

Establishing climate–growth relationships for yelloweye rockfish (*Sebastes ruberrimus*) in the northeast Pacific using a dendrochronological approach

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ABSTRACT

We applied dendrochronology (tree-ring) methods to develop multidecadal growth chronologies from the increment widths of yelloweye rockfish (*Sebastes ruberrimus*) otoliths. Chronologies were developed for the central California coast, a site just north of Vancouver Island, British Columbia, and at Bowie Seamount west of the Queen Charlotte Islands, British Columbia. At each site, synchronous growth patterns were matched among otoliths via the process of cross-dating, ensuring that the correct calendar year was assigned to all increments. Each time series of growth-increment measurements was divided by the values predicted by a best-fit negative exponential function, thereby removing age-related trends. These detrended time series were averaged into a master chronology for each site, and chronologies were correlated with monthly averages of sea surface temperatures, upwelling, the Northern Oscillation Index, and the Pacific Decadal Oscillation. The two northern growth chronologies positively correlated with indices of warm ocean conditions, especially from the prior summer through the spring of the current year. During the same period, the California chronology positively correlated with indices of cool ocean conditions, indicating an opposing productivity regime for yelloweye rockfish between the California Current and the Gulf of Alaska. Overall, this study demonstrates how tree-ring techniques can be applied to quickly develop annually resolved chronologies and establish

climate–growth relationships across various temporal and spatial scales.

Key words: climate, dendrochronology, North Pacific, otolith, sclerochronology, yelloweye rockfish

INTRODUCTION

Climate variability is increasingly recognized as a major influence on the structure and function of northeast Pacific ecosystems. Significant changes in the physical environment may act from the bottom-up via impacts on primary and secondary productivity, or from the top-down through controls on key predator populations, potentially inducing substantial, wide-ranging, and complex responses both within and among marine communities (Francis *et al.*, 1998). For example, the 1976–77 shift to a warm regime in the North Pacific initiated a widespread increase in zooplankton in the Gulf of Alaska, which was coupled with increases in walleye pollock (*Theragra chalcogramma*), starfish, cephalopods, and a variety of groundfishes (Hollowed and Wooster, 1992; Hollowed *et al.*, 2001). Yet at the same time, populations of pandalid shrimp, capelin (*Mallotus villosus*), various crab species, and Atka mackerel (*Pleurogrammus monopterygius*) declined (Anderson and Piatt, 1999; Mueter and Norcross, 2000). On a broader spatial scale, the increase in lower trophic productivity noted in the Gulf of Alaska was concomitant with declines in the California Current following the 1976–77 regime shift (Brodeur *et al.*, 1996; Francis *et al.*, 1998), a pattern also exhibited in salmon (*Oncorhynchus* spp.) populations (Francis and Sibley, 1991; Hare *et al.*, 1999). Given these potentially profound and varied effects on the biomass, age structure, and growth rates of organisms within and among ecosystems of the North Pacific, a detailed understanding of climatic impacts is critical for developing fisheries management strategies. Defining climate–growth relationships would allow fisheries managers to better disentangle the effects of climate from those of overfishing, particularly on depleted stocks, and also offer predictive

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capabilities to help forecast the effects of future climate changes.

Establishing the effects of climate on growth requires multiple decades of observations to ensure adequate statistical power and span phase shifts in major climate oscillations. In the northeast Pacific, an ideal time series would capture strong El Niño or La Niña years and include a warm and a cool regime of the Pacific Decadal Oscillation. To date, a number of time series of direct observations exist for several fisheries of the northeast Pacific including such variables as catch (Spencer and Collie, 1997; Hare *et al.*, 1999; Field and Ralston, 2005), recruitment (Hollowed and Wooster, 1992; Hollowed *et al.*, 2001), and body size and fecundity (Harvey *et al.*, 2006). These datasets provide invaluable insight into long-term patterns of variability and their relationships with climate. However, repeated sampling is costly, especially on multidecadal time scales. Also, data must be gleaned from records of commercial catches or scientific surveys that may require generations of researchers to complete. For these reasons the number of lengthy time series of direct measurements is limited.

