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Time Series of Growth in the Genus *Sebastes* from the Northeast Pacific Ocean

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ABSTRACT: Marine fish populations respond to their physical and biotic environment in complex ways. While direct studies may discern short-term responses at the individual level, time series are needed to describe or predict the population level response to environmental variation or cycles. The ageing technique presented in this paper extracts historical growth information from otoliths through sectioning and careful measurement in order to establish time series of growth. Otoliths of two long-lived species, *Sebastes pinniger* and *S. diploproa*, were collected off the west coast of North America in 1977–84. Fish ages ranged from 1 to 86 years; corresponding birth dates were as early as 1896. Otolith measurements allow description of growth at ages 1–6 for several decades of this century. Although the technique has certain limitations, significant interannual variability in growth is observed, and its relationship to the species' environment is interpreted. Within species, coherence in growth among age groups was not always evident; first year growth in *S. diploproa* was particularly different from growth in other years. For both species, growth responses to environmental factors were not clear; the dominant signal in the time series appears to be increased growth rates after about 1970. This signal is apparently related to density-dependent factors (most likely prey availability) associated with stocks depleted by fishing pressure.

Long-term changes in marine fish populations can be caused by physical and biotic factors as well as man-induced changes. An important goal of fisheries research is to evaluate the effect of fishing on population levels, and this task is easily accomplished if natural variability is understood. Determining causal relationships and superimposing fishing mortality can lead to predictive capability; indeed, many studies in fisheries oceanography model past changes in fish stocks with the objective of forecasting future trends in populations for purposes of fisheries management. Long-term biological data sets are also valuable for ecosystem research, particularly in evaluating the range of natural variability (Wolfe et al. 1987). Historical catch records have been used to assess long-term changes in marine fish populations or stock sizes, and such data from many decades are available for some Pacific salmonid stocks (Mysak et al. 1982; Rogers 1984), for several North Atlantic fisheries (Cushing 1982), and in the Southern Hemisphere for Tasmanian fish populations (Harris et al. 1988). Changes in species assemblages and biotic interactions in the California Current region have been described on both the decade scale (Loeb et al. 1983; Moser et al. 1987) and the century scale (Soutar and Isaacs 1974).

Long-term time series are developed either from continuous data collection or by the extraction of information stored naturally as a chronographic record. Continuous data collection must occur over generations of biologists; starting a new series may not allow achievement of objectives for 30 or more years, so available time series, which are often collected for other purposes, are used. A classic example of extracting data from a chronographic record is the study of fluctuations in population abundance of *Engraulis mordax*, *Sardinops sagax*, and *Merluccius productus* by Soutar and Isaacs (1974). By enumerating fish scales preserved at different depths in anoxic, varved sediments, they defined natural cycles of abundance of these species over 150 years. This approach has recently been applied by Shackleton (1987). Chronological information is also stored in fish otoliths (Radtke 1984; Campana and Neilson 1985). Estimating age of fishes and using otoliths for back calculation are simple examples of extraction of historical information. In addition, the isotopic composition of otoliths has been used to define past thermal habitats occupied by individual fish (Mulcahy et al. 1979; Radtke 1987) and to identify stocks (Mulligan et al. 1987).

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Because studies on fish growth are generally conducted at a single time, time series on the order of several decades are either rare or absent. Some available time series are often produced from different studies, which may not have used the same techniques for sampling, ageing, or interpretation (Boehlert and Kappenman 1980). Using fish scales and interopercular bones from two flatfish species collected over approximately 15 years, Kreuz et al. (1982) established time series of growth and found that growth was negatively correlated with temperature. Width and length of otoliths can be used to estimate length of fish so that past growth patterns can be estimated with back-calculation techniques on otoliths from older fish. Extreme longevity has been documented in the scorpaenid genus *Sebastes* (Bennett et al. 1982; Leaman and Nagtegaal 1987), and ages in excess of 80 years have been reported for several species (Archibald et al. 1981; Boehlert and Yoklavich 1984; Leaman and Beamish 1984). Thus, otoliths of these species can potentially be used to estimate growth from several decades ago.

In this paper, we describe an otolith-based technique for obtaining a historical time series of growth. We apply this technique to two species, the canary rockfish, *Sebastes pinniger*, and the splitnose rockfish, *S. diploproa*, and describe the resultant time series of growth in light of physical and biological factors.

MATERIALS AND METHODS

Otoliths from *S. pinniger* and *S. diploproa* were collected during rockfish surveys conducted by the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, in 1977 (Boehlert 1980), 1980 (Boehlert and Yoklavich 1984), and 1983 (Wilson 1985). Collection techniques followed Gunderson and Sample (1980). Our objective was to represent as many years of growth as possible; therefore, otolith selection was based upon age alone, and old fish greatly outweighed their relative abundance in a random sample. Additional otoliths from *S. pinniger*, collected off the central Oregon coast in 1984, were obtained from the Oregon Department of Fisheries and Wildlife.

Technical aspects of our methods, described in Boehlert and Yoklavich (1987), are repeated here for completeness because the original information is not widely available. For otolith sectioning and age determination, we followed Boehlert and Yoklavich (1984). Briefly, otoliths were affixed to cardboard tags, embedded in polyester casting resin, mounted on a diamond lapidary saw, and fed onto a pair of thin diamond blades separated by acetate spacers. Dorsal-ventral sections through the focus and perpendicular to the sulcus, approximately 0.4 mm thick, were removed from the center of the otolith, attached to microscope slides, and ground to eliminate artifacts. Total ages were determined from these sections by identifying the first translucent annulus (winter growth zone) and counting sequential growth zones from the center toward the dorsal edge; dorsal annuli at ages near 8–10 years were followed from the dorsal edge to the interior dorsal quadrant, and subsequent annuli were counted to the internal surface.

Annulus measurements, used as a proxy of annual fish growth, were limited to the first 6 years of growth. This limit was imposed because otolith increments became smaller with increasing age; eventually, linear growth stopped, and the otolith began to thicken (Bennett et al. 1982; Boehlert 1985). Two different techniques for otolith measurement were used. In the faster growing *S. pinniger*, whose otoliths are clearer, measurements were from the focus to the dorsal distal edge of each increment (Fig. 1). In *S. diploproa*, whose otoliths are typically more opaque and whose annual increments are smaller, the focus was difficult to identify; for this species, measurements were from the dorsal to ventral distal edges of increments 1–6.

