Abstract—Errors in growth estimates can affect drastically the spawner-perrecruit threshold used to recommend quotas for commercial fish catches. Growth parameters for sablefish (Anoplopoma fimbria) in Alaska have not been updated for stock assessment purposes for more than 20 years, although aging of sablefish has continued. In this study, length-stratified data (1981-93 data from the annual longline survey conducted cooperatively by the Fisheries Agency of Japan and the Alaska Fisheries Science Center of the National Marine Fisheries Service) were updated and corrected for discovered sampling bias. In addition, more recent, randomly collected samples (1996-2004 data from the annual longline survey conducted by the Alaska Fisheries Science Center) were analyzed and new length-at-age and weight-at-age parameters were estimated. Results were similar between this analysis with length-at-age data from 1981 to 2004 and analysis with updated longline survey data through 2010; therefore, we used our initial results from analysis done with data through 2004. We found that, because of a stratified sampling scheme, growth estimates of sablefish were overestimated with the older data (1981-93). and growth parameters used in the Alaskan sablefish assessment model were, thus, too large. In addition, a comparison of the bias-corrected 1981-93 data and the 1996-2004 data showed that, in more recent years, sablefish grew larger and growth differed among regions. The updated growth information improves the fit of the data to the sablefish stock assessment model with biologically reasonable results. These findings indicate that when the updated growth data (1996-2004) are used in the existing sablefish assessment model, estimates of fishing mortality increase slightly and estimates of female spawning biomass decrease slightly. This study provides evidence of the importance of periodically revisiting biological parameter estimates, especially as data accumulate, because the addition of more recent data often will be more biologically realistic. In addition, it exemplifies the importance of correcting biases from sampling that may contribute to erroneous parameter estimates.

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Interdecadal change in growth of sablefish (*Anoplopoma fimbria*) in the northeast Pacific Ocean

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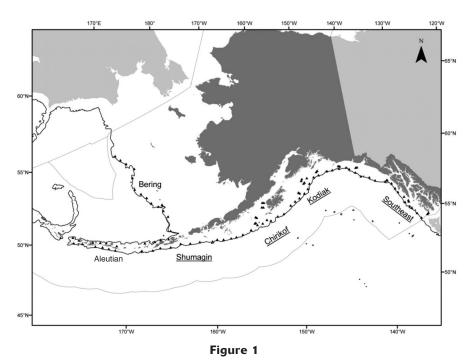
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Sablefish (Anoplopoma fimbria) are a long lived, commercially important finfish abundant along the upper continental slope in the North Pacific, with catches ranging from 10,000 to 35,000 metric tons (t) in Alaskan waters during the last 2 decades (Hanselman et al., 2010). Using data provided by the NOAA National Marine Fisheries Service (NMFS) annual domestic longline survey, we modeled the sablefish population with statistical catch-atage split by sex (Hanselman et al., 2006). To estimate fish abundance accurately, age-structured models require several biological parameters, such as growth, maturity, natural and fishing mortality, and annual age or length data, as well as annual abundance estimates and catches (Quinn and Deriso, 1999). Errors in growth estimates can drastically affect the spawner-per-recruit threshold used to recommend quotas for commercial fish catches. Overestimation of growth rates may result in overestimation of biomass and, therefore, recommendation of harvest rates that are too high (Quinn and Deriso, 1999). Conversely, underestimation of fish growth can lead to underutilization of a resource and lost economic yield. Growth parameters for Alaskan sablefish have not been updated

for stock assessment purposes since Sasaki's published research (1985). When age-length conversion matrices were first added to the Alaskan sablefish stock assessment in 1995, they were constructed from data (1981–93) that were collected under a lengthstratified sampling scheme. These data were randomized according to the method of Kimura and Chikuni (1987), but they were collected in limited areas and over just a few years and were aggregated in a way that put too much weight on large fish (>66 cm FL). For these reasons, we speculated that size estimates used in the assessment of the sablefish population of Alaska have been too large. Meanwhile, many more sablefish have been aged over a larger geographic area. Additionally, since the last update on sablefish growth rates, significant changes in lengthat-age have been discovered for other demersal species, such as Pacific halibut (*Hippoglossus stenolepis*) and other flatfish species in the northeast Pacific Ocean. These changes have caused substantial changes in stock assessment results (Walters and Wilderbuer, 2000; Clark and Hare, 2002). Because both sablefish and Pacific halibut have similar fisheries and are such commercially valuable fishes, a change in the assessment



Map showing the 6 management regions covered by the NMFS sablefish (*Anoplopoma fimbria*) longline survey during the period of 1981–2004 and used for growth comparisons in our study: eastern Bering Sea, Aleutian Islands, and the Gulf of Alaska management regions of Shumagin, Chirikof, Kodiak, and Southeast. Underlined regions are those considered to be in the Gulf of Alaska. Triangles represent individual survey stations.

of one of these fishes suggests that an update of the assessment of the other fish is needed.

A growth analysis of sablefish in the Gulf of Alaska (Sigler et al., 1997) revealed values similar to results from the earlier analysis by Sasaki (1985); therefore, the earlier growth estimates for sablefish in Alaska have continued to be used in models for sablefish stock assessment. In the last 20 or more years, however, more sablefish from a wide geographic area have been aged and another evaluation of growth is warranted.

The overall goal for this study was to evaluate whether changes in growth of sablefish in Alaska have occurred since 1985. Specifically, our objectives were 1) to reevaluate estimates of length at age and weight at age, 2) to compare these new estimates among regions and over time for each sex, 3) to evaluate the sensitivity of the current stock-assessment model using this new growth information and evaluate the implications for management of sablefish in Alaska, and 4) to search for biological or environmental reasons for any discovered changes.

