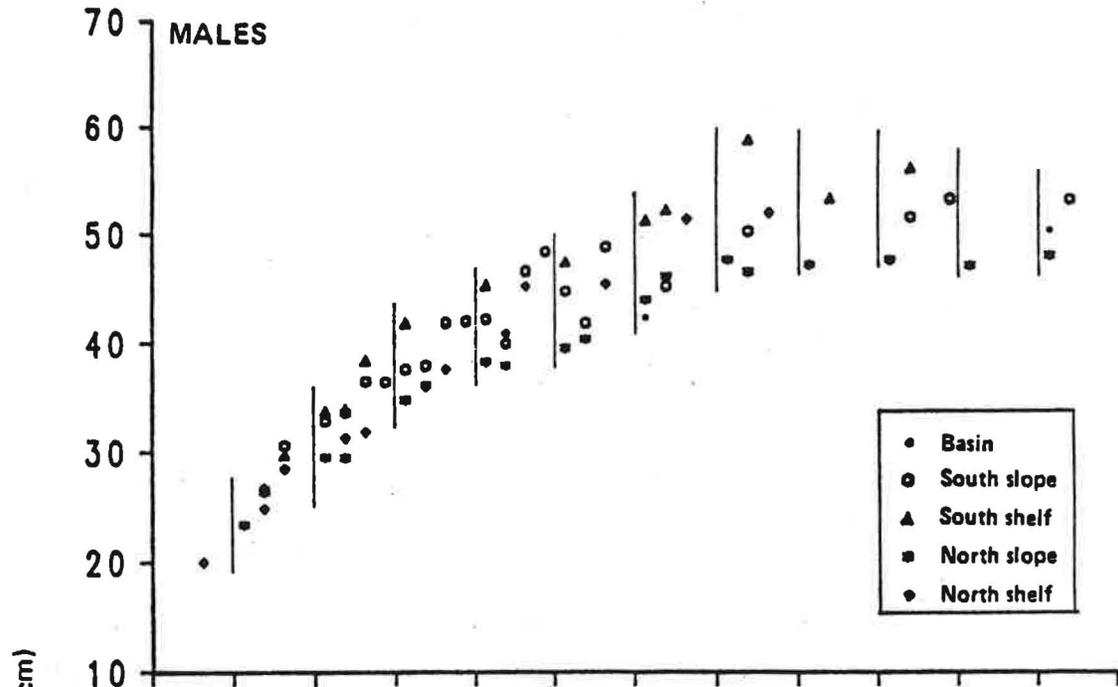


Fig. 5. Continued.