Data from each fish included sex, fork length, date of collection, location, total age, and widths of the increments measured from the otoliths for ages 1–6. The first increment width was a true reflection of first year growth; subsequent measurements, however, integrated past growth. That is, a large growth increment in year 1 could bias the measurement in years 2–6. To remove this correlation and to provide a measure of growth in each year, our analysis used growth increments (GI(i), where i = 1–6) determined by differencing successive measurements. Thus, growth in a given year was not cumulative and generally did not reflect past growth.

Age was subtracted from the year of collection to determine the year of birth. For each fish, each growth increment (1–6) was associated with a specific "year of growth" in the following manner: Increment 1 represented the year of birth or first year growth, increment 2 represented the following year, and so forth. Data on 6 years of growth were available for each fish with the ex-

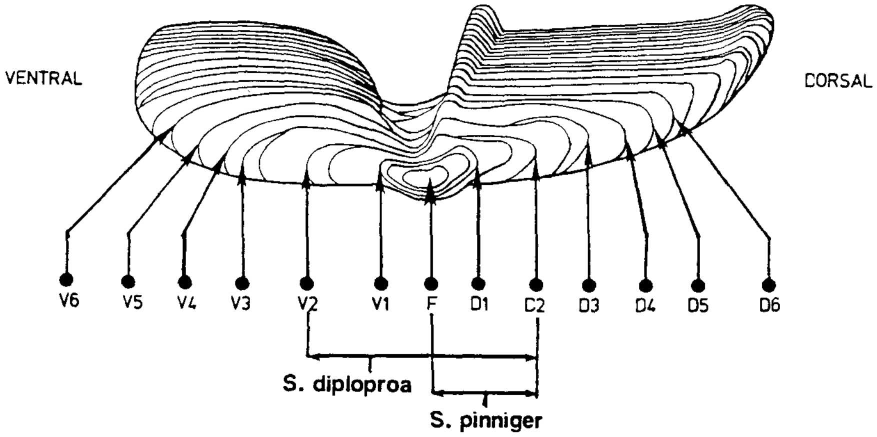

FIGURE 1.—Schematic drawing of an otolith section from *Sebastes* spp. showing the axes of measurements. Measurements for *S. pinniger* were from focus to dorsal distal increment margin (i.e., F to D2); measurements for *S. diploproa* were from dorsal to ventral distal increment margins (i.e., V2 to D2).

ception of those younger than 6 at the time of sampling. As an example, a fish collected in 1980 and aged at 40 years was determined to be born in 1940; therefore, growth measurements from this individual were available for years 1940 (GI(1)) through 1945 (GI(6)).

Most otoliths in our study were from males; otoliths from older females were also included to increase the sample size earlier in the time series. Length at age for these species did not differ between sexes until after sexual maturity, which occurred after age 6 (Boehlert 1980; Boehlert and Kappenman 1980). Still, to test for differences in growth between sexes, we separated the data by sex and then aggregated the data for each GI(i) so that each year of birth had a single, mean value. A paired t-test was used to test for differences in respective growth increments for all years in which both male and female data were available. Growth did not significantly differ between sexes for either species ($P > 0.10$), so data were combined in subsequent analyses.

Certain aspects of the technique, associated with errors in otolith increment measurement and age estimation, may have led to variability in results. From a methodological standpoint, three errors were quickly apparent. First, small changes in the location where the section was removed from the otolith (Fig. 1) may have resulted in slightly different increment measurements; we expected this to introduce relatively minor errors, however, since the sectioning technique (Boehlert and Yoklavich 1984) was designed to be the same. The second source of error occurred in the estimate of total age. Errors in this estimate will result in the assignment of an incorrect year of birth and, thereby, incorrect years of growth for each growth increment; this type of error is probably the most serious, because it will tend to decrease the reliability of real differences between adjacent years. This type of error will increase with increasing age (Boehlert and Yoklavich 1984), and therefore, the reliability of between-year differences in growth will decrease somewhat with increasing age. Finally, errors in selection of annuli (for example, selecting 2–7 instead of 1–6) can occur when making measurements on the section. The cumulative effects of these errors, averaged over many individual samples for each year, should not significantly mask long-term trends in the data. The errors could mask correlations with high frequency environmental features but should not affect correlations with low frequency phenomena.

An additional concern stemmed from the implicit assumption that there is no linkage between longevity and growth; this concept, associated with Lee's phenomenon, is related to size-selective mortality (Ricker 1969). If long-lived individuals are characterized by either faster or slower growth rates during the first 6 years of life than are individuals with shorter lifespans, then we can encounter problems comparing growth of young and old fishes. In lightly exploited populations of *S. alutus*, for example, very old age groups may have smaller mean lengths than younger age groups, suggesting some type of growth-dependent mortality (Leaman[1]). Markedly smaller mean lengths at age have not been observed, however, for very old specimens of either *S. pinniger* or *S. diploproa* (Boehlert and Yoklavich 1984; Wilson 1985). A genetic basis for differences in growth and age at sexual maturity has been suggested for cod, *Gadus morhua* (Borisov 1979) and brown trout, *Salmo trutta* (Favro et al. 1979). An investigation of the biochemical genetics of *S. diploproa* by using electrophoresis at 29 loci has shown no variation associated with age (L. W. Seeb and G. W. Boehlert unpubl. data). Although negative results cannot rule out a difference, our growth results did not show a consistent trend supporting a genetic basis for growth differences.

Data Analysis and Interpretation

Yearly means of GI(i)'s were calculated and were the values upon which further analysis was made. Standardized growth anomalies (Z-scores) were calculated so that each time series of growth for both species had a mean of zero and a standard deviation of one. This allowed comparison of the growth anomalies in different growth years, standardized for the effects of growth increment magnitude. Comparisons between species were also facilitated by this conversion. A growth anomaly value of zero corresponded to normal growth rate, averaged over the period of the data record.