Apart from direct observations, various proxies can be analyzed to reconstruct aspects of fishery productivity. Among these, scales and other hard parts of fishes that have been preserved in annually varved sediments provide records of abundance that extend across multiple centuries (Soutar and Isaacs, 1974). From sediment cores of the Effingham Inlet, located on the western coast of Vancouver Island, British Columbia, Wright *et al.* (2005) developed a 3500-yr record for a fish community dominated by Pacific herring (*Clupea pallasii*) and northern anchovy (*Engraulis mordax*). Applying a similar technique in freshwater lakes on Kodiak Island, Alaska, Finney *et al.* (2002) reconstructed sockeye salmon (*Oncorhynchus nerka*) abundance over the past 2200 yr. Although these records are not annually resolved, they yield valuable information on low-frequency interdecadal-to-intercentennial patterns of variability. By contrast, analysis of annually formed growth increments can yield multidecadal records of fish growth at high temporal resolution. Tree rings are the archetypal example of such growth-increment data, and have been successfully applied to reconstruct various aspects of marine productivity. Given close couplings between the ocean and atmosphere, Clark *et al.* (1975) used a network of western North American tree-ring chronologies and catch records to generate a 300-yr reconstruction of albacore tuna (*Thunnus alalunga*) productivity for a region north of San Francisco. Tree rings in riparian forests of the Pacific Northwest and

southeast Alaska also reflect salmon abundance via a shared sensitivity to ocean variability and fertilization from the marine nutrients released during salmon decomposition (Drake *et al.*, 2002; Drake and Naiman, 2007).

As in trees, bony fish form annual growth increments, and various attributes of these increments can be used to reconstruct fisheries productivity with methods borrowed from the tree-ring sciences (dendrochronology). In an early example, Pereira *et al.* (1995) constructed a 110-yr growth-increment chronology from the otolith ring widths of freshwater drum (*Aplodinotus grunniens*) in the Red Lakes of Minnesota. Applying a similar methodology, growth increments in fin ray samples were measured to develop a 50-yr chronology of lake sturgeon (*Acipenser fulvescens*) in southeastern Canada and the northeastern United States (LeBreton and Beamish, 2000). Similarly, scale annuli widths were used to generate a 22-yr chronology of rock bass (*Ambloplites rupestris*) in the Ozark region of the southeastern United States (Guyette and Rabeni, 1995). Although the majority of examples represent freshwater habitats, the same analyses are possible in marine environments, as demonstrated specifically in the northeast Pacific. In the first such study, Boehlert *et al.* (1989) developed multidecadal growth chronologies at ages 1 through 6 for canary (*Sebastes pinniger*) and splitnose rockfish (*Sebastes diploproa*). Chronologies extended multiple decades, related to indices of the physical environment, and suggested compensatory growth following a period of increased fishing pressure (Boehlert *et al.*, 1989).

More recently, Black *et al.* (2005) employed the dendrochronology technique of cross-dating to develop a high resolution, 40-yr chronology from otolith growth increments of splitnose rockfish. Ubiquitously applied in tree-ring studies, cross-dating ensures annual resolution in the final chronology. The procedure is based on the principles that at least one climatic variable limits growth, and values of these climatic variables fluctuate over time. Under such conditions, climatic variability induces synchronous growth patterns in all individuals within a given region. These synchronous growth patterns, much like bar codes, can then be cross-matched among samples to verify that all growth increments have been correctly identified and assigned the correct calendar year. Such annually-resolved chronologies provide detailed growth histories, and also strongly relate to records of environmental variability such as the Pacific Decadal Oscillation and El Niño Southern Oscillation (Black *et al.*, 2005). Yet despite the potential for assessing long-term trends and establishing

climate–growth relationships, these techniques remain far underutilized outside of terrestrial environments. Thus, to better investigate the potential of cross-dating and other dendrochronology methods in fisheries, we applied them to the otoliths of yelloweye rockfish (*Sebastes ruberrimus*), a long-lived (at least 118-yr-old) bottom-dwelling species most common in water depths from 91 to 180 m (Love *et al.*, 2002), and for which the annual periodicity of growth-increment formation has been validated by radiometric techniques (Andrews *et al.*, 2002). A total of three growth-increment chronologies were developed from northern California to northern British Columbia with the specific objectives of (i) describing interannual to interdecadal growth patterns within each chronology, (ii) assessing the influence of climate variables including the Pacific Decadal Oscillation, the Northern

Oscillation Index, upwelling, and sea surface temperatures, and (iii) comparing growth patterns and climate–growth relationships across the broad spatial scales in the northeast Pacific.