5E



5F

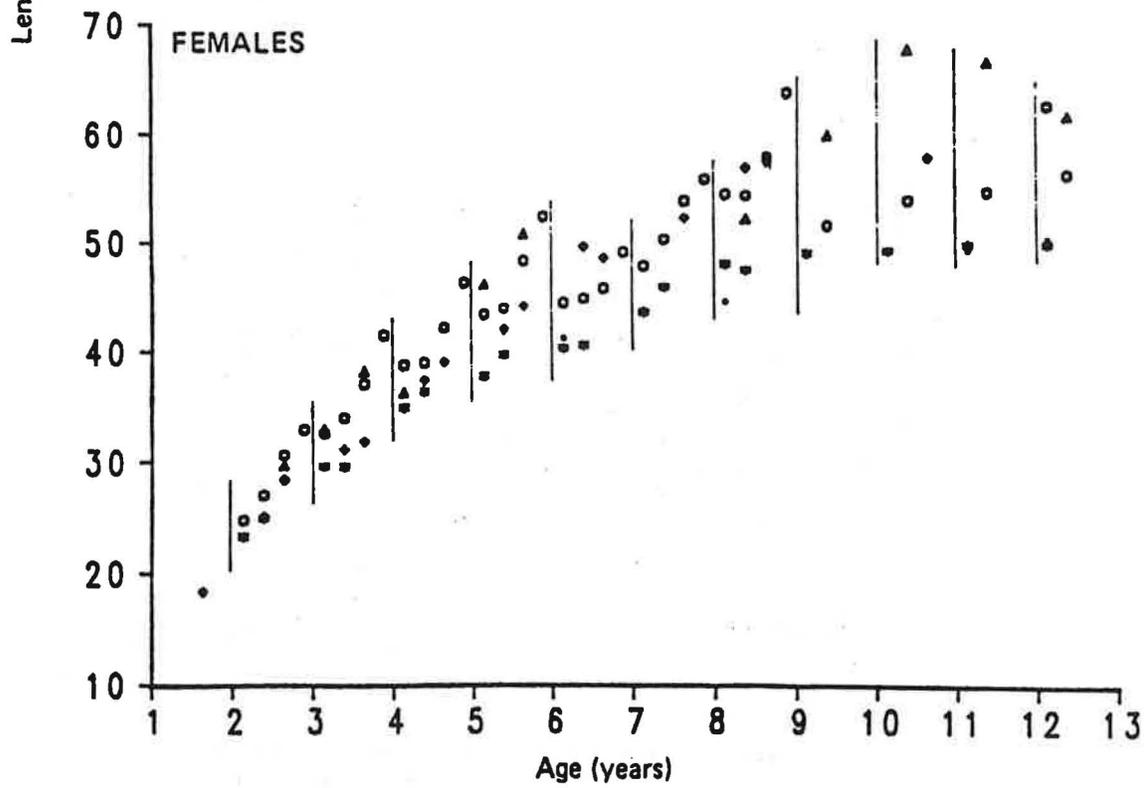
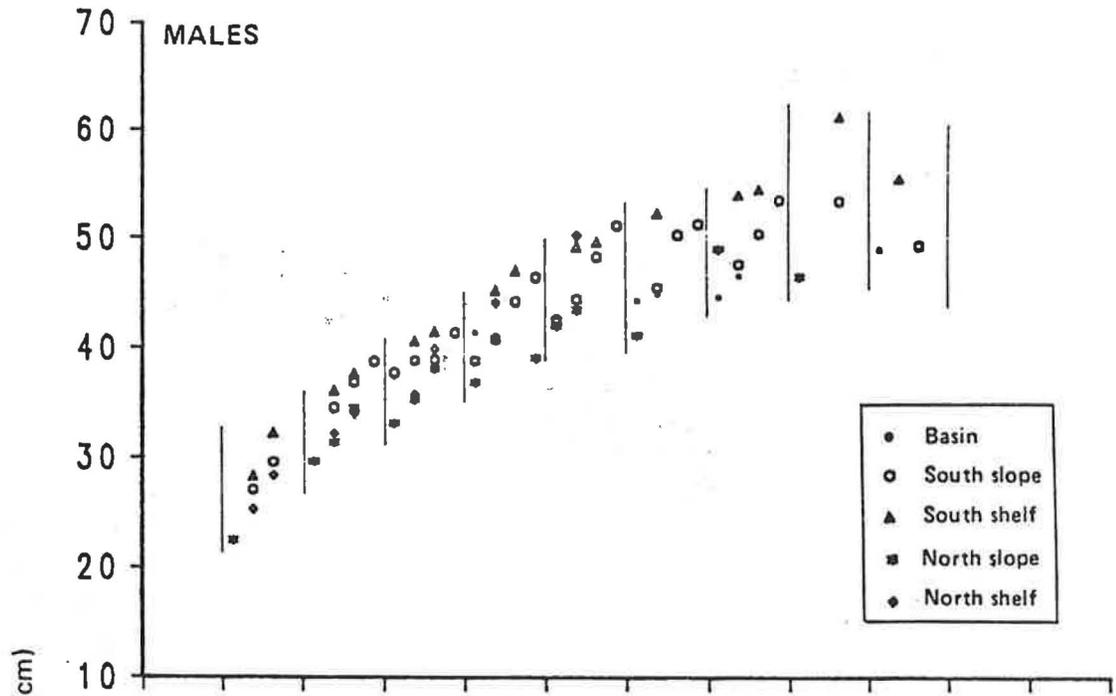


Fig. 5. Continued.