Within species, there were both similarities and differences between the time series of different age groups. Covariability between different age groups was extracted by principal component analysis (Hotelling 1933) of the six-by-six cross correlation matrix, which expressed interrelationships among the six series of standardized growth anomalies of each species over the period of analysis. The principal component expansion of growth increments can be written as

$$\mathrm{GI}(x,t) = \sum_{n=1}^{6} F_n(x) a_n(t); \tag{1}$$

where x is the age class (1–6), t is time, and the index n corresponds to component number (1–6). The loadings $F_n(x)$ are the eigenvectors of the cross correlation matrix. The amplitude time series $a_n(t)$ are referred to as the principal components of covariability. The dominant loadings across age groups (those reducing the largest proportions of total variance in the original data set) and the associated principal component time series were interpreted in terms of physical and biological processes influencing growth rate variability. An attempt was made to relate the principal component time series as dimensionless, uncorrelated expressions of growth for each species to time series of environmental and biological data. Environmental data (upwelling, wind speed, and wind stress curl at lat. 45°N, long. 125°W; sea-surface temperature at Neah Bay, WA, lat. 48°22′N) from 1946 to 1977 were provided by the Pacific Fisheries Environmental Group, Monterey, CA. Sea level data from San Francisco (lat. 38°N) were taken from Prager and MacCall[2].

RESULTS

A total of 942 *S. pinniger* (616 males and 326 females) and 802 *S. diploproa* (651 males and 151 females) were used in this study. Specimens of *S. pinniger* ages 2–60 years corresponded with birth dates from 1920 to 1978 (Fig. 2A); *S. diploproa* ages 1–86 years corresponded with birth dates from 1896 to 1979 (Fig. 2B). Total numbers of growth increments measured were 5,600 for *S. pinniger* and 4,714 for *S. diploproa*.

Mean annual size of growth increments for both species showed a reduction with age group, which is typical in fishes. Mean size of increments decreased dramatically (between twofold and threefold) from age groups 1 and 2, then slowly from age groups 2–6 (less than twofold). Growth anomalies for all ages were characterized by significant interannual variability for both species (Figs. 3, 4). The standardized time series for *S. pinniger* (Fig. 3) showed a general, gradual decreasing trend in growth rates for age groups 2–4 from the beginning of the record until about 1965 or 1970. Age group 1 showed a generally decreasing trend prior to about 1957 and an increasing trend thereafter. Age groups 5 and 6 showed a gradually increasing trend virtually

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[1] B. M. Leaman, Pacific Biological Station, Nanaimo, B.C., Canada, pers. commun. November 1987.

[2] Prager, M. H., and A. D. MacCall. 1986. An environmental data base describing coastal southern California in the years 1920–1984. Part 1: Procedures and summaries. Natl. Mar. Fish. Serv., Southwest Fish. Cent. Adm. Rep. LJ-86-31, 50 p.

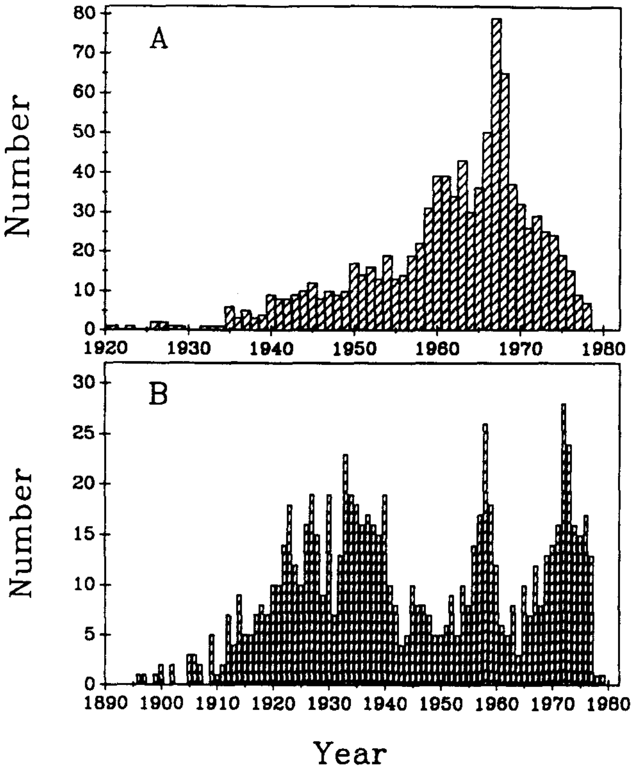

FIGURE 2.—Distribution of the years of birth; males and females are combined. A. *Sebastes pinniger*. B. *S. diploproa*.

throughout the time series. After about 1972, all age groups showed concordance in a relatively abrupt increase in growth rates. This increase may have been shorter lived for age groups 5 and 6, as suggested by the decrease in positive growth rates for the last few years of the record. Positive growth rates continued to increase to the end of the record in the 5 yr running averages for age groups 1–4, though with some significant year-to-year variability in the yearly data.

The time series for *S. diploproa* (Fig. 4) was much longer than for *S. pinniger* (Fig. 3). Age groups 2–4 generally showed a gradual decreasing trend in growth rates prior to about 1965 or 1970. This pattern was similar to that observed for *S. pinniger* age groups 2–4 over the more limited record length. This long-term trend in decreasing growth rates was less evident in *S. diploproa* age groups 1, 5, and 6. Growth rates for age group 5 were nearly normal throughout the record. Growth rates for age group 6 were relatively low in the early part of the record and slightly higher than normal for the period 1930–55. They decreased briefly from 1955 to 1960, then were steady, near-average, or slightly increasing until about 1970. Age groups 2–6 of *S. diploproa* increased in growth rates during the 1970's, coinciding with the high growth rates of all age groups of *S. pinniger* after about 1972. Growth rates for age group 1 of *S. diploproa* were strikingly different from all other age groups of both species of *Sebastes*, with a predominance of variability over much shorter time scales (ca. 5 years) and no evidence of a rapid increase during the 1970's.

