Abstract.–Growth of otoliths of adult widow rockfish, *Sebastes entomelas*, and yellowtail rockfish, *S. flavidus*, inhabiting the coastal waters off central and northern California was reduced in 1983. This reduction (12.6% and 20.5%, respectively) coincided with a strong El Niño event that dominated oceanographic conditions that year. Otolith growth from 1980 to 1987 was significantly correlated with ocean temperature, upwelling, and sea level anomaly. Specifically, in 1983, the highest ocean temperature, largest positive sea level anomaly, and lowest amount of coastal upwelling corresponded to the smallest mean otolith growth increment.

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Reduction of growth in otoliths of widow and yellowtail rockfish (*Sebastes entomelas* and *S. flavidus*) during the 1983 El Niño

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In 1983, one of the strongest El Niño events of the century occurred in the east-central Pacific Ocean (Cane, 1983; Rasmusson, 1984; Glynn, 1988). This event had strong negative effects on the growth of many marine organisms inhabiting waters along the west coast of North America, including giant kelp (Zimmerman and Robertson, 1985), yellowtail rockfish (Lenarz and Wyllie Echeverria, 1986), coho and chinook salmon (Pearcy and Schoener, 1987), Pacific herring (Spratt, 1987), Pacific kelp (Germann, 1988), Pacific hake (MacLellan and Saunders, 1995), and blue rockfish (VenTresca et al., 1995).

Atypically narrow annuli (annual growth increments) formed during 1983 were observed during routine aging of otoliths from adult yellowtail rockfish, *Sebastes flavidus* (Fig. 1). Because otolith growth is generally proportional to fish growth, a reduction in the width of the 1983 annulus could correspond to poor fish growth caused by the El Niño-induced anomalous oceanographic and biotic conditions present that year. Widths of annually formed increments on the hard parts of animals and plants have been used to correlate growth with a range of environmental conditions. A common example is the relation between the widths of tree rings and annual precipitation. In the marine environment, a reduction in annual shell growth of geoduck clams was observed to correspond with increased pollution (Noakes and Cambell, 1992). Boehlert et al. (1989) used otolith annuli to provide historical time series of growth in *Sebastes* that were compared with environmental factors. In a similar study, MacLellan and Saunders (1995) noted a reduction in the 1983 annulus of Pacific hake otoliths inhabiting northeastern Pacific waters, attributing it to the negative effect of the 1983 El Niño.

In this study, otolith growth from 1980 to 1987 was measured from two commercially important rockfish species: yellowtail rockfish and widow rockfish (*S. entomelas*). These species range from British Columbia to southern California (Gunderson and Sample, 1980). They are semipelagic, associated with bottom structure located on the shelf. The measurements of otolith growth were compared with physical oceanographic variables collected during the same period.

Methods

Otolith growth

Otoliths from female yellowtail rockfish inhabiting Cordell Bank, California (Fig. 2), were collected during research cruises conducted from 1986 to 1992. As noted earlier, during otolith age determination procedures, the 1983 annulus was observed to be narrower than adjacent annuli. To quantify this observation, measurements of annuli were made on these otoliths, as well as additional otoliths obtained from an ongoing port sampling program. Otoliths were collected from male and female widow and yellowtail rockfish landed at Eureka, California, and female widow rockfish landed at Bodega Bay, California, during 1989 and 1990.

The annulus was defined as otolith growth from the end of one summer to the end of the following summer (approximately October through September). Using reflected light on the distal surface of whole otoliths, I observed that summer growth appears as a white ring and winter growth as a dark ring (Fig. 1). Annuli from 366 otoliths were measured by using one of the two following methods. With the first method, a camera lucida was mounted atop a dissecting microscope, which was used to trace the surface annuli from 115 female yellowtail rockfish otoliths collected at Cordell Bank. A digitizing pad was used to measure the area of each annulus from the tracings. One or two otoliths per hour could be processed with this method. The remaining 251 otoliths were analyzed by using an image enhancement system comprising a personal computer interfaced with a dissecting microscope and a high resolution closed-circuit video camera. A mouse-driven crosshair was used to trace the annuli displayed on the monitor. This method increased production by sixfold. The area of each annulus (mm^2) was square-root–transformed prior to analysis. To compare the two methods, annuli from five otoliths measured by the first method were remeasured by using the second method. The differences in the estimated growth from these five otoliths ranged from 0.2 to 11.4%, with a mean of 2.9%, which represented a minor error compared with observed interannual growth differences.