5G



5H

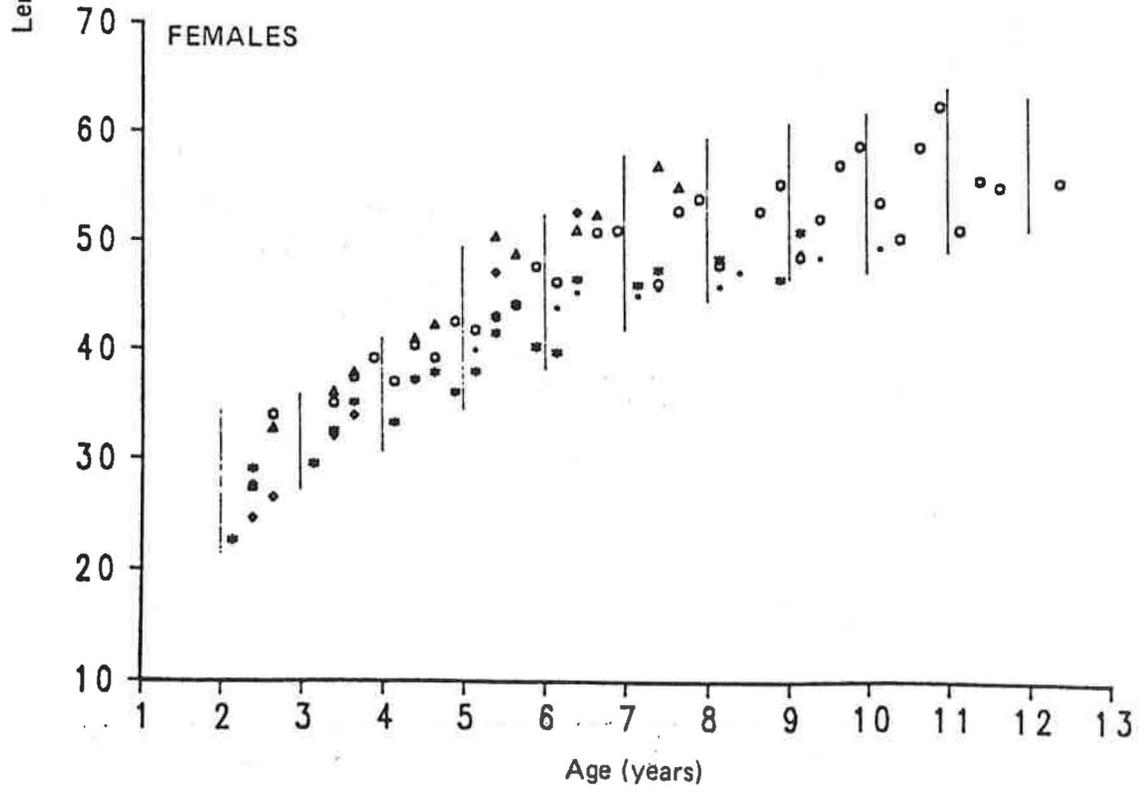
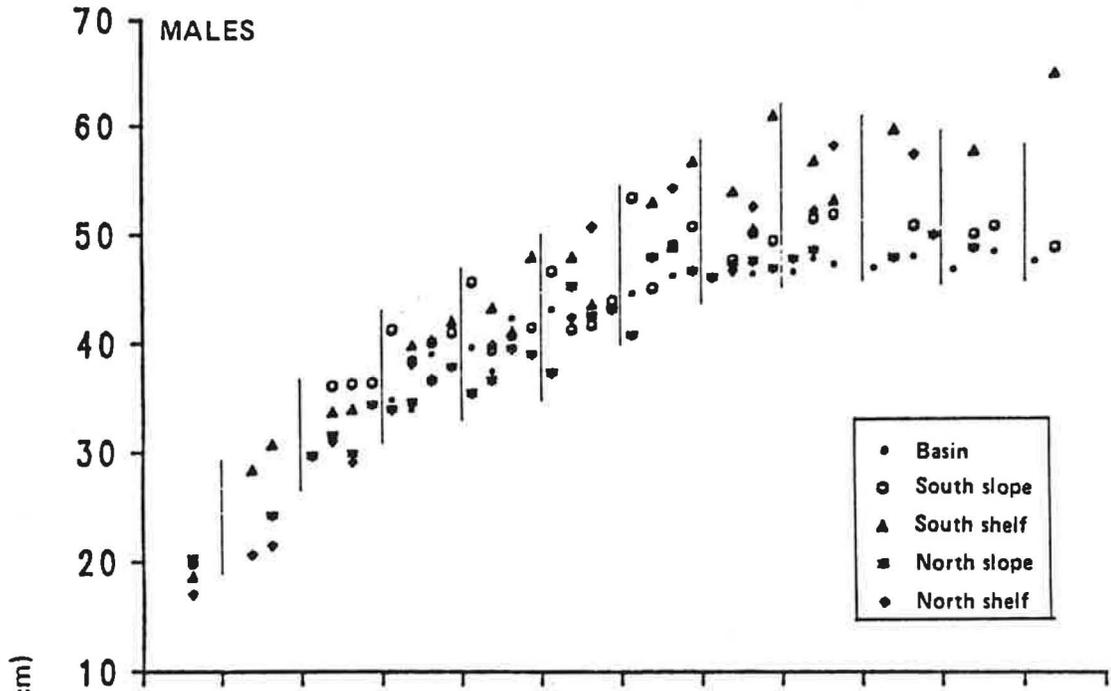


Fig. 5. Continued.