The relationship between growth variability in different age groups summarized above from the time series in Figures 3 and 4 were compactly described by the principal components of the six age group time series. We included only years for which yearly mean values of growth were

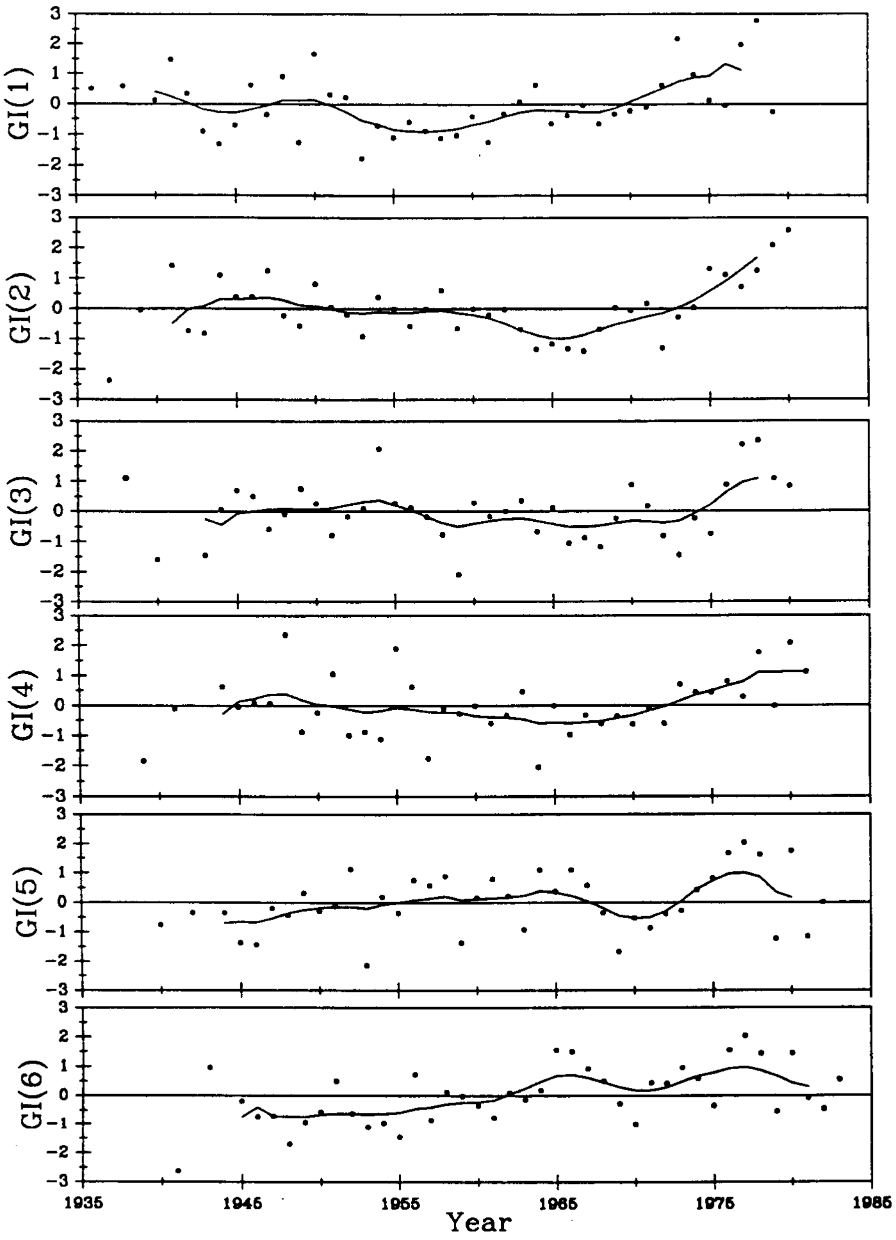

FIGURE 3.—Plot of mean growth anomalies in years of growth 1–6 for *Sebastes pinniger*. Data points represent the yearly mean growth anomalies; the curve represents the double 5-yr running average. Only years with means based upon four or more observations are used.