Potential problems arise when measuring all the annuli in an otolith. When these rockfish species reach sexual maturity and somatic growth slows, the reduced growth rate is reflected in their otoliths. Therefore, it would be impossible to determine if a reduction in otolith growth was caused by poor environmental conditions or from energy being diverted into gonadal development. In addition, annuli formed after the onset of maturity are deposited disproportionately on the proximal surface of the otolith. It is easier to measure annuli deposited during the immature phase on the distal side of the otolith. To minimize these concerns, measurements were restricted to the five annuli formed prior to sexual maturity. Both male and female widow rockfish have an age of 50% maturity of five years, whereas male and female yellowtail rockfish are mature at six and seven years,

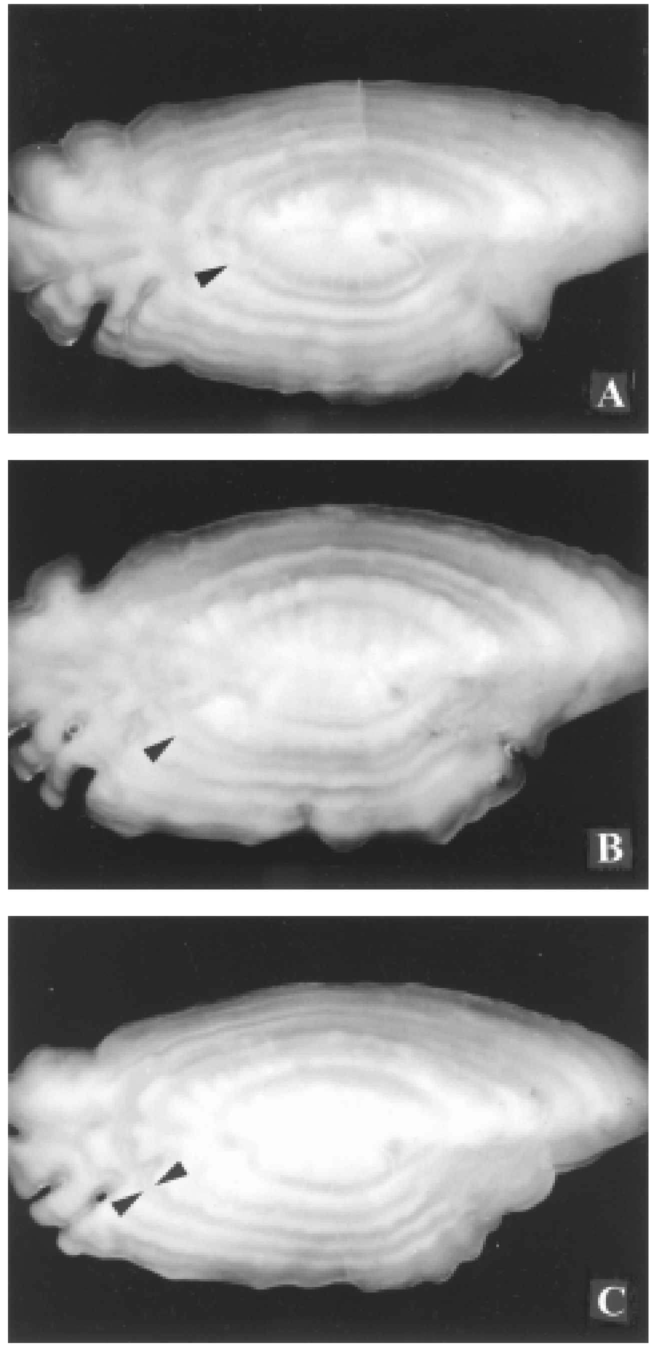

Figure 1

Otoliths from female yellowtail rockfish collected at Cordell Bank, California, showing narrow 1983 annulus (arrow): (**A**) 1982, (**B**) 1981, and (**C**) 1980 year classes.

Table 1

Sample sizes for each combination of rockfish species, port, sex, and yearclass.

			Yearclass					
Species	Port	Sex	1979	1980	1981	1982	1983	Total
Yellowtail	Eureka	Female	2	22	10	6	11	51
Yellowtail	Eureka	Male	1	27	19	1	10	58
Yellowtail	Cordell Bank	Female	16	38	47	13	1	115
Widow	Eureka	Female	9	9	22	11	1	52
Widow	Eureka	Male	12	10	21	11	4	58
Widow	Bodega Bay	Female	7	4	15	6	0	32
Total			47	110	134	48	27	366

respectively (Wyllie Echeverria, 1987). An additional concern arises from the protracted parturition season exhibited by these species. Interannual differences in birthdate distributions (Woodbury and Ralston, 1991) result in interannual differences in otolith growth during the first year of life. Therefore, measurements of the first annulus were not included in the analysis because they might have biased the data. Only measurements of otolith growth for the years 1980–87, comprising ages 1–4 and otoliths from fish belonging to the 1979–83 year classes (Table 1) were used.