Materials and methods

Data collection

We used data available from the annual longline survey conducted cooperatively by the Fisheries Agency of

Japan (1981–94) and the NMFS Alaska Fisheries (AFSC) (1988–present). The Fisheries Agency of Japan conducted the survey solely from 1981 to 1987. Starting in 1988, the NMFS conducted the survey cooperatively with Japan between 1988 and 1994, creating survey overlap between the efforts of the 2 countries. NMFS took over conducting the survey solely in 1995. Samples were collected from June through September, 1981 to 2004, in all 6 management regions defined by the North Pacific Fishery Management Council (NPFMC). Four of these regions are in the Gulf of Alaska (GOA): Southeast, Kodiak, Chirikof, and Shumagin. The other 2 management regions are in the eastern Bering Sea (EBS) and Aleutian Islands (AI) (Hanselman et al., 2010; Fig. 1). Predefined stations have been sampled along the upper continental slope at depths of 200-1000 m in the GOA annually from 1981 to the present and in the BSAI at 2 different schedules annually from 1981 to 1994 and in alternating years from 1996 to the present (EBS in odd years and AI in even years). At each station, 7200 hooks baited with cut squid (Illex spp.) and spaced 2 m apart are set (Sigler and Fujioka, 1988).

Length measurements and otoliths of sablefish have been collected since the inception of the Japan-U.S. cooperative longline survey in 1981, and data collection has continued as part of the current NMFS domestic longline survey that started in 1988. However, these data were collected under 2 different sampling designs.

In the first sampling design, fish samples from the Japan-U.S. cooperative survey (1981–93) were stratified by length (5 fish were aged per centimeter length per sex per area). The sex and fork length (FL) of all collected fish were recorded. No assessment of weight was performed.

A change of sampling method took place in 1996 in the NMFS domestic longline survey. A random subsample of fish was collected (if the first hook of a skate contained a sablefish, it was sampled) to acquire age and weight data (Hanselman et al., 2010). A "skate" is a unit of gear that is 100 m long and contains 45 hooks. As before, fork-length measurements and sex of all fish brought aboard were recorded. Age was determined from otoliths stored in 50% ethanol by using the break and burn technique (Beamish and Chilton, 1982; Nielsen and Johnson, 1983).

Length-at-age analysis

Mean length-at-age was calculated from the age-length data in 3 ways by 3 different strata: 1) by sex, region, and survey period, 2) by sex and survey period, and 3) by sex and region. Data were split between the 2 sexes because it was already known that male and female sablefish have different growth rates (Sasaki, 1985) and because the current sablefish assessment model is split by sex. Data were split into 2 periods by using the shift in sampling design: 1981–93 and 1996–2004 (no otoliths were collected in 1994 and 1995). Fish aged 31 years and older were pooled into a 31+ age category (Hanselman et al., 2010). Only the 6 regions sampled consistently across the entire time series (Southeast, Kodiak, Chirikof, Shumagin, EBS, AI; Fig. 1) were used in regional comparisons.

Estimates of mean length-at-age produced by simple averaging with length-stratified data are biased. This bias is caused by aging smaller and larger specimens more often than would be aged under a random sampling design. The mean size-at-age for early age groups is too small, and the mean size-at-age for the oldest age groups is too large (Goodyear, 1995; Sigler et al., 1997; Bettoli and Miranda, 2001). As a result, we determined that size estimates used in the assessment of the sablefish population in Alaska have been too large. To account for stratification, the length-frequency distribution from the survey catch data was used in combination with the length-stratified age samples to create bias-corrected age-length estimates for 1981–93 (Goodyear, 1995; Sigler et al., 1997). The following equation was used (Bettoli and Miranda, 2001):

$$L_{a} = \frac{\sum_{j} N_{j} (n_{a,j} / n_{j}) l_{j}}{\sum_{i} N_{j} (n_{a,j} / n_{j})} \ . \tag{1}$$

Here, $L_{\rm a}$ = the estimated mean length at age a; $l_{\rm j}$ = the median of the length group j; $N_{\rm j}$ = the number of fish in the jth length group;

 n_j = the number of fish subsampled for age determination in the jth length group; and

 $n_{a,j}$ = the number of fish in age group a in the subsample from the jth length group.

Sablefish growth was modeled with the von Bertalanffy (VB) age-length model, which was fitted by non-linear least squares weighted by sample size,

$$\bar{L}_a = L_{_{\infty}}(1 - e^{-k(a - t_o)}) + \varepsilon_a. \tag{2}$$

Here, L_{∞} = the average maximum length;

 κ = the mean growth coefficient;

 t_0 = the mean theoretical age a fish would have been at zero length; and

 ε_{a} = an additive normally distributed error term.

Standard errors, correlation estimates, and 95% confidence intervals for growth curve parameters were estimated by the Hessian method of second partial derivatives (Quinn and Deriso, 1999).

Individual parameters of growth models were compared using the univariate Fisher-Behrens test. Likelihood ratio tests (LRTs) were carried out to determine whether growth curves differed between the 2 survey periods, among regions, or both survey period and region (Kimura, 1980; McDevitt, 1990; Sigler et al., 1997). The LRT for comparing nested models was log-transformed and calculated as follows:

$$-N\ln(RSS_{\scriptscriptstyle E}/RSS_{\scriptscriptstyle P}) \sim \chi^2. \tag{3}$$

Here, N = the total number of observations (of length-at-age); and

 RSS_F and RSS_R = the estimated residual sum of squares (RSS) of the full (F) and reduced (R) models, respectively (Kimura, 1980; Quinn and Deriso, 1999).

The degrees of freedom for the test are the difference in the number of parameters between the full and reduced models. The increase in the RSS between each of the reduced models and the full model was used to test for temporal and spatial effects. This increase also was used to further test for differences among pairs of regions and between survey periods within each region if a regional or temporal effect was discovered.

Weight-at-age analysis

Weight-at-age curves were fitted to data by sex and region strata. Sasaki (1985) reported sablefish weight estimates; however, no weight data were collected before 1996 in the domestic longline survey; therefore, no temporal changes were investigated. Because weight data were collected only from random samples, no correction for stratification was needed. Fish of ages >31 were pooled into a 31+ age category (Hanselman et al., 2010). To determine weight-at-age for the stock assess-

ment model, first the length-weight relationship was determined by using the typical nonlinear allometric relationship:

$$\hat{W}_{\alpha} = \alpha \cdot l + \varepsilon. \tag{4}$$

Here, length l, α , and β are parameters estimated by procedures for nonlinear least squares. This equation was combined with the length-at-age model to construct the weight-at-age model. The weight-at-age model was log-transformed to the following equation because the data had a multiplicative error structure:

$$\ln \hat{W}_{\alpha} = \ln W_{\alpha} + \beta \cdot \ln(1 - e^{(-k(a - t_0))}) + \varepsilon, \tag{5}$$

where ε = a normally distributed error term.