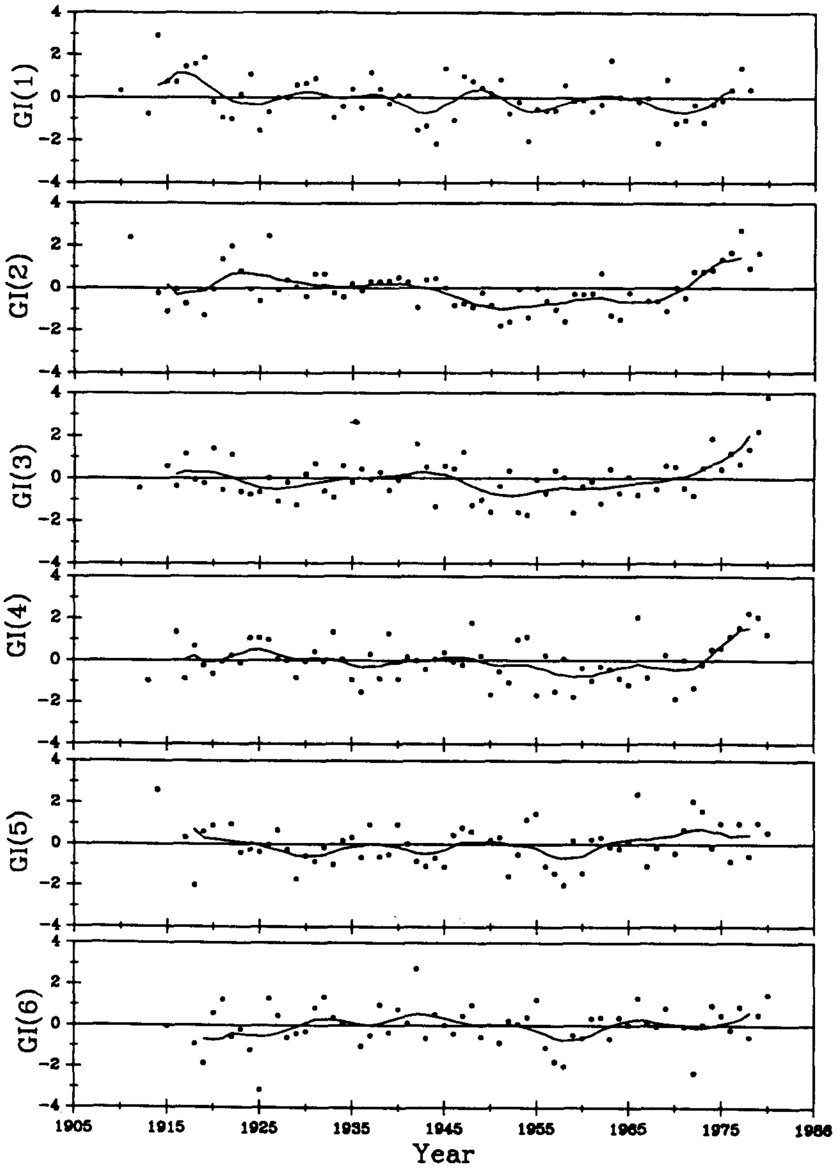

FIGURE 4.—Plot of mean growth anomalies in years of growth 1–6 for *Sebastes diploproa*. Data points represent the yearly mean growth anomalies; the curve represents the double 5-yr running average. Only years with means based upon four or more observations are used.

computed from four or more observations. The first three principal components of *S. pinniger* variability explained 75% of the total variance summed over the six growth anomaly time series; loadings are shown in Figure 5A. Corresponding principal component time series (Fig. 6), or "modes of variability," effectively filter the data to draw attention to the dominant signals discussed above (Fig. 3). By considering the loading values (and thus the relative contribution of each age class) along with the trends in the principal component time series, we described the dominant signals in the time series of the original data. The loadings of the first mode were approximately the same for all six age groups (Fig. 5A); this principal component represented the dominant mode of coherent variability with about the same amplitude in all age groups. The corresponding principal component time series (Fig. 6) is nearly averaged from 1940 to 1970, followed by an abrupt increase beginning about 1972, and represented the high growth rates for all age groups after 1972 (cf. Fig. 3). This was the most pronounced signal in the record, accounting for 36% of the variability over the six age groups.

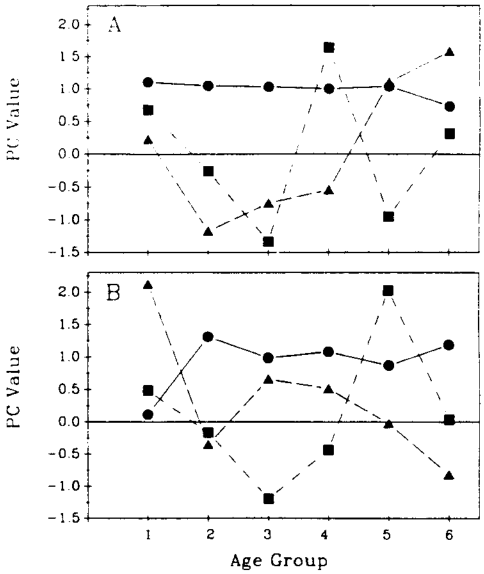

FIGURE 5.—Component (age group) loadings to the three principal components (PC's) explaining the greatest amount of variability in the growth time series. A. *Sebastes pinniger*. B. *S. diploproa*. Circles represent the loadings of the first PC, triangles the second, and squares the third.

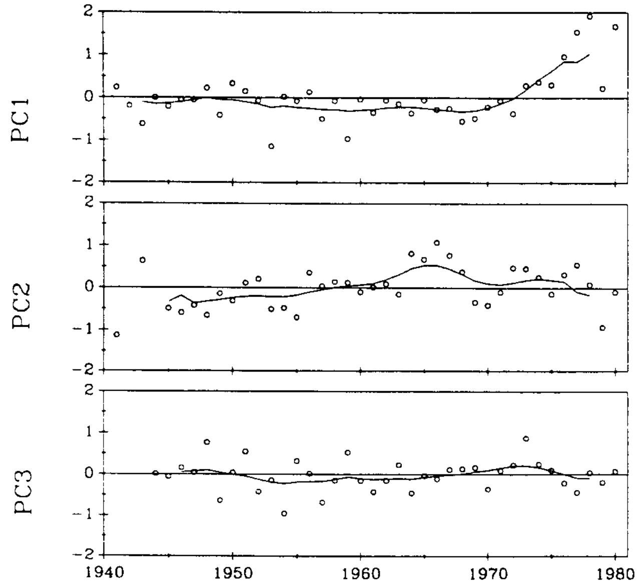

FIGURE 6.—Principal component time series for the three modes explaining 75.0% of the total variance in growth of *Sebastes pinniger* from the six time series in Figure 3. The curve represents the double 5-yr running average.

The second principal component of *S. pinniger* growth variability extracted the coherent trends in the time series evident prior to 1965 (Fig. 3). The loadings (Fig. 5A) were negative for age groups 2–4 and positive for age groups 5 and 6; the loading value for age group 1 was zero, indicating that its variability is not related to this mode. The principal component time series of this second mode of variability (Fig. 6) generally showed a gradually increasing trend from 1945 to 1965, followed by a decreasing trend thereafter. This time variability described well the trends evident in Figure 3 for age groups 5 and 6, for which the loading values (Fig. 5A) were positive. Since the loading values of the second mode were negative for age groups 2–4 (Fig. 5A), this mode of variability (the product of the loading value and the principal component time series, see Equation (1)) corresponded to a gradually decreasing trend in age groups 2–4 growth rates prior to 1965, followed by an increasing trend thereafter. We have no explanation for the difference in the early trends in growth between age groups 5 and 6 and age groups 2–4. Further, growth increments in 1964–68 (Fig. 3) reinforced this difference and produced a peak in the principal component time series in those years (Fig. 6). This second mode of variability describing the trends in growth rates accounts for 24% of the variance in the data.

The loading values of the third principal component of *S. pinniger* growth variability (Fig. 5A) showed no obvious coherent relationship among age groups. The values oscillated from positive to negative among the age groups, and the corresponding principal component time series (Fig. 6) showed no remarkable characteristics. Thus, this mode of variability has no obvious physical interpretation.