The results of this study are dependent upon the accuracy of the ages assigned to each otolith. It is not uncommon for ages to vary by one or more years between readers or among readers re-aging the same otolith. The 1983 annulus was observed over a period of several years during which one additional annulus was deposited each subsequent year for year classes prior to 1983. By using the distinctive 1983 annulus (Fig. 1) as a natural tag (MacLellan and Saunders, 1995), I was able to assign an age to each otolith in this study that was accurate.

To test the validity of the 1983 annulus in this study, twelve otoliths that had previously been aged were re-examined without knowledge of their date of capture. On the basis of only the pattern of annuli widths, 11 of the 12 otoliths were assigned to their previously determined year class. The one misinterpretation was for an otolith from a fish born in 1984, which did not have the 1983 annulus. This error would be unlikely in the data used for this study because the otoliths were first aged by the break-and-burn method, in which the year of birth was determined from counting all the annuli. The narrow 1983 annulus could then be used to ensure that the correct age was obtained.

The following additive model (Weisburg, 1993) was used to calculate treatment effects on annual otolith growth for each species over all years.

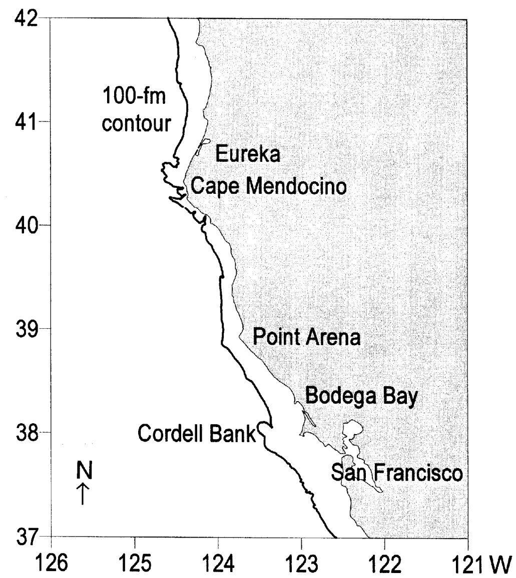

Figure 2

Sampling locations at Eureka, Bodega Bay, and Cordell Bank.

$$\Delta_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_k + \delta_l + \varepsilon_{ijkl},$$

where Δ_{ijkl} = index of annual otolith growth of a species;
μ = mean square-root of annual growth;
α_i = year "i" fixed effect;
β_j = age "j" fixed effect;
γ_k = port "k" fixed effect;
δ_l = sex "l" fixed effect; and
ε_{ijkl} = normal error term.

This model assumes no significant interaction among any of the four main effects. This assumption was evaluated in Figures 3 and 4, where annual least-square means are plotted against year for each species-sex-port combination by using both a combined model with no interaction term for the age-by-year effect, and a model with interactions that estimates a distinct otolith growth effect for each age-by-year combination. These figures show that although there are statistically significant interactions, the signal for the year effect is not strongly effected by excluding the interaction terms from the model. The additional variance explained by the model with interactions was only 3.5% and 4.2%, for yellowtail and widow rockfish, respectively. Because inclusion of an interaction term contributes little to the explanatory power of the model, and analyses that include interaction terms are much more restrictive in terms of data requirements, the simple, combined additive model was used, thereby allowing the computation of a longer time series of annual otolith growth effects (1980–87).