Because of high parameter correlation with only one dependent variable, the allometric parameter β was fixed, determined from the length-weight relationship. The 3 remaining parameters, W_{∞} , κ , and t_0 were estimated by a nonlinear procedure (Quinn and Deriso, 1999).

Two age-weight models were fitted to each sex to test whether sablefish weight-at-age differed by region. The full model used separate growth curves fitted to each of the 6 regions, and the reduced model relied on one growth curve fitted to pooled data. Equation 3 was used to compare the full model against the reduced model at a significance level of α =0.05 (Sigler et al., 1997; Quinn and Deriso, 1999).

Biological and oceanographic explanations for observed changes

Several hypotheses have been formulated to explain the possible change in growth of sablefish in Alaska: interspecific competition with healthy arrowtooth flounder (Atheresthes stomias) populations, intraspecific density-dependent processes, and changing environmental conditions (Hanselman et al., 2006; Maloney and Sigler, 2008). We explored the possibility that temporal growth changes can be attributed to density-dependent effects or to environmental factors, including winter sea-surface temperature (SST), summer SST, and the Pacific Decadal Oscillation (PDO) index.

To test for intra- and interspecific density-dependence, linear regressions were performed between each of the response variables (the growth parameter k, mean length at age 4, and mean length at age 6), and each of the explanatory variables (biomass values for age-2 sablefish, age-4+ sablefish, and age-4+ arrowtooth flounder). Biomass estimates were obtained from the 2008 Alaskan sablefish stock assessment (Hanselman et al., 2007) and 2008 Alaska arrowtooth flounder stock assessment (Turnock and Wilderbuer, 2007). Growth estimates were taken from data pooled across the entire series, 1981–2004, for all regions, fitted to the von Bertalanffy growth curve. Significance was determined using a level of α =0.05, and then the coefficients of

determination (r^2) were used to assess the explanatory power of the model.

To discern the effect of density-dependence while sablefish were in the juvenile stage, abundance estimates for sablefish and arrowtooth flounder were lagged by 2, 3, and 4 years. This calculation was made to compare the growth rate and size of sablefish at age 4 and age 6 with the abundance of sablefish and arrowtooth flounder exposed to while young of the year (YOY), and at age 1, age 2, and age 3.

To examine the influence of environment on growth, linear regressions were performed between each of the response variables (mean length at age 4 and mean length at age 6), and each of the explanatory variables (winter SST, summer SST, and an index used to quantify the PDO). Because YOY and juvenile sablefish are more susceptible to surface temperatures and are considered to be more susceptible to oceanographic variability than are adults, we lagged the SST by 2, 3, and 4 years to compare the size of an age 4 sablefish with the SST exposed to while as a YOY, and at age 1, and age 2, and we lagged the SST by 4, 5, and 6 years to compare the size of an age 6 sablefish with the SST exposed to as a YOY, and at age 1 and age 2.

Monthly values of the PDO index were obtained from the Joint Institute for the Study of Atmosphere and Oceans (Mantua et al., 1997; http://jisao.washington. edu/pdo/PDO.latest, accessed January 2008; http:// www.beringclimate.noaa.gov/data/index.php, accessed January 2008), which incorporated data from the United Kingdom's Meteorological Office's (UKMO) Historical SST Dataset and Reynolds' Optimally Interpolated SST. SST values for the Bering Sea (http://www.beringclimate.noaa.gov/data/BCresult.php, accessed January 2008) and the GOA (Kaplan et al., 1998; http://www. esrl.noaa.gov/psd/data/timeseries/, accessed January 2008) were taken from a data set of SST anomalies, Kaplan Extended SST V2, provided by the Physical Sciences Division of NOAA's Earth System Research Laboratory, Boulder, Colorado.

Management implications

We examined the sensitivity of the current stock assessment model to the use of the new growth information from our study. The AFSC models the Alaskan sable-fish population with statistical catch-at-age methods. It uses a penalized maximum likelihood function to estimate parameters simultaneously to obtain the best fit between predicted and observed data. Data in the sablefish stock assessment model include catch, several abundance indices, and age and length data from the longline survey and from the fishery. For details of the assessment model, see Hanselman et al. (2010).

This assessment model in its current form uses agelength conversion matrices, not empirical age-length keys, to describe the probability that a fish of a given age is of a certain length. This model uses these age-length conversion matrices to predict lengths. The weight-at-age is input as a fixed vector for the whole

Table 1

Growth parameters (L_{∞} =average maximum length, κ =mean growth coefficient, t_0 =mean theoretical age a fish would have been at zero length) for male sablefish ($Anoplopoma\ fimbria$) in Alaska estimated with data from the annual longline survey conducted cooperatively by the Fisheries Agency of Japan and the Alaska Fisheries Science Center of the National Marine Fisheries Service in 1981–93 and by the Alaska Fisheries Science Center during 1996–2004. Estimates were made for 6 management regions with the von Bertalanffy model fitted to age-length data stratified by region and survey period, where n is the number of agelength observations and an asterisk (*) indicates a significant difference between the 2 periods, 1981–93 and 1996–2004, in that particular region. The 6 regions are the Chirikof, Kodiak, Shumagin, and Southeast, all in the Gulf of Alaska, and the eastern Bering Sea and Aleutian Islands. Standard errors of the mean (SE) are provided in parentheses. RSS=residual sum of squares.