POLLOCK 1982

5I



5J

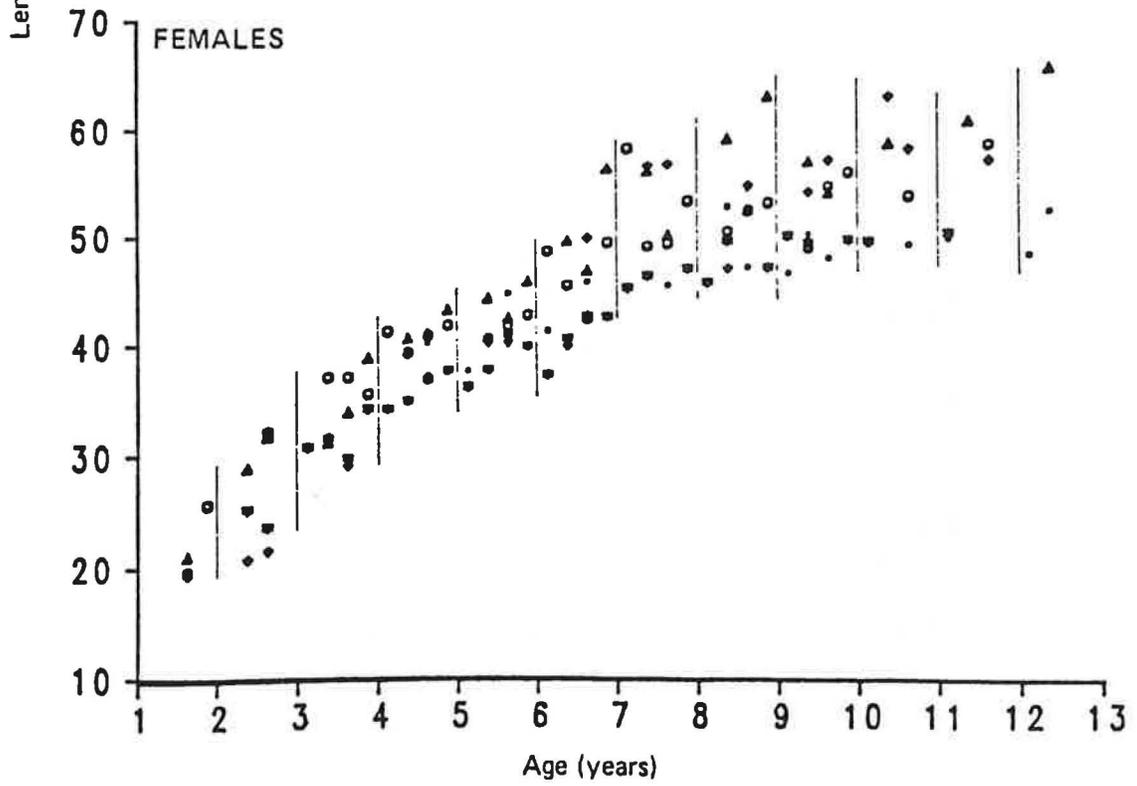
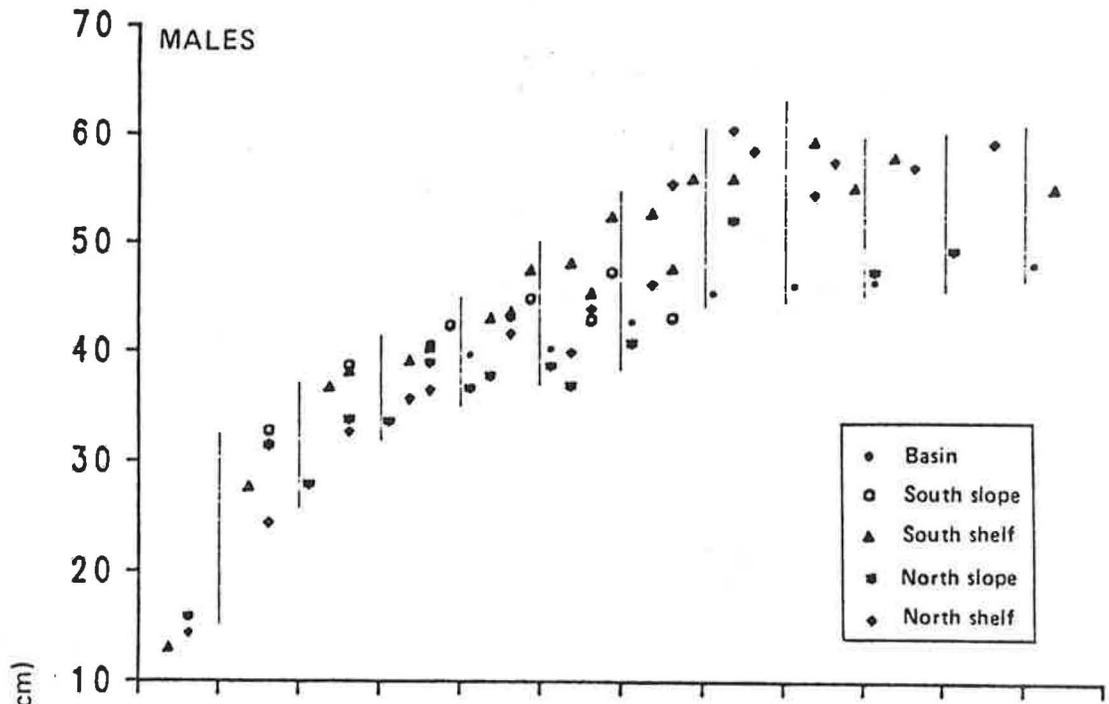