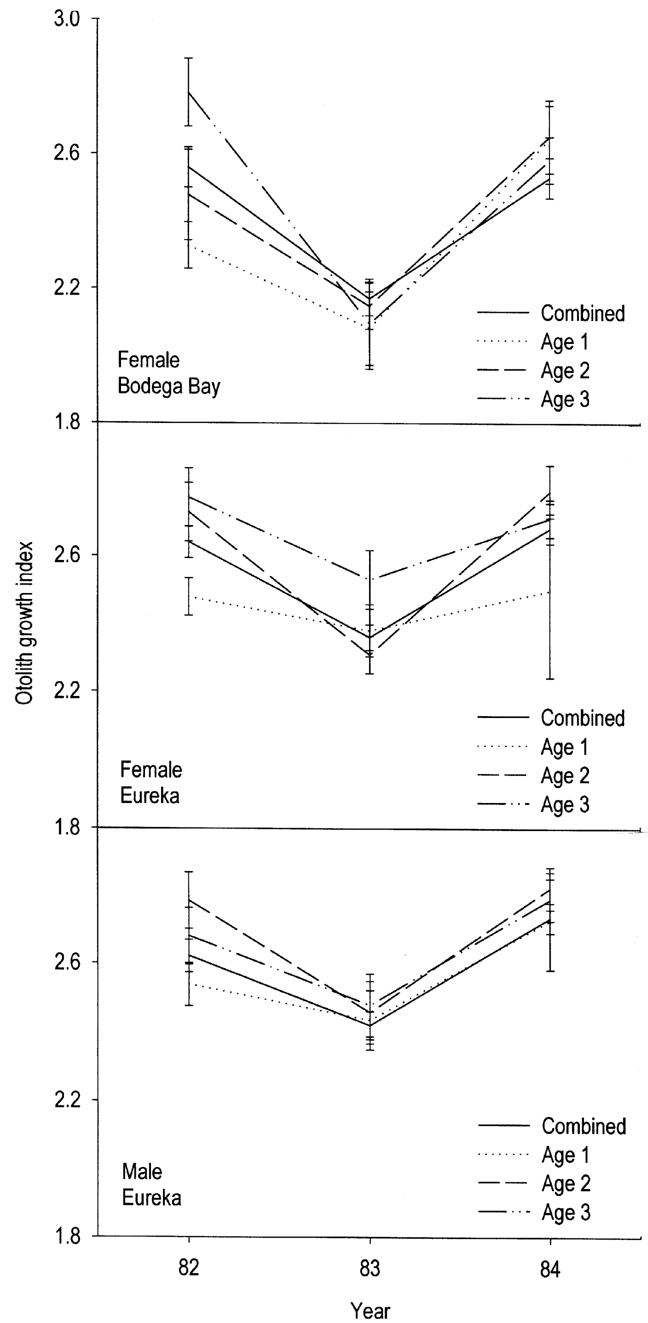

Figure 3

Comparison of mean annual otolith growth indices (1982–84) among models with and without interaction terms for widow rockfish. Bars represent ±1 standard error of the mean.

Oceanographic databases

Thirteen oceanographic variables were analyzed to determine their relation with otolith growth patterns. These included eight measures of ocean temperature, three upwelling indices, a sea level statistic, and the northeast Pacific atmospheric pressure index. All ocean temperature data were obtained from the Fleet Numerical Oceanography Center, Master Oceanographic Observations Data Set (Sharp and McClain, 1993). The data included temperature at the sea surface, at 100 m, at 200 m, and the depth of the 10°C isotherm. Measurements were summarized from two coastal areas (i.e. 36–39°N × 121–125°W and 39–42°N × 123–127°W), which together encompass the region where the fish were collected. Annual means for 1980–87 were calculated from the monthly means of October through September, the otolith growth year as defined in this study. Annual upwelling indices (Bakun, 1975) were calculated from daily upwelling statistics. In this instance, the mean of the February to April monthly means was computed, as these three months bracket the spring transition (Strub et al., 1987) when nutrient-rich water is first upwelled to the surface, initiating the biological production cycle (Cushing, 1975). Upwelling data were summarized from three localities (i.e. 36°N, 39°N, and 42°N), which represent the area of fish collections. Sea level data compiled at the San Francisco tidal station were used to compute monthly anomalies, after correcting for differences in atmospheric pressure (University of Hawaii[1]). Annual mean sea level anomalies were then calculated from the monthly means of October through September. Lastly, the northeast Pacific atmospheric pressure index is an indicator of atmospheric forcing upon ocean waters (Beamish and Bouillon, 1993). This index is the mean monthly difference in surface atmospheric pressure between 40°N, 120°W (Reno,

[1] Sea Level Center, Univ. Hawaii, Honolulu, Hawaii. 1994. Unpubl. data.

Nevada) and 50°N, 170°W (Aleutian Islands) (NOAA[2]). A plot of the data revealed an increase in the intensity of the pressure differences during the winter months. Therefore, annual means were calculated from the monthly means for November to March.