The first four principal components of *S. diploproa* variability explained 81% of the total variance summed over the six growth anomaly time series; the loadings for the first three modes are shown (Fig. 5B), with corresponding principal component time series (Fig. 7). The loading values of the first principal component, accounting for 30% of the variance, were approximately the same for age groups 2–6 and zero for age group 1. This highlighted the fundamental difference between growth rate variability in age group 1 and that in the other age groups.

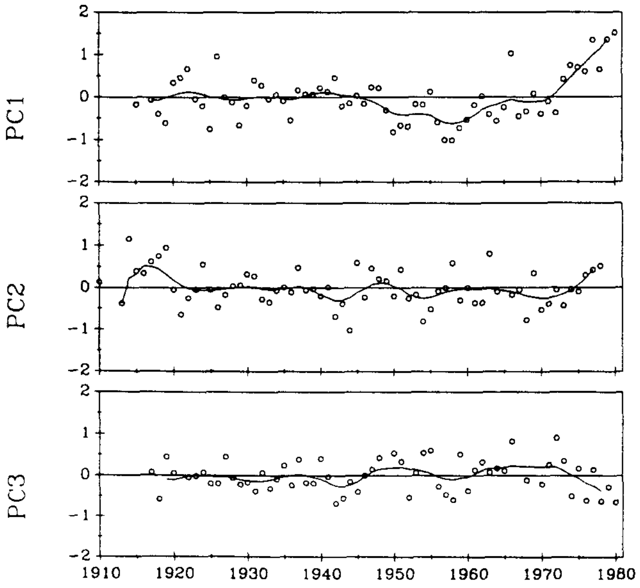

FIGURE 7.—Principal component time series for the three modes explaining 64.6% of the total variance in growth of *Sebastes diploproa* from the six time series in Figure 4. The curve represents the double 5-yr running average.

The principal component time series of this first mode of variability (Fig. 7) showed growth rates as nearly normal in 1915–45, moderately decreasing in 1945–70, and abruptly increasing after about 1972. This was consistent with the earlier interpretation of variability in the individual time series (Fig. 4). The increased growth rates after 1972 coincided with the same signal described by the first principal component of *S. pinniger* growth rates (Fig. 6).

The second principal component of *S. diploproa* growth rates extracted the independent nature of variability in age group 1 and accounted for 19% of the total variance over the six growth anomaly time series. The loading values of this second mode of variability (Fig. 5B) were near zero for all age groups except age group 1. The corresponding principal component time series (Fig. 7) was almost identical to the time series of *S. diploproa* age group 1 (Fig. 4); periods of positive, normal, and negative growth rates in both time series closely corresponded. This further supported the interpretation of this mode of variability as describing age group 1 growth rates. As will be expanded upon in the following section, the lack of linkage between growth rates in age group 1 and the other age groups is likely related to the fact that *S. diploproa* inhabits an environment during the first year of life that is quite different from that during later states of life (Boehlert 1977) and is thus subject to different environmental factors influencing growth rates.

As with *S. pinniger*, the third principal component of *S. diploproa* growth rates has no obvious physical interpretation. The loading values (Fig. 5B) oscillate from positive to negative across the age groups, and the principal component time series (Fig. 7) was nearly normal over the entire record length.

DISCUSSION

The study of growth in marine fishes has typically been concerned with relatively short-term trends in growth of cohorts or populations, most often with fished stocks. Differences in growth may have existed between stocks (Templeman and Squires 1956; Borisov 1979), geographical regions (Boehlert and Kappenman 1980), stock densities, and years (Margetts and Holt 1948; Jones 1983). Such growth differences may be due to genetic factors (Borisov 1979), density dependence (Margetts and Holt 1948; Peterman and Bradford 1987), or environmental factors, most importantly temperature (Brett 1979; Kreuz et al. 1982). The dramatic reduction in stock sizes of many *Sebastes* spp. (Archibald et al. 1983; Ito et al. 1987) has led several authors to suggest density-dependent increases in growth (Gunderson 1977; Boehlert and Kappenman 1980). Recent changes in ageing methodology for *Sebastes* (Boehlert and Yoklavich 1984), however, have rendered long-term comparisons of growth difficult without a historical collection of otoliths.

Analogous to historical time series derived from tree rings (Fritts 1976), the technique described in our paper uses uniform methodology to develop time series of growth for long-lived fishes. Reading of otoliths, however, has more inherent variability than that for tree rings, and the resultant ageing biases described earlier must be considered. The impacts of ageing errors will be most apparent in high frequency signals in the time series and are probably not well resolved by our data; this is the main reason we used the running averages to low-pass filter the data, making the low frequency signals more apparent to the human eye (Figs. 3, 4, 6, 7).

An interesting biological feature of our results is the differing pattern of growth of age group 1 *S. diploproa* (Fig. 4), the only age group not contributing significantly to the variance described by the first principal component for either species. In contrast, first year growth in *S. pinniger* was similar to that in age groups 2–6. *Sebastes pinniger* have a relatively narrow seasonal spawning peak (Westrheim 1975; Gunderson et al. 1980), and pelagic young apparently recruited to their juvenile benthic habitats within about 6 months (Richardson and Laroche 1979). *Sebastes diploproa*, however, seemed to spawn during most months of the year (Snytko 1975), and pelagic prejuveniles were present year-round, at least in the Southern California Bight (Boehlert 1977). Assuming that the first annulus is laid down on a seasonal basis, first year growth was probably quite variable. Further, *S. diploproa* are deepwater (200–500 m) members of this genus, but their first year is spent in surface waters, probably in the upper meter of the water column (Boehlert 1977, 1981); thus, the factors influencing growth in the first year may differ from those affecting growth in subsequent years. Temperature can have an important impact on juvenile rockfish growth (see summary in Boehlert and Yoklavich (1983)), but it may not show coherent cycles between deep and shallow water over the continental shelf off Oregon (Kruse and Huyer 1983); thus, differences between growth rates for age group 1 and later age groups are not surprising.