Fig. 5. Continued.

5K



5L

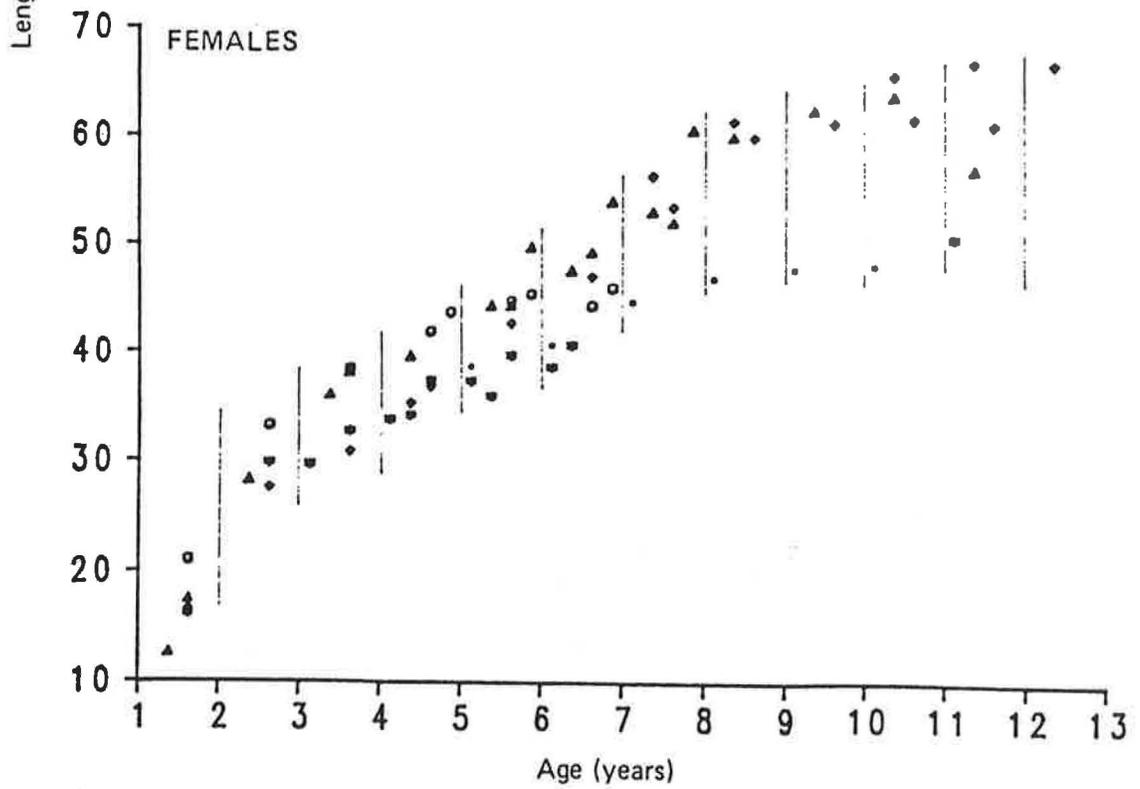


Fig. 5. Continued.