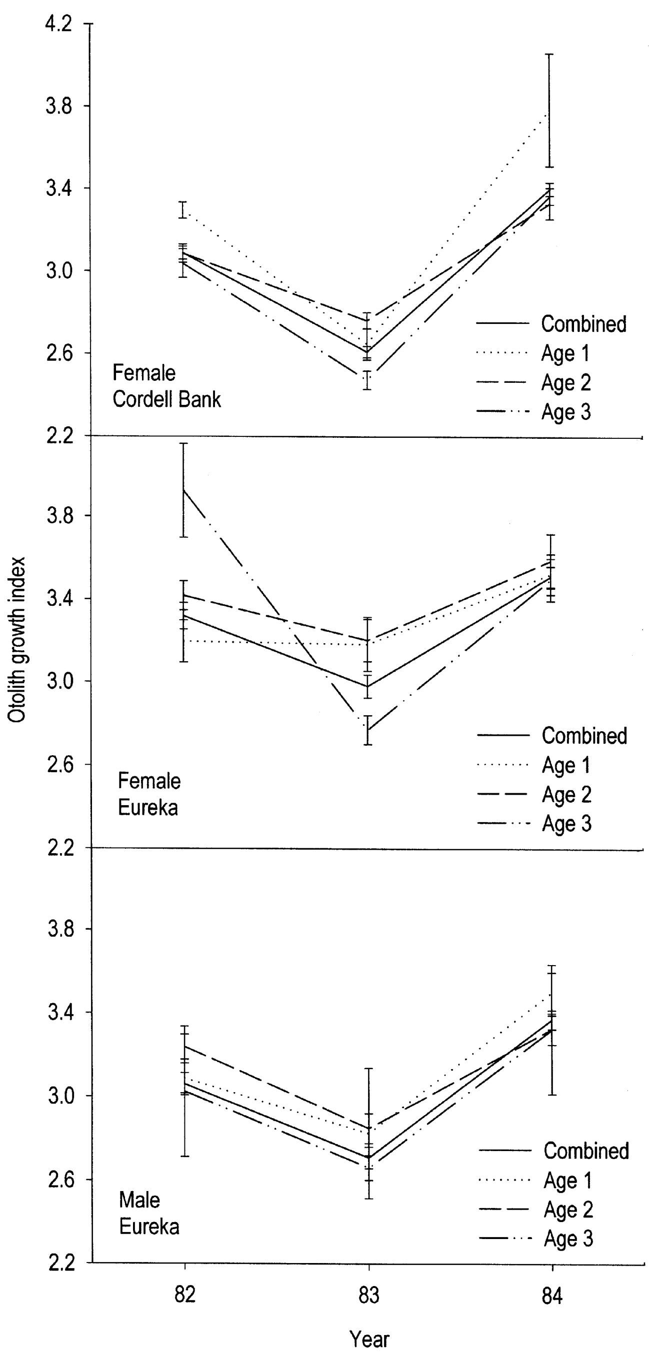

Figure 4

Comparison of mean annual otolith growth indices (1982–84) among models with and without interaction terms for yellowtail rockfish. Bars represent ±1 standard error of the mean.

Owing to strong interdependence among these 13 oceanographic variables, a principal component analysis (SAS Institute Inc., 1988) was conducted to reduce the dimensionality of the information and to insure statistical independence of the data. The ordination was conducted on the correlation matrix, so that each variable was weighted equally. The otolith data were then compared with the principal components of the oceanographic data to quantify the impact of the 1983 El Niño event on the growth of yellowtail and widow rockfish otoliths.

Results

Patterns of annual otolith growth were similar in widow and yellowtail rockfish from 1980 to 1987 (Fig. 5). A 12.6% and 20.5% reduction in otolith growth occurred during 1983 for widow and yellowtail rockfish, respectively. This year of reduced otolith growth was followed by enhanced growth, especially for yellowtail rockfish. The growth estimates calculated for 1980 and 1987 were based on samples from one year, i.e. the 1979 and 1983 year classes respectively, and these estimates should be viewed with caution.

Although most of the variance in otolith growth is explained by the year effect, the other effects in the model are worth noting (Table 2). There was a significant difference in otolith growth between sexes for yellowtail rockfish (i.e. otoliths from females grew faster than those from males); however, this was not the case for widow rockfish. Growth of the otolith at age differs between species (Fig. 6), which may be the result of somatic growth rate differences between the species. In a simple simulation, similar curves were produced by varying the von Bertalanffy growth coefficient (k). Yellowtail rockfish exhibit faster growth than do widow rockfish, thus yielding relatively lower indices of otolith growth with increasing age. There was a significant difference in otolith growth between the two ports for both species (i.e. otoliths from fish collected in Eureka grew faster than those from Bodega). Further analysis revealed that these differences began in 1983. Figure 7 shows results of four separate ANOVAs run on each of the four species-port combinations. In these analyses, sex and port were excluded as effects in the model. Otolith growth was similar at the two ports prior to 1983. Al-

[2] Pacific Marine Environmental Laboratory, National Oceanic and Atmospheric Administration, Seattle, Washington. 1994. Unpubl. data.

Table 2

Analysis of variance results for the growth model used in this study.