Region	Survey period	$L_{\scriptscriptstyle\infty}$	k	t_0	RSS	n
All regions combined	1981–93	64.6 (0.38)	0.287 (0.03)	-2.07 (0.60)	3644	3429
	1996-2004*	67.7 (0.16)	0.292(0.01)	$-2.25\ (0.21)$	904	2614
	1981-2004	66.2(0.28)	0.30 (0.03)	-2.19(0.51)	18,954	6043
Chirikof	1981-93	$70.2\ (1.02)$	0.239 (0.03)	-2.288(0.70)	448	128
	1996-2004*	67.3* (0.48)	$0.335\ (0.06)$	$-1.617\ (1.02)$	487	294
	1981-2004	67.8 (0.45)	$0.327\ (0.03)$	-1.287(0.48)	1230	422
Aleutian	1981-93	67.0 (0.55)	0.195 (0.03)	1329	726	
	1996-2004	68.1 (0.48)	0.243(0.02)	-2.898(0.59)	478	543
	1981-2004	67.0 (0.55)	$0.195\ (0.03)$	$-5.101\ (1.23)$	2235	1269
Kodiak	1981-93	65.1 (0.66)	0.352(0.06)	-1.685(0.79)	1737	598
	1996-2004*	66.6 (0.34)	0.357 (0.07)	-2.052(1.21)	606	542
	1981-2004	$66.0\ (0.39)$	$0.365\ (0.04)$	$-1.423\ (0.55)$	3239	1140
Shumagin	1981-1993	64.3 (0.50)	0.440 (0.07)	-0.793(0.60)	1625	684
-	1996-2004*	70.1 (0.98)	0.193 (0.03)	-4.501(1.08)	438	267
	1981-004	$65.3\ (0.49)$	0.352(0.05)	$-1.669\ (0.63)$	2914	951
Bering	1981-1993	64.9 (0.64)	0.197 (0.04)	-6.264(1.67)	1154	757
	1996-2004*	69.3* (0.50)	0.237 (0.03)	-3.48(0.86)	600	363
	1981-2004	66.7 (0.71)	$0.186\ (0.03)$	$-6.250\ (1.69)$	4695	1120
Southeast	1981-1993	67.0 (0.79)	0.219 (0.04)	-3.827(1.19)	1998	536
	1996-2004*	68.3 (0.37)	0.307 (0.04)	-1.714 (0.73)	829	605
	1981-2004	67.7 (0.45)	0.271 (0.03)	-2.384(0.65)	4136	1141

time series. If the conversion matrices and the weightat-age vector are developed with growth data that do not correspond with the true underlying growth, they can bias the stock assessment (Hanselman et al., 2007). Using the updated growth curves from the 2 survey periods reported in this study, we created new lengthage conversion matrices and a new weight-at-age vector and applied them to the current stock assessment model (Hanselman et al., 2007).

Results

Length-at-age analysis

Our results indicate that previously used growth estimates in the stock assessments of sablefish in Alaska (assessments before 2007) obtained from length-stratified sampling were erroneously too large. A comparison of growth estimates from 1981–93 data updated to correct for this bias with estimates from more recent data (1996–2004) indicates that sablefish are growing to a larger maximum size in more recent years. The

estimates of average maximum length (L_∞) used in the stock assessment of Alaskan sablefish in 2007 (Sasaki's [1985] estimate from length-stratified data) were 69 cm FL for males and 83 cm FL for females (Hanselman et al., 2006). Maximum lengths were smaller in our biascorrected estimates for the same time period (1981–93; Tables 1, 2) than in the 2007 stock assessment model: males=64.6 cm FL, females=75 cm FL. Our estimates for the more recent period (1996–2004; Tables 1, 2) are significantly larger (males=67.7 cm FL, females=80.1 cm FL) than the bias-corrected estimates from the earlier period, but these estimates for the recent period are still smaller than the estimated lengths incorrectly used in earlier stock assessments.

The growth rates of male and female sablefish in Alaska differed significantly across areas and survey periods (P<0.05; Tables 3, 4). In the data from the earlier period, both male and female sablefish display smaller asymptotic lengths (L_{∞}) and younger ages t_o than do sablefish in data from the more recent time period (Fig. 2). Significant differences were detected between the 2 male growth curves (P<0.001; Table 1). Test results on the female data showed that the L_{∞}

Table 2

Growth parameters (L_{∞} =average maximum length, κ =mean growth coefficient, t_0 =mean theoretical age a fish would have been at zero length) for female sablefish ($Anoplopoma\ fimbria$) in Alaska estimated with the von Bertalanffy model fitted to age-length data stratified by region and time period, where n is the number of age-length observations and an asterisk (*) indicates a significant difference between the 2 survey periods, 1981–93 and 1996–2004, for that particular region. Standard errors of the mean (SE) are presented in parentheses. RSS=residual sum of squares.

Region	Survey period	$L_{\scriptscriptstyle\infty}$	k	t_0	RSS	n
All regions combined	1981–93	75.0 (0.35)	0.263 (0.01)	-2.00 (0.29)	3945	4788
	1996-2004*	80.1* (0.26)	0.223(0.01)	-1.92(0.14)	1191	3493
	1981–2004	77.1 (0.77)	$0.25\ (0.02)$	-1.91(0.32)	23,963	8281
Chirikof	1981-93	75.3 (1.29)	0.298(0.04)	$-0.798 \ (0.58)$	1275	165
	1996-2004	77.5 (0.51)	$0.294\ (0.02)$	$-0.802\ (0.40)$	609	485
	1981-2004	76.8(0.56)	0.302(0.02)	$-0.697\ (0.33)$	2201	650
Aleutian	1981-93	73.8 (0.84)	0.197 (0.04)	-3.888(1.30)	4839	1037
	1996-2004*	77.9* (1.31)	0.218 (0.03)	-2.246(0.69)	2191	795
	1981–2004	73.8(0.69)	0.248(0.03)	$-2.210\ (0.70)$	9466	1832
Kodiak	1981-93	74.5 (0.84)	$0.305\ (0.04)$	-1.288(0.51)	3334	831
	1996-2004*	78.6*(0.50)	0.311 (0.03)	-0.49(0.42)	1081	602
	1981–2004	76.7 (0.63)	0.292(0.03)	$-1.220\ (0.40)$	7231	1433
Shumagin	1981-93	73.2(0.69)	0.295(0.03)	$-1.724\ (0.58)$	1993	975
	1996-2004*	81.6* (1.30)	0.177*(0.02)	-3.046(0.49)	877	563
	1981-2004	74.7(0.72)	0.256(0.02)	-2.028(0.48)	4830	1538
Bering	1981-93	68.3 (0.59)	0.351 (0.05)	-1.79(0.76)	1925	993
	1996-2004*	76.4* (0.87)	0.223*(0.02)	-2.746(0.62)	695	533
	1981-2004	$70.2\ (0.74)$	0.306(0.05)	$-2.163\ (0.82)$	6979	1526
Southeast	1981-93	78.3 (1.02)	0.189 (0.03)	-3.579(0.95)	4488	787
	1996-2004*	80.8* (0.50)	0.273* (0.02)	-0.816*(0.42)	964	515
	1981-2004	79.3 (0.72)	0.217 (0.02)	-2.489(0.61)	8949	1302

Table 3

Comparison of 4 age-length models used for analyses of regional and temporal effects on growth of male sablefish (Anoplopoma fimbria) in Alaska. The most reasonable model, indicated with an asterisk (*), is the reduced model with a residual sum of squares (RSS) not significantly greater than the RSS for the full model. n=the number of observations, and χ^2 =the chi-squared value.