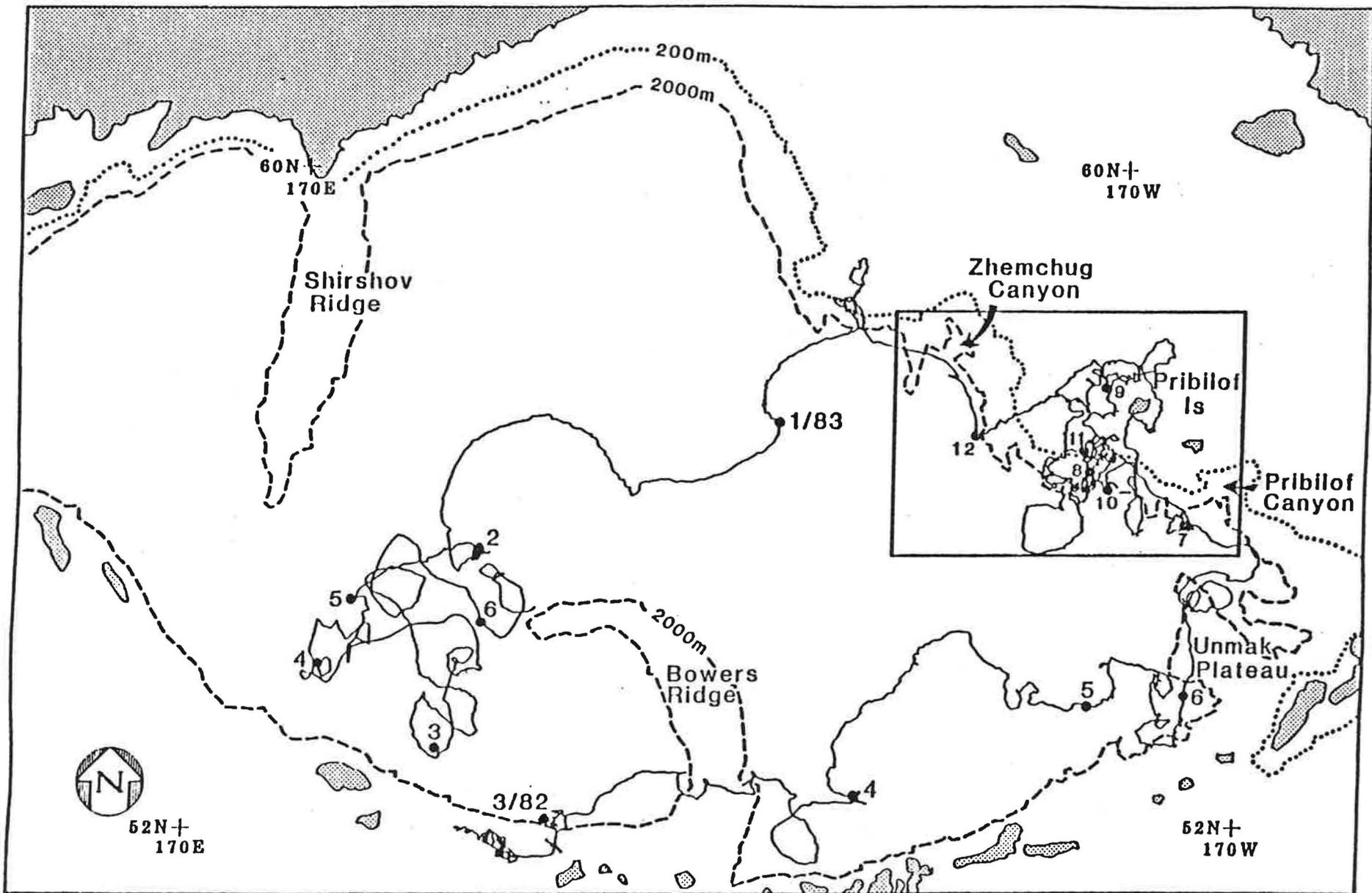


Fig. 6. The Bering Sea showing the trajectory of the surface drifter released in February 1982. The first day of each month is indicated. January 1983 is indicated as 1/83. (From Royer and Emery, 1984).