Source	df	Sum of squares	Mean square	F-Value	$P>F$
Widow rockfish (r^2=0.318)					
Model	12	19.9617	1.6635	21.57	0.0001
Year	7	13.6558	1.9508	25.29	0.0001
Age	3	2.3318	0.7773	10.08	0.0001
Port	1	0.9860	0.9860	12.78	0.0004
Sex	1	0.1064	0.1064	1.38	0.2408
Error	555	42.8046	0.0771		
Corrected total	567	62.7663			
Yellowtail rockfish (r^2=0.542)					
Model	12	96.8742	8.0728	87.09	0.0001
Year	7	77.8370	11.1196	119.96	0.0001
Age	3	3.3136	1.1045	11.92	0.0001
Port	1	3.5704	3.5704	38.52	0.0001
Sex	1	3.8560	3.8560	41.60	0.0001
Error	883	81.8491	0.0927		
Corrected total	895	178.7233			

though both species exhibited significant reduction in otolith growth in 1983, the effect was more pronounced at Bodega, consistent with a decreasing effect of El Niño with increasing latitude, as was observed in Pacific hake (MacLellan and Saunders, 1995). Although otolith growth recovered quickly for both species at Eureka and for yellowtail rockfish at Bodega, otolith growth for widow rockfish collected from Bodega was relatively slow to recover.

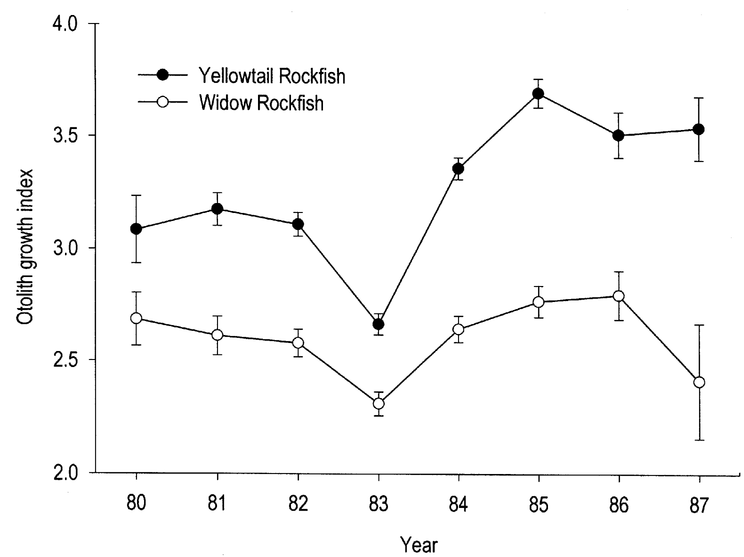

Figure 5

Mean annual otolith growth indices (1980–87) for each species. Bars represent ±2 standard errors of the mean.

Results of the principal component analysis on the oceanographic data (Table 3) show that only the first two components are very informative (eigenvalue ≥1; first three principal components shown). Note that the first component explained 70% of the combined variation among all 13 oceanographic variables, whereas the second component accounted for an additional 18%. As the loadings on the first principal component indicate, temperature and sea level anomaly are closely linked. Upwelling loads higher with increasing latitude, which may relate to increased upwelling from south to north along that section of coast. Upwelling also demonstrates an inverse relation with temperature and sea level anomaly. Finally, the atmospheric pressure statistic does not contribute substantially to the first principal component, although it is much more influential in the second component.

A multiple regression of otolith growth on the first two principal components showed that the second component was neither significant nor informative, and it was therefore dropped from the analysis. An ordinary regression of otolith growth on the first principal component resulted in a significant relationship for both widow and yellowtail rockfish (P=0.033

and 0.030, respectively). Plots of mean annual otolith growth index against the first principal component score (Fig. 8) reveal the extreme conditions that prevailed in 1983. In 1983, the lowest measurements of otolith growth corresponded to the highest sea temperature, highest positive sea level anomaly, and lowest upwelling index. As previously noted, this particular El Niño was one of the strongest on record for the east-central Pacific Ocean. Its signature was noted off the California coast by high sea temperature at 100 m, being the warmest observed since records were first kept starting in 1944 (Sharp and McClain, 1993). A converse relationship between enhanced otolith growth and lower sea temperature, lower sea level anomaly, and higher upwelling index is not as evident, although above normal growth did occur in 1985, which was the "coldest" year.

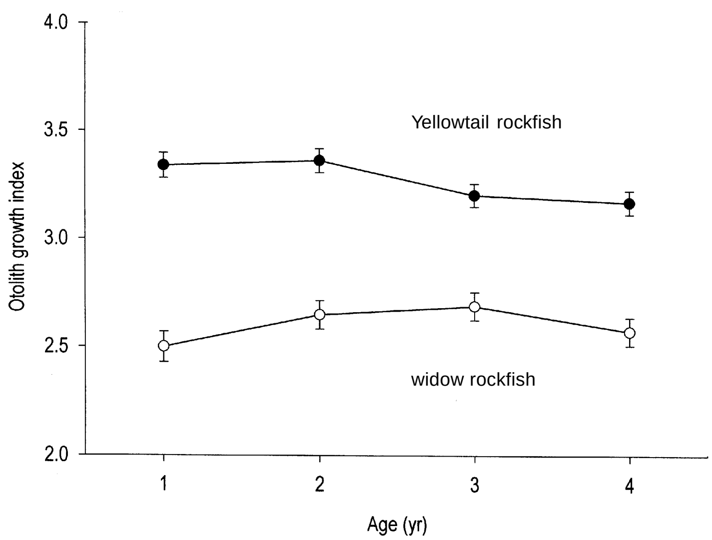

Figure 6

Mean otolith growth indices at age for widow and yellowtail rockfish. Bars represent ±2 standard errors of the mean.