Model	RSS	χ^2	P	No. of parameters	n
Data split by each combination of region and survey period *	11,729			36	
Data split into 2 survey periods	16,354	114.7	< 0.001	6	
Data split into 6 regions	18,449	156.3	< 0.001	18	
All data pooled	21,642	211.3	< 0.001	3	6043

estimates (P<0.001) and the growth curves were significantly different (P<0.001; Table 2) between the 2 periods.

A comparison of male growth curves between the 2 survey periods, stratified by region, showed a consistent pattern of slower growth and smaller asymptotic lengths during the earlier survey period. There were significant differences between growth curves fitted to the 2 periods in 5 of the 6 management regions (Fig. 3, Table 1). Fish from most regions had a smaller asymp-

totic length and slower growth during the earlier survey period than during the more recent period. In contrast, during the earlier survey period versus the more recent one, males in the Shumagin region reached a smaller maximum length but grew faster and males in the Chirikof region displayed a larger asymptotic length and grew more slowly.

Age-length relationships for females between the 2 survey periods differed significantly in 5 of the 6 management regions (Fig. 4, Table 2). Female asymptotic

Table 4

Comparison of 4 age-length models used for analyses of regional and temporal effects on growth of female sablefish ($Anoplo-poma\ fimbria$) in Alaska. The most reasonable model, indicated with an asterisk (*), is the reduced model with a residual sum of squares (RSS) not significantly greater than the RSS for the full model. n=the number of observations, and χ^2 = the chi-squared value

Model	RSS	χ^2	P	No. of parameters	n
Data split by each combination of region and survey period *	24,271			36	
Data split into 2 survey periods	48,717	238.9	< 0.001	6	
Data split into 6 regions	39,656	168.4	< 0.001	18	
All data pooled	68,900	357.9	< 0.001	3	8281

lengths ranged from 68.3 to 78.3 cm FL during the earlier survey period, with the lowest maximum lengths occurring in the EBS region and highest lengths in the Southeast. In the more recent period, asymptotic lengths were much larger, ranging from 76.4 cm (EBS) to 81.6 cm FL (Shumagin region). During the earlier time period, compared to the more recent one, AI, Kodiak, and Southeast females grew slower and Shumagin, Chirikof, and EBS females displayed the opposite pattern.

Several tests for differences in growth between pairs of regions were significant (P<0.05) for both sexes. Male sablefish showed fewer differences in growth between regions, with Chirikof males differing significantly from Shumagin (P=0.02), AI (P=0.01) and EBS (P=0.01) males, and EBS males differing significantly from males in the Southeast (P=0.04). For female sablefish, most regional comparisons were highly significant, with the exception of the difference between AI and Shumagin (P=0.55), Chirikof and Kodiak (P=0.12) and Southeast (P=0.12), and Kodiak and Southeast (P=0.37).

A consistent pattern of smaller estimates of t_0 , the theoretical age at zero length, was seen for both male and female sablefish in the earlier survey period, than estimates for the more recent survey period. These smaller values could be a result of small sample sizes of fish <4 years old in the older data sets (Sigler et al., 1997).

Weight-at-age

The age-weight relationship differed significantly among regions in both males (P<0.001, Table 5) and females (P<0.001, Table 6). Maximum weights for male (Table 7) and female (Table 8) sablefish in all regions combined were smaller than the values used in the current stock assessment model, likely because of differences in age at length. Female sablefish in pooled regions reached a higher average maximum weight-at-age than did male sablefish, 5.5 kg versus 3.2 kg, respectively.

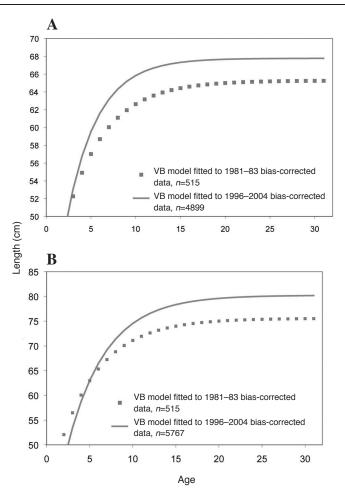
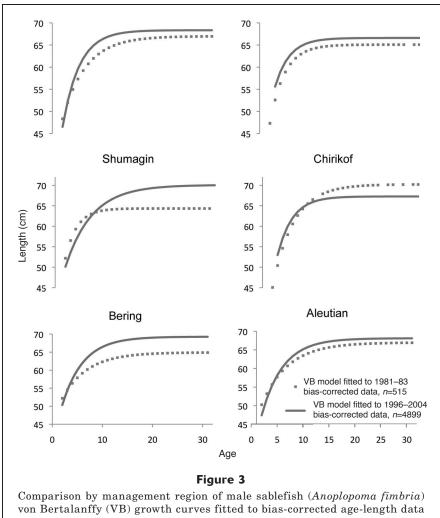


Figure 2

Comparison of (A) male and (B) female sablefish (Anoplopoma fimbria) von Bertalanffy (VB) growth curves (for all of the 6 management regions in Alaska combined) fitted to biascorrected age-length data from 1981 through 1993 (shown as a dashed line) and fitted to age-length data from 1996 through 2004 (shown as a solid line). Note the different scales on the y-axis of each figure. Sample sizes (n) contributing to the VB analysis are listed in the legends.



Comparison by management region of male sablefish ($Anoplopoma\ fimbria$) von Bertalanffy (VB) growth curves fitted to bias-corrected age-length data from the period 1981–93 (shown as a dotted line) and fitted to age-length data from the period 1996–2004 (shown as a solid line). Sample sizes (n) contributing to the VB analysis are listed in Table 1.