METHODS

A yelloweye rockfish chronology was developed at each of three locations in the northeast Pacific: the continental shelf of northern California (36°–40° latitude); Triangle Island, located off the northern tip of Vancouver Island, British Columbia (50°50′ latitude 128°40′ longitude); and at Bowie Seamount, approximately 100 km west of the Queen Charlotte Islands, British Columbia (53°20′ latitude 135°40′ longitude) (Fig. 1). California otoliths were obtained by commercial and sport fishing vessels between 1977

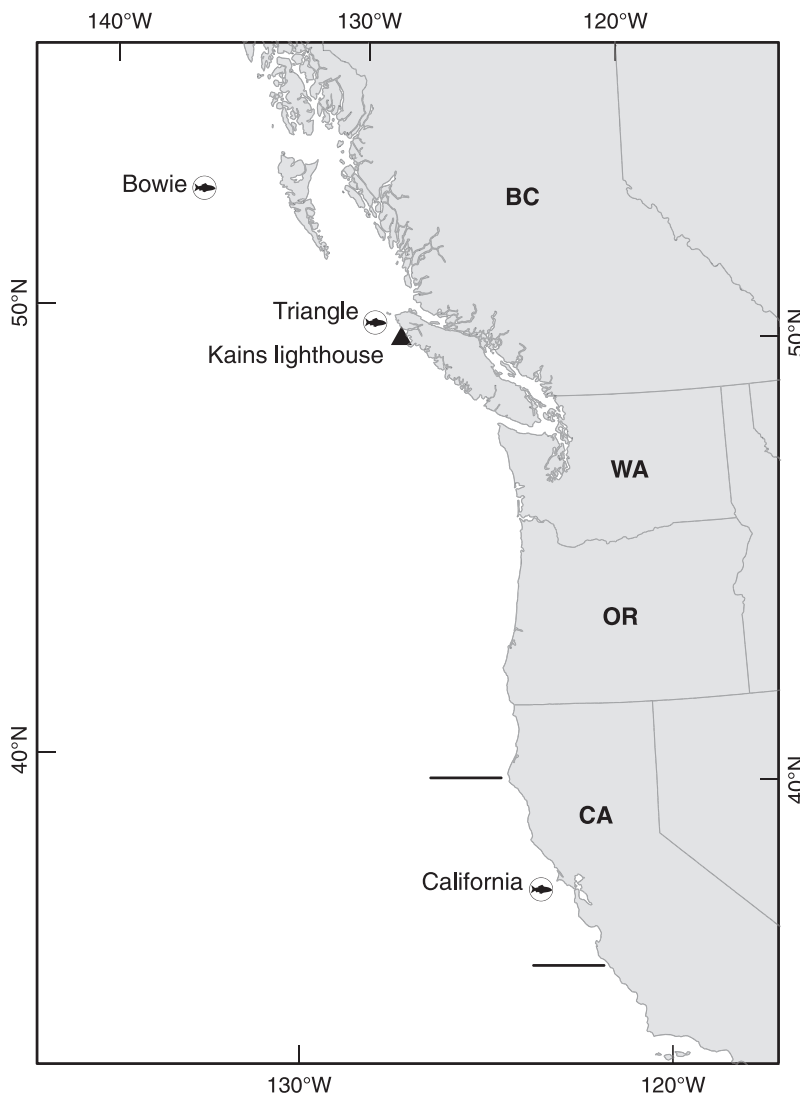


Figure 1. Map of the northeast Pacific with yelloweye rockfish chronology locations: California (sampled on the continental shelf between approximately 36° to 40° latitude, with boundaries marked by black lines), Triangle (50°50′ lat. 128°40′ long.), and Bowie (53°20′ lat. 135°40′ long.). Also shown is the location of Kains lighthouse from which sea surface temperature records were obtained for climate–growth analyses. Abbreviated states or provinces are CA (California), OR (Oregon), WA (Washington), and BC (British Columbia).

and 2004. In British Columbia, the Canadian Department of Fisheries and Oceans collected samples at Bowie Seamount in the summers of 1999 and 2000, and at Triangle Island in May 2003. At each of the two locations in British Columbia, the area sampled was less than 400 km².

Otoliths were embedded in resin, and the resin block was then mounted on a diamond lapidary saw with two blades separated by acetate spacers. Thin sections approximately 0.4 mm in width were cut along a dorsal-ventral axis perpendicular to the sulcus, passing through the focus (Boehlert *et al.*, 1989). Each section was mounted on a glass slide and polished using 2000 grit sandpaper and 0.5 µm lapping film. We selected only the oldest and clearest otoliths at each of the three study sites for chronology development. Otoliths then were visually cross-dated using the 'list year' technique in which synchronous patterns were identified by noting growth increments that were conspicuously narrow or wide relative to immediately surrounding increments (Yamaguchi, 1991). Referred to by dendrochronologists as 'signature years', these prominent growth increments were generally synchronous among samples, reflecting the high-frequency growth variability induced by climate. The process of cross-dating began at the marginal growth increment, which is known to have formed at the calendar year of capture. From this dated increment, synchronous growth patterns were used to verify dates of successively earlier increments, ending with the innermost increment (Black *et al.*, 2005). When all growth increments were correctly identified, years of especially narrow or wide increments corresponded among all specimens. Between these prominent years, less conspicuous yet synchronous growth patterns could be used to verify cross-dating.

Once visual cross-dating was complete, we measured all samples using the program IMAGEPRO PLUS v. 6.0 (Media Cybernetics, Silver Spring, MD, USA). Images were captured with a Leica DC300 7.2 megapixel digital camera attached to a Leica MZ9_s dissection scope. Transmitted light was best for viewing the growth increments, though reflected light produced superior results in a small subset of samples. Growth increments were measured continuously from the dorsal distal margin to within 5 yr of the focus, or as close to the focus as possible. The first years of growth were excluded in case young fish have different habitat and food requirements or respond differently to the environment. Also, measurements were halted if growth increments became unclear, as tended to occur near the margin and the center of the otolith. A total

of one axis was measured per otolith, which always followed the direction of growth (i.e., perpendicular to the growth increments).

At each site, cross-dating was statistically verified using the International Tree-Ring Data Bank Program Library program COFECHA, available through the University of Arizona Laboratory of Tree-Ring Research <http://www.ltrr.arizona.edu/pub/dpl/> (Holmes, 1983; Grissino-Mayer, 2001). This procedure involved isolating high-frequency variability in each set of measurements via the process of detrending, and then cross-correlating the detrended measurements to verify that all samples aligned with one another. In COFECHA, detrending was accomplished by fitting each set of otolith measurements with a cubic spline set at a 50% frequency response of 22 yr (Cook and Peters, 1981; Grissino-Mayer, 2001). The frequency response is analogous to the length of a window used in calculating a moving average whereby the flexibility of the function increases with decreasing window length (Grissino-Mayer, 2001). Cubic splines with a frequency response of 22 yr provided optimal cross-dating verification results in splitnose rockfish and were therefore applied in this study (Black *et al.*, 2005). Once fitted, each set of otolith measurements was divided by the values predicted by the cubic spline, thereby removing low-frequency variability, homogenizing variance, and equally weighting each set of measurements to a mean of one (Holmes, 1983; Grissino-Mayer, 2001). Any remaining autocorrelation was removed to ensure that all detrended time series met the assumptions of serial independence. Each detrended set of otolith measurements was then correlated with the average of all other detrended sets of otolith measurements in the sample. In so doing, the high frequency growth pattern of each individual was compared to the high frequency growth pattern of all other individuals. Isolating only the high frequency, serially-independent growth pattern prevented spuriously high correlations among individuals, and also mathematically mimicked the process of visual cross-dating.