The dominant signal apparent in all of the time series of growth, except age group 1 of *S. diploproa* (Figs. 3, 4), and in the first principal component for both species (Figs. 6, 7) was that of increased growth after about 1972. Many of the fish used to calculate the growth anomaly values for this period would have been captured before the age at full recruitment to the fishery, which is 12 years for *S. pinniger* (Wilson 1985) and 14 years for *S. diploproa* (Boehlert 1980). A potential concern with the use of fish younger than the age at full recruitment is that the gear will be selective for larger, faster growing individuals; thus, fish younger than the age at full recruitment might conceivably be characterized by more rapid growth rates, resulting in the increased growth rates observed late in the time series (Figs. 3, 4). If true, then the size of growth increments for fish born in a given year should decrease with time from first recruitment until the age at full recruitment (as is true in Lee's phenomenon). Our samples, however, were taken with sampling gear of much smaller mesh than used in the commercial fishery (Gunderson and Sample 1980). Nonetheless, to test for more rapid growth of younger age fish, we compared the six growth indexes of *S. pinniger* born in 1973–77 and collected in 1980 ($N = 41$, ages 3–7) with those collected in 1984 ($N = 51$, ages 7–11). This timespan covered the most rapid increase in growth (Figs. 3, 4). The growth indexes did not significantly differ (paired *t*-test, $P > 0.10$); this suggests that the size of growth increments did not change as fish born in 1973–77 were collected 4 years closer to the age at full recruitment (1984 versus 1980).

An alternative explanation of increased growth in the 1970's was density dependence. Density-dependent growth has been observed in a variety of fish stocks, generally in association with exploitation (Margetts and Holt 1948) or strong year classes (Jones 1983), and is most evident in immature fish (see summary in Ware (1980)). There is little question that stocks of several *Sebastes* spp. have declined under the influence of fisheries (Gunderson 1984; Bracken 1987; Lenarz 1987; Westrheim 1987). Ito et al. (1987) have suggested that stocks of *S. alutus* off Oregon, Washington, and British Columbia declined from a virgin biomass of about 144,000 metric tons (t) to about 13,500 t in the early 1970's. No direct work documents density-dependent changes in growth in this species, although Gunderson's (1977) model of the stock used increased growth as a compensatory mechanism at low stock density. The best evidence for density-dependent growth changes in the genus is for *S. mentella* (Sorokin et al. 1986). For *S. diploproa*, length frequencies from 1977 (Boehlert 1980) were shifted to much smaller sizes than those from 1961 to 1962 (Alverson et al. 1964); this decrease may have been a result of fishing pressure (Boehlert 1980). Faster growth in the region north of California has been described for this species (Boehlert and Kappenman 1980); density-dependent growth increase (since the major stock reduction occurred in the north) was suggested as one of the factors responsible for the geographical growth differences.

The decrease in stock size of many deepwater *Sebastes* spp. along the west coast of North America and the Gulf of Alaska may be related to the growth increase after about 1972 for both species. The major removals of this group by foreign fisheries occurred in the mid-1960's to 1970's (Bracken 1987; Ito et al. 1987; Westrheim 1987). Time series of reliable biomass estimates for *S. pinniger* and *S. diploproa* are not available, but estimates for *S. alutus* have been made using the stock reduction analysis method (Ito et al. 1987). All three species inhabit similar environments and depend upon similar food resources, so biomass estimates for *S. alutus* can be used as a proxy of biomass for the other two species. A comparison of the first principal component time series of *S. pinniger* and *S. diploproa* with the stock size of *S. alutus* on the west coast (Ito et al. 1987) shows that the increase in growth begins slightly after the major stock decline (Fig. 8). The stock size of *S. alutus* is negatively correlated with the first principal component (and thus growth indexes) for both species ($P < 0.01$).

If decreased stock size is responsible for the increased growth evident in both species, it apparently occurs in age groups 1–6 for *S. pinniger* (Figs. 3, 5A) and in age groups 2–6 for *S. diploproa* (Figs. 4, 5B). The ecological differences between age group 1 and older *S. diploproa* (described above) may explain why density-dependent growth does not occur in the young fish. Density-dependent growth in the first year of life has been described for several fishes (van der Veer 1986; Peterman and Bradford 1987) that

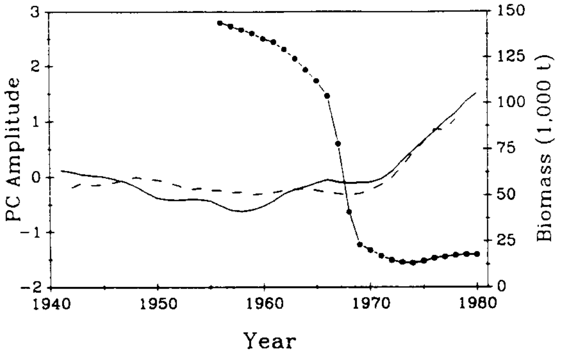

FIGURE 8.—Comparison of the smoothed first principal component time series of *Sebastes pinniger* (dashed line) and *S. diploproa* (solid line) with data on the stock size of *S. alutus* (circles) from Oregon, Washington, and British Columbia (Ito et al. 1987).

typically have a limiting juvenile habitat (often estuarine) and a much more extensive adult habitat. Indeed, Peterman and Bradford (1987) have suggested that density-dependent growth of English sole, *Parophrys vetulus*, off the coast of Oregon occurs only in the first year of life but not later. In *S. diploproa*, the opposite occurs. The adult habitat is restricted bathymetrically and latitudinally, whereas the pelagic prejuveniles occur in a very extensive epipelagic habitat subject to different environmental factors, competitors, and food resources. It is doubtful that variations in density of *Sebastes* in this habitat would impact growth significantly. In the adult habitat of both *S. pinniger* and *S. diploproa*, however, the immense virgin biomass of members of this genus has been reduced significantly. Further, most rockfish species commercially exploited by the trawl fishery rely on the same food resource, with euphausids as the principal prey (Phillips 1964; Brodeur and Pearcy 1984). The increased availability of prey resources associated with stock decline could conceivably result in increased growth in most species. Snytko and Fedorov (1974) suggested that some rockfish species have increased their geographic ranges at the expense of the decreased stocks of *S. alutus*; density-dependent growth could be a corollary of such a range extension.