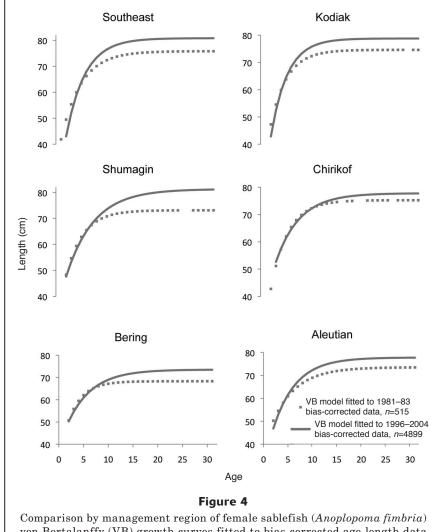
Table 5

Comparison of 2 age-weight models used for analyses of regional effects on growth of male sablefish (*Anoplopoma fimbria*) in Alaska. The most reasonable model, indicated with an asterisk (*), is the reduced model with a residual sum of squares (RSS) not significantly greater than the RSS for the full model. n=the number of observations, and χ^2 =the chi-squared value.

Model	RSS	χ^2	P	No. of parameters	n
Data split into 6 regions*	144.4			24	
All data pooled	151.8	174.6	< 0.001	4	2614

Maximum average weights among male sablefish varied slightly, but still significantly (P<0.05), by region (Table 7). The lightest males, with maximum weight of 3.0 kg, were found in the Kodiak region, and the heaviest males, with maximum weight of 3.4 kg, were observed in the EBS region. Females showed a larger

range of average maximum weights, from 4.7 kg in the EBS region to 5.8 kg in the Shumagin region (Table 8). Several maximum weights differed significantly between regions for both sexes; similar age-weight relationships were seen only for females in the AI and Shumagin regions and the Kodiak and Southeast regions.



Comparison by management region of female sablefish ($Anoplopoma\ fimbria$) von Bertalanffy (VB) growth curves fitted to bias-corrected age-length data from the period 1981–93 (shown as a dotted line) and fitted to age-length data from the period 1996–2004 (shown as solid line). Sample sizes (n) contributing to the VB analysis are listed in Table 2.

Table 6

Comparison of 2 age-weight models used for analyses of regional effects on growth of female sablefish ($Anoplopoma\ fimbria$) in Alaska. The most reasonable model, indicated with an asterisk (*) is the reduced model with a residual sum of squares (RSS) not significantly greater than the RSS for the full model. n=the number of observations, and χ^2 =the chi-squared value.

Model	RSS	χ^2	P	No. of parameters	n
Data split into 6 regions *	262	145 5	0.001	24	0.400
All data pooled	277	145.5	< 0.001	4	3493

Male sablefish in all of the 6 regions displayed highly significant differences in weight-at-age, although their growth curves appeared similar. These minor growth differences may not be of biological importance and may not need to be considered for assessment purposes.

Biological and oceanographic explanations for observed changes

There was no evidence of a common climatic forcing factor among the management regions in relation to

Table 7

Estimates of weight-at-age parameters (W_∞ =average maximum weight, κ =mean growth coefficient, t_0 =mean theoretical age a fish would have been at zero weight) for male sablefish ($Anoplopoma\ fimbria$) in Alaska determined with the von Bertalanffy model fitted to age-weight data for the pooled survey periods of 1996–2004 stratified by region and combined for Alaskan waters (W_∞ = average maximum weight, κ =mean growth coefficient, t_0 =mean theoretical age a fish would have been at zero weight). Standard errors of the mean (SE) are presented in parentheses. β was fixed at 3 and is, therefore, not included in this table. n=the number of age-weight observations.

	W_{\sim}	k	t_0	RSS	n
All regions pooled	3.2 (0.03)	0.355 (0.01)	-1.113 (0.18)	152	4889
Aleutian	3.3 (0.09)	0.285(0.03)	-1.949(0.50)	38.1	543
Bering	3.4 (0.07)	0.313 (0.03)	-1.630(0.47)	17.4	363
Chirikof	3.1 (0.06)	0.460 (0.07)	0.019(0.59)	13.9	294
Kodiak	3.0 (0.03)	0.762 (0.10)	1.106(0.35)	23.2	542
Shumagin	3.3 (0.15)	0.272(0.04)	-2.252(0.73)	18.3	267
Southeast	3.2 (0.04)	0.421 (0.03)	0.019 (0.30)	33.5	605

Table 8

Estimates of weight-at-age parameters for female sablefish (Anoplopoma fimbria) determined with the von Bertalanffy model fitted to age-weight data for the pooled survey period of 1996–2004 stratified by region and combined for all Alaskan waters (W_{∞} = average maximum weight, κ =mean growth coefficient, t_0 =mean theoretical age a fish would have been at zero weight). Standard errors (SE) are presented in parentheses. β was fixed at 3 and is, therefore, not included in this table. n=the number of age-length observations.

	$W_{\scriptscriptstyle \infty}$	k	t_0	RSS	n
All regions pooled	5.5 (0.06)	0.238 (0.01)	-1.387 (0.13)	277	5767
Aleutian	5.5(0.22)	0.209(0.02)	-2.092(0.37)	71.5	795
Bering	4.7 (0.16)	0.267(0.02)	-1.598(0.42)	34.2	533
Chirikof	5.0 (0.12)	0.326(0.03)	-0.206(0.33)	29.5	485
Kodiak	5.2 (0.10)	0.336(0.02)	-0.064(0.27)	42	602
Shumagin	5.8 (0.33)	0.197(0.02)	-2.349(0.37)	47.9	563
Southeast	5.5 (0.11)	0.300 (0.02)	-0.114(0.27)	38.2	515

changes in sablefish growth. Arrowtooth flounder biomass likewise was unrelated to sablefish growth. Intraspecific, density-dependent effects appeared to be a more plausible explanation for changes in growth of Alaskan sablefish because measures of age-4+ biomass at some lags (in years) were correlated with reduced growth. Significant relationships included mean length at age 6 regressed on the total age-4+ biomass (coefficient of determination $[r^2]$ =0.28, P=0.02), and mean length at age 4 regressed on the age-4+ biomass from 3 years prior, when the sablefish were age 1 (r^2 =0.5, P=0.04). Both of these analyses revealed a decrease in average length with an increase in biomass. Although not significant, a negative correlation between the growth coefficient k and both age-2 and age-4+ biomass also was evident.

Management implications

The use of updated growth data (length-at-age fitted to 2 survey periods and weight-at-age from the more recent

survey period) improved the fit of the current AFSC assessment model of sablefish to the data and slightly increased the recommended fishing-induced mortality. The updated growth also had an effect on the estimated time series of female spawning biomass (Fig. 5). Three prominent changes in the estimates of female spawning biomass were observed when the assessment model that used the estimates of Sasaki (1985) was run with our updated growth estimates: 1) the initial estimated spawning biomass in 1960 was substantially higher, 2) the minima in female spawning biomass are lower, and 3) the estimated spawning biomass was slightly lower for recent years (2000 to present). The increase, between the use of Sasaki estimates and our bias-corrected data, in estimated spawning biomass in 1960 is biologically reasonable because fishing mortality before 1960 was low (Hanselman et al., 2007). The lower spawning biomass minima in the updated series imply that the resource was not managed as conservatively as expected during the periods of lowest biomass. Results from our study show that recent estimates of female spawning biomass from our updated growth data are slightly lower but appear to be rising at a steeper trajectory than recent estimates determined with Sasaki's growth data in the current model.

Discussion

Although a specific cause (changes in sampling method, environmental factors, or differences in fish abundance) and time of the changes observed in sablefish growth were not identified, these changes have occurred. The division of the sablefish age-and-length data set into 2 growth regimes was not based on any detectable shift in growth but on a change in the sampling design of the longline survey. Separating the data into 2 time intervals might not completely capture the temporal pattern of changes in growth. Sablefish growth, for example, might have changed slowly, instead of in a stepwise fashion. However, we also analyzed growth data by individual years, and no obvious temporal patterns were noted. It is unlikely that other changes in the survey could explain apparent differences in growth over the time series because of the standardization in most other aspects of the survey design between the 2 periods (Hanselman et al., 2007). In addition, both the ages and the abundance indices for the sablefish stock assessment are treated as separate

surveys (Japan-U.S. cooperative and domestic NMFS

longline surveys) with different catchability values and

sensitivities, and therefore updated growth estimates

fitted to these 2 survey periods (which theoretically

represent the 2 surveys) follow accordingly.

Aging error could be a very plausible cause for seeing changes in growth when in fact growth has not changed. Although Heifetz et al. (1999), among others, have validated the currently accepted aging practices (Beamish and Chilton, 1982) and have examined sources of error in the aging of sablefish, there is still much disagreement on the possibility of obtaining reliable ages from sablefish otoliths (Pearson and Shaw, 2004). We feel aging error is an unlikely cause for the growth changes seen in this study. The NMFS stock assessment of sablefish in Alaska uses an aging error matrix, one with known ages that make it particularly realistic. Aging error should not have a major effect on growth estimation if the aging error is imprecise but not biased, and Heifetz et al. (1999) found bias to be at a minimum for younger ages when most growth is occurring. In addition, otoliths for Alaskan sablefish have been read consistently by the same age-reader using the same protocol during the timeline of this study and agereader agreement tests have been in place throughout that entire time thus, removing the possibility of an age-reader effect.

The best documented causes for change in growth of various fish species (juvenile sablefish; Pacific halibut; yellowtail flounder [Limanda ferruginea]; haddock

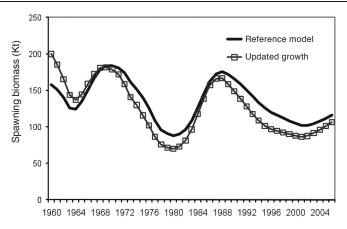


Figure 5

Comparison of time series of spawning biomass, measured in kilotons (kt), of female sablefish (*Anoplopoma fimbria*) in Alaska from the sablefish reference model (Hanselman et al., 2006; shown as a solid line) and from the same model with updated growth parameters from our study (shown as line with open boxes).

[Melanogrammus aeglefinus]; and Pacific chub mackerel [Scomber japonicas] have been density dependence and environmental conditions (Ross and Nelson, 1992; Clark et al., 1999; Wilson, 2000; Sogard and Olla, 2001; Watanabe and Yatsu, 2004). In our study, we did find evidence that changes in growth may be the result of intraspecific density-dependent mechanisms. It appears that sablefish growth is most influenced by fish density that fish are exposed to while in the larval and juvenile stages. This response in turn is linked highly to favorable environmental conditions for recruitment and YOY survival (McFarlane and Beamish, 1992; Sigler and Lunsford, 2001; Sogard and Olla, 2001). Results of our growth analysis show that sablefish from the more recent time period of our study (1996–2004), when compared to sablefish from earlier time period of our study (1981-93), exhibited faster growth rates and reached larger sizes-at-age as biomass steadily declined (Hanselman et al., 2007). Although the Alaskan sablefish population is considered to be at a sustainable, healthy level and is neither overfished nor approaching an overfished level, it is by no means close to its peak abundances of the late 1980s and early 1990s (Hanselman et al., 2010). Across the time series, abundance of Alaskan sablefish was characterized by relatively consistent high values (e.g., age-4+ abundance of 489 kt in 1986) during the early period of this study and consistently lower values (e.g., age-4+ abundance of 223 kt in 2000) during the more recent period (Hanselman et al., 2010). Since 1988, abundance has decreased substantially, whereas growth has increased significantly (Hanselman et al., 2007).

Although no direct relationships were observed between sablefish growth and any of the tested environmental factors, it is important to note that evaluating

which environmental variables are appropriate proxies for the ambient conditions that influence growth may be done best with data from smaller time and space scales than with the data available for the purposes of this study and that environmental data at fine temporal or spatial scales are likely to be difficult to interpret for fish species that move long distances (Heifetz and Fujioka, 1991; Kimura et al., 1998). The use of broad geographic and time-averaged representations of environmental effects misses short-term changes in temperature regimes brought on by weather events, such as wind-driven mixing and upwelling. In the future, to determine an appropriate scale, results from the extensive tagging studies with sablefish should be examined (the Fisheries Agency of Japan and NMFS have been tagging sablefish throughout the entire geographic range of the annual longline survey since 1972). Further, analysis should be done with the El Niño-Southern Oscillation as an environmental variable in a similar manner to work done by Kimura et al. (1998) who found growth of groundfish species to be significantly enhanced by events of the El Niño-Southern Oscillation.

There appear to be significant differences in growth patterns among management regions; the GOA regions consistently displayed the largest (in asymptotic length and average size) sablefish for both sexes in this study and in past research (McDevitt, 1990; Sigler et al., 1997). Sasaki (1985) reported regional differences in mean sizes between young sablefish from the EBS, AI, and GOA and a temporal increase in weight-at-age in the EBS from the 1960s to the late 1970s similar to the temporal increase in growth (length-at-age) reported here. Sasaki's reported differences were minor and not significant. McDevitt (1990) reported significant growth differences between the EBS and GOA but did not find significant differences in growth between the AI and EBS and the AI and GOA. She speculated that her findings were the result of high variability of the data from the AI. Consequently, differences between the AI and EBS regions were not detected because of the low power of the tests. In accord with our results, Sigler et al. (1997) found that female sablefish in the Shumagin and Southeast regions of the GOA differed significantly in growth, but no regional differences were detected for males.

In both the AI and EBS regions, poor model fits and atypical rates of growth and average maximum sizes were noted in this and past studies (McDevitt, 1990). Both of these regions displayed notably high estimates of the growth parameter k, likely because samples from these two regions consisted mostly of larger (>66 cm FL) fish, and smaller (<57 cm FL) fish are required for an accurate estimate of k. Data from both of these regions exhibit the highest variability (large residual population variances) and the poorest fit to the growth curves, compared with data from other regions in this study. The most notable differences among observed sablefish were consistently found in the EBS region, where smaller asymptotic lengths were reported than those for sablefish found in all other regions.

Alaskan sablefish are assessed by the AFSC as one stock, and therefore sablefish found throughout Alaskan waters are assumed to display similar growth rates; however, this stock is highly mobile (Heifetz and Fujioka, 1991; Maloney and Sigler, 2008). Younger fish move into deeper waters onto the slope, moving from the Eastern Gulf of Alaska (EGOA) in a counter clockwise direction through the Central Gulf of Alaska (CGOA) to the Western Gulf of Alaska (WGOA), returning to the EGOA as larger, older fish (Heifetz and Fujioka, 1991; Maloney and Sigler, 2008). In theory, one would not expect there to be many regional differences in sablefish growth and average size-at-age because a large part of the sablefish population moves each year, maintaining a well-mixed population (Heifetz and Fujioka, 1991). Several competing hypotheses are available to explain these observed regional differences: geographic differences in food abundance, oceanographic condition, or sablefish abundance. Any explanation for these regional differences, however, has to be consistent with this observed movement pattern. As with observed geographical variation for the northern anchovy (Engraulis mordax) along the west coast of North America, geographical variation in age composition could have influenced the observed variation in mean size of sablefish in the 6 management regions (Parrish et al., 1985; Saunders et al., 1997). Sablefish in the GOA may have displayed apparently faster growth and larger asymptotic lengths and weights than have sablefish in the AI and EBS regions because size-dependent migration results in a mixture of faster-growing young fish with older spawning fish (Heifetz and Fujioka, 1991). In contrast, in the EBS region, which primarily comprises fish >4 years of age, sablefish might have displayed slower growth because of the absence of the youngest, fastest-growing fish (Quinn and Deriso, 1999; Sogard and Olla, 2001).

Alternatively, varying growth rates might be explained in part by regional differences in abiotic factors, such as oceanographic conditions (Sasaki, 1985; McDevitt, 1990; Saunders et al., 1997; Kuznetsova, 2003). If fish are grouped within a highly migratory population, environmental effects would appear as growth differences between the 6 management regions. Temperature differences may explain the divergence in growth rates between fish in the EBS region and fish in regions in the GOA, such as the Southeast region. Several marine species (e.g., northern anchovy; Atlantic cod [Gadus morhua L.]; walleye pollock [Theragra chalcogramma]; turbot [Scophthalmus maximus]; and blacknose shark [Carcharhinus acronotus]) are of larger sizes and are faster growing in the southern extent of their ranges than in other areas of their distributions (Parrish et al., 1985; Imsland et al., 2001; Kuznetsova, 2003; Armstong et al., 2004; Driggers et al., 2004; Stark et al., 2007).

For the purposes of the management of Alaskan sablefish, updated and corrected growth estimates divided into the 2 survey periods, 1981–93 and 1996–2004, have been incorporated into the Alaskan sablefish stock assessment conducted by the AFSC. We ran the model

used in our study with the data updated through 2010 and found results that were not significantly different from the results of our analysis with data collected through 2004. Therefore, our initial results were used: VB parameter estimates for females from 1996–2010, L_{∞} =79.9, k=0.22, t_0 =-2.23; VB parameter estimates for males from 1996–2010, L_{∞} =68, k=0.273, t_0 =-3.01. The updated growth estimates provide a better fit to the data, and they are the result of decades more age and growth collections with previous size biases corrected. We view these updated growth estimates as a needed and substantial increase in biological realism for the Alaskan sablefish stock assessment model. In the future, growth will be revisited periodically, but as data accumulate, the addition of the newest data should have only nominal effects on recommendations for harvest rates (Hanselman et al., 2007).

Conclusions

In moving closer to estimating true underlying sablefish growth, we have revealed that, historically, the sizes of sablefish modeled in the Alaskan sablefish stock assessment were slightly too large. This study aids in describing the population of sablefish in Alaska more realistically as having a smaller maximum size. The use of these improved estimates will result in more conservative management in the short term but more harvest stability in the future. Although a specific cause and time for the changes in sablefish growth was not identified, these changes have occurred. To properly manage this important economic resource, the updated estimates for growth should continue to be used for the NMFS assessment of the Alaskan sablefish stock.

This study provides an example of the importance of identifying and correcting for biases that may be produced from different data collection strategies and of scientists periodically revisiting life history parameter estimates used in assessment of various stocks. The result of such efforts could mean the difference in overestimation or underestimation of abundance and, in turn, could have an effect on allotted harvest recommendations.

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