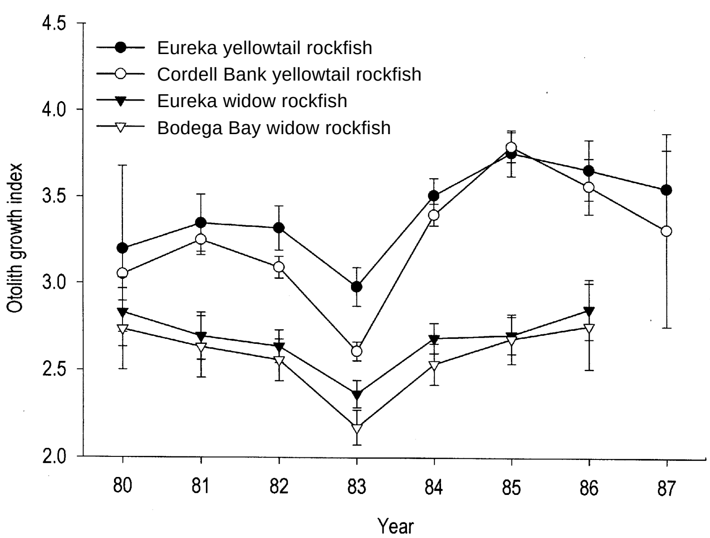

Figure 7

Mean annual otolith growth indices (1980–87) for widow and yellowtail rockfish from two geographic areas. Bars represent ±2 standard errors of the mean.

Discussion

In this paper, the reduction in growth of widow and yellowtail rockfish otoliths during 1983 was quantified by measuring annuli surface areas. Otolith growth is postulated to represent a conservative measure of somatic growth. Casselman (1990) determined that otoliths from several species of freshwater fish grew relatively faster than their body during periods of slow body growth. Francis et al. (1993) argue that otolith growth in *Pagrus auratus* can occur even if somatic growth has stopped. Therefore, the reduction observed from this study may indicate an even larger reduction in somatic growth, perhaps affecting reproductive capacity as well. This was observed by VenTresca et al. (1995) who noted a reduction in both the somatic and gonadal indices of blue rockfish (*S. mystinus*) inhabiting California coastal waters in 1983.

It appears that the oceanographic perturbations caused by El Niño had a negative effect on the growth of these fish. Temperature has been implicated as a major contributor to influencing both otolith and somatic growth. Lombarte and Lleonart (1993) stated that environmental conditions, mainly temperature, regulate the quantity of material deposited during the formation of the otoliths. Dorn (1992) found that growth of Pacific whiting (*Merluccius productus*), which inhabit similar waters, is most affected by temperature during younger ages.

Although physical oceanographic conditions and otolith growth were found to be significantly correlated, the causal relationship may well be based on preferred food availability. Central California represents the southernmost range of both widow and yellowtail rockfish. Pearson and Hightower (1991) reported slower growth of widow rockfish in this area as compared with growth from more northerly distributed populations. This may be related to diet because more northerly distributed populations consume more fish and euphausiids, whereas populations in the south feed more on gelatinous zooplankters. Lorz et al. (1983) reported the diet of yellowtail rockfish in Queen Charlotte Sound comprised both fish and euphausiids, whereas off Washington it comprised mainly euphausiids. Pereyra et al. (1969) found that fish dominated the diet of both yellowtail and widow rockfish collected near Astoria Canyon, off northern Oregon. Brodeur and Pearcy (1984) noted that yellowtail rockfish preyed on a diverse assemblage, dominated by euphausiid, fish and squid, depending on the season. Adams (1987) reported that widow rockfish collected off northern California fed primarily on gelatinous zooplankters. At Cordell Bank, during late fall, winter, and in years of reduced productivity (e.g. 1983), yellowtail rockfish have been found to feed primarily on gelatinous zooplankton, which has a lower nutritional value than their preferred diet of euphausiids (MacFarlane[3]). Owing to the lack of upwelling and reduced productivity during 1983, these fish were probably forced to feed on less nutritional prey. Although lacking stomach analysis data for 1983, Lenarz and Wyllie Echeverria (1986) found a significant reduction in visceral fat of yellowtail rockfish collected at Bodega Bay during 1983 as compared with 1980, a "normal" year.