The nonstationary characteristic due to the sudden increases in growth late in the time series makes correlations of growth indexes with environmental factors difficult to evaluate. Further, sea level, wind stress curl, and the first principal component time series of *S. diploproa* and *S. pinniger* were all serially correlated in the 1946–77 data base, indicating temporal trends that decrease the number of independent degrees of freedom in the sample correlation estimates and that introduce potentially spurious correlations (Chelton 1983, 1984; Bakun 1985). Correlations of the relationship of growth data to time series of physical factors (sea level, sea-surface temperature, upwelling index, and wind stress curl) were determined (Table 1); the 95% significance levels were calculated using the formula in Chelton (1983), which accounts for the reduced number of degrees of freedom from serial correlations. For *S. pinniger*, a significant, positive correlation existed between the second principal component and both the April-September upwelling index and sea level (Table 1); a significant, positive correlation also existed between both growth for age group 6 (G6 in Table 1) and the second principal component with the April-September upwelling index for the prior year. Growth in age group 6 contributed significantly to the variance described by the second principal component (Fig. 5A), so the similarity was not surprising. Feeding by *S. pinniger* increased during the spring-summer upwelling period when *Euphausia pacifica* was the dominant diet item and the frequency of empty stomachs was lower (Brodeur and Pearcy 1984). This must also be the time that fat deposition occurs in this species since the peak fat content was in fall (Guillemot et al. 1985). The effects of upwelling in a prior year on growth may be related to delayed growth using the energy from stored fat reserves built up during the prior upwelling season. The importance of upwelling in rockfish feeding is shown by the decreased fat storage in El Niño years in *S. flavidus* (Lenarz and Echeverria 1986).

For *S. diploproa*, wind stress curl was negatively correlated with the growth indexes for age groups 2, 4, and 6, with mean growth for age groups 2–6 (G26), and with the first principal component (Table 1), which reflects most closely growth from ages 2–6 (Fig. 5B). Negative wind stress curl is associated with offshore convergence (Nelson 1977), which could concentrate prey (such as euphausids) and potentially increase feeding efficiency during the spring-summer upwelling season when maximum feeding takes place. Sea-surface temperature is negatively correlated with growth in year 2, whereas it is positively (but nonsignificantly) correlated with growth in year 1; the correlation between the second principal component (which reflects growth in year 1) and sea-surface temperature is significant, however, suggesting a real difference between the response of these age groups to temperature. This difference may be involved with an ontogenetic shift in the temperature for optimum growth for this species as noted by Boehlert (1981).

TABLE 1.—Pearson correlation matrices for six age group growth indexes (G1–6), mean growth indexes (G for *Sebastes pinniger*, G26 for *S. diploproa*), and principal component time series of the three dominant modes of variability (PC 1–3) with environmental factors from 1946 to 1977; mean yearly values (as opposed to smoothed values) are used in these calculations. The mean growth index for *S. diploproa* is for ages 2–6 because of differences in growth in age group 1. The significance levels of coefficients were calculated following Chelton (1983). CURL, wind stress curl at lat. 45°N, long. 125°W; UP, yearly average Bakun upwelling index at lat. 45°N; SSTNB, sea-surface temperature at Neah Bay, WA; UP49, upwelling index averaged for April–September; and SLSF, sea level at San Francisco.

Index	CURL	UP	SSTNB	UP49	SLSF
S. pinniger					
G1	−0.288	0.105	−0.254	0.163	−0.033
G2	0.065	−0.057	−0.032	−0.165	−0.236
G3	0.049	−0.296	−0.078	−0.261	−0.344
G4	−0.058	0.205	−0.173	−0.013	−0.182
G5	−0.066	0.162	−0.140	0.344	0.083
G6	−0.500	0.123	−0.088	0.274	0.429
G	−0.262	0.085	−0.243	0.127	−0.069
PC 1	−0.228	0.077	−0.247	0.109	−0.113
PC 2	−0.344	0.192	−0.061	0.416*	0.459*
PC 3	−0.178	0.261	−0.091	0.081	0.089
S. diploproa					
G1	0.007	0.034	0.363	−0.079	0.075
G2	−0.567*	−0.122	−0.351*	−0.025	−0.041
G3	−0.270	0.127	−0.072	0.062	0.277
G4	−0.453*	−0.392*	0.267	−0.326	−0.140
G5	−0.310	−0.024	−0.293	0.200	−0.216
G6	−0.349*	−0.056	−0.094	0.021	−0.350
G26	−0.619*	−0.163	−0.148	−0.027	−0.120
PC 1	−0.635*	−0.172	−0.145	−0.044	−0.130
PC 2	0.032	0.016	0.438*	−0.126	0.229
PC 3	−0.092	0.029	−0.175	0.200	−0.239

* = $P < 0.05$.

With the exception of the correlations noted above, the general lack of strong relationships of fish growth with physical parameters may be due to several causes. First, errors in methodology may cause lower resolution in the growth time series than would be necessary to demonstrate the associations. Second, the complexity of factors having an impact upon fish growth (Weatherley 1976; Brett 1979) makes detecting relationships of growth with individual physical factors difficult; furthermore, fish growth may be related to environmental factors in a nonlinear fashion. Higher resolution in the measuring technique and minimization of ageing errors will be necessary to address the first of these problems. The second problem can be addressed through nonlinear analysis of the relationships and continuation of the time series of growth anomalies, which will help define the relationships of growth with physical and biological factors.

CONCLUSION

The research we describe develops a new technique for constructing historical time series of fish growth and conducts analysis into the causes of growth variation in *Sebastes diploproa* and *S. pinniger*. The technique is applicable to a variety of marine organisms for which chronographic records are deposited in some calcareous structures. Our analysis of the record for *S. diploproa* and *S. pinniger* is characterized by a strong signal of increased growth late in the record. Although this signal is confounded by questions associated with size-selective mortality and Lee's phenomenon, we interpret it to indicate a density-dependent response to stocks depleted by overfishing. Our interpretation can be tested; if stocks of *Sebastes* are allowed to rebuild, the dominant signal of increased growth evident in the time series (Figs. 3, 4, 6, 7) should return to more normal values. We recommend that these time series be continued and that the techniques be applied to other species. The interrelationships among species and further investigation of the role of environmental factors in annual fish growth variation could provide valuable insights into population responses of fishes to their physical and biological environment.

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