Once cross-dating verification was complete we began developing a master chronology for each site by detrending the original measurement time series with negative exponential functions. Negative exponential functions removed age-related growth declines while preserving any remaining low-frequency variability, much of which could have been induced by climate. Exceptions to negative exponential functions were made for two measurement time series that excluded early growth years, did not show age-related growth declines, and were instead better fit by the series mean

(a horizontal line). At each site, all detrended series were then averaged into a master chronology using a biweight robust mean to reduce the effects of outliers (Cook, 1985). All chronology development was conducted using the program ARSTAN (developed by Ed Cook and Paul Krusic; available at <http://www.ldeo.columbia.edu/res/fac/trl/public/publicSoftware.html>) (Cook, 1985). Once completed, the quality of the chronology was quantified using the expressed population signal (EPS) statistic, which describes the strength of the synchronous growth pattern relative to growth patterns unique to individual samples (i.e., 'noise'). Though there is no significant threshold for this statistic, an EPS value of 0.85 or greater is considered adequate by dendrochronologists for climate reconstruction, a level more than sufficient for the purposes of our study (Wigley *et al.*, 1984).

Each yelloweye rockfish master chronology was correlated with monthly averages of the Pacific Decadal Oscillation (PDO) and the Northern Oscillation Index (NOI). The NOI is the difference in sea level pressure between the North Pacific High and Darwin, Australia, and captures the strength of atmospheric circulation between the tropics and the North Pacific, particularly with respect to the El Niño Southern Oscillation in the North Pacific (Schwing *et al.*, 2002). The PDO is the leading principal component of North Pacific sea surface temperatures poleward of 20°N latitude, and it exhibits a spatial 'fingerprint' similar to the El Niño Southern Oscillation, but acts on much longer temporal scales (Mantua *et al.*, 1997). In addition to these basin-wide variables, we also correlated the master chronologies with monthly averages of local sea surface temperature and upwelling. NOI (1948 to present) and upwelling (1946 to present) records were obtained through the Pacific Fisheries Environmental Laboratories live access server at <http://www.pfeg.noaa.gov/>. PDO data were obtained from University of Washington Joint Institute for the Study of the Atmosphere and Ocean at

<http://jisao.washington.edu/pdo/>. For the two British Columbia chronologies, we used SST data recorded at the Kains Lighthouse (1935 to present) available at (http://www.pac.dfo-mpo.gc.ca/sci/osap/data/SearchTools/Searchlighthouse_e.htm). California sea surface temperatures were obtained from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) and averaged between 36 and 40° latitude, and from -130° longitude to the coast, the approximate sampling locations of the fish used to develop the chronology. Monthly averages were used in the correlation analysis to determine the periods of the year in which environmental variability most strongly affected growth.

RESULTS

Unlike most tree-ring analyses in which narrow signature years are primarily used for cross-dating, wide signature years were equally useful in the yelloweye rockfish dataset. Although signature years were not shared among sites, strongly synchronous growth patterns occurred within sites. Important signature years for the California chronology were 1992, 1983, 1966, 1942 (narrow) and 1991, 1965 (wide). Signature years for Triangle Island were 1997, 1979, 1957 (narrow) and 1992, 1970, 1958 (wide), and those for Bowie Seamount 1993, 1977, 1963 (narrow) and 1998, 1964 (wide).

Among the 47 thin-sectioned otoliths from Bowie Seamount, 45 thin-sectioned otoliths from Triangle Island, and 65 thin-sectioned otoliths from northern California, a total of 18, 21, and 27, respectively, were sufficiently clear and old for developing the master chronologies (Table 1). Mean otolith age was 70 yr for Bowie, 68 yr for Triangle, and 50 yr for California, though only the clearest portions of these otoliths were used for chronology development. The earliest years of growth tended to be the least clear and least suitable for measurement, particularly at Bowie and Triangle.

Chronology	Otolith sample size*	Mean sensitivity†	Interseries correlation‡	Mean series length (yr)	First-order autocorrelation
California	27	0.20	0.54	25.7	-0.51
Triangle	21	0.20	0.65	44.7	-0.16
Bowie	18	0.20	0.68	32.5	-0.29

*The number of otoliths used in developing each chronology.

†An index of high-frequency variability.

‡The average correlation between each detrended measurement time series (using a 22-yr cubic spline) and the average of