An assumption of this study is that the widow and yellowtail rockfish sampled during this study did not migrate to less productive waters during 1983 and then return. Most species within the *Sebastes* genus spend their adult life within a relatively small area (Stanley et al., 1994). Both widow and yellowtail rockfish lead an epibenthic schooling existence, inhabiting the area above benthic structures. Several tagging studies have been conducted on yellowtail rockfish to study the movement of these fish. Carlson and Haight (1972) noted homing behavior in yellowtail rockfish that were captured and transplanted to different areas in Alaska. Pearcy (1992) tagged 25 yellowtail rockfish on Heceta Bank off central Oregon and noted little displacement during a one-month period. However, Stanley et al. (1994) noted displacement of several tagged yellowtail rockfish from Alaskan and Canadian waters after they had been at large for several years. Although no tagging studies have been conducted on widow rockfish, it is worth noting

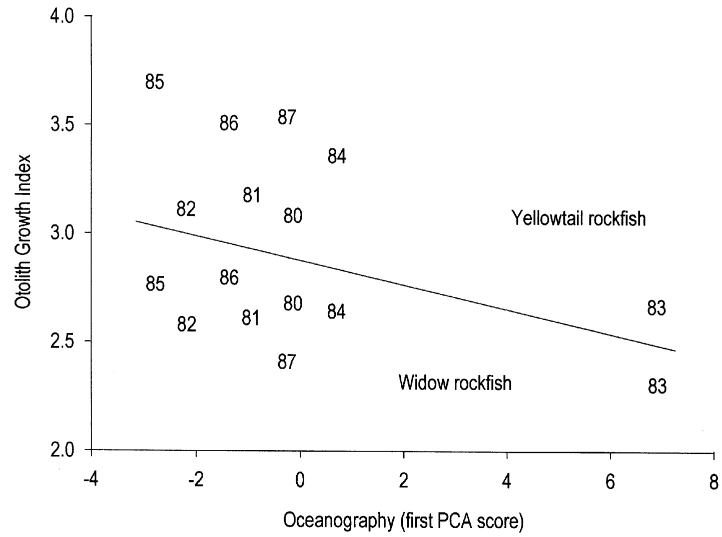

Figure 8

Mean annual otolith growth indices compared to the first principal component annual scores of oceanographic variables.

Table 3

Principal component analysis results for the thirteen oceanographic variables (1980–87).

	Principal component		
	1	2	3
Eigenvalue	9.10	2.36	0.96
Percent variance	70.0	18.1	7.4
Cumulative variance	70.0	88.1	95.5
Eigenvectors			
Sea surface temp at 39–42°N	0.259	0.269	–0.417
Sea surface temp at 36–39°N	0.287	0.255	–0.265
100 m temp at 39–42°N	0.313	0.119	0.276
100 m temp at 36–39°N	0.304	0.053	0.382
200 m temp at 39–42°N	0.302	–0.135	–0.321
200 m temp at 36–39°N	0.301	–0.165	–0.299
Depth of 10°C isotherm at 39–42°N	0.301	0.259	0.129
Depth of 10°C isotherm at 36–39°N	0.301	0.141	0.349
Sea level anomaly	0.296	–0.214	0.296
Upwelling index at 42°N	–0.321	–0.135	–0.024
Upwelling index at 39°N	–0.271	0.357	0.035
Upwelling index at 36°N	–0.148	0.524	0.238
Atmospheric pressure index	0.109	0.498	-0.239

[3] MacFarlane, R. B. 1994. Tiburon Laboratory, NMFS, 3150 Paradise Dr., Tiburon, CA. Personal commun.

that otoliths collected from fish sampled from southern California to British Columbia show distinct growth patterns, indicating little large-scale movement.

One of the best applications of the anomalous 1983 annulus is its use as a chronological marker to improve the accuracy of assigned ages, thus increasing the veracity of age-structured models used in stock assessments (MacLellan and Saunders, 1995). Although the narrow 1983 annuli was most pronounced on young fish at the time of the event, the ring was easily discerned from older fish when their otoliths were broken, burnt, and viewed with reflected light. Therefore, it could be used for decades to aid in the accurate determination of ages of fish born prior to 1983 (Boehlert et al., 1989).

Although the poor environmental conditions present during 1983 appeared to have detrimental effects on the growth of widow and yellowtail rockfish, the effects were short-lived as noted in the increased otolith growth the following years, especially for yellowtail rockfish. As these fish are long-lived (for decades), they have the capacity to absorb occasional years of lower productivity without permanent detrimental effects on the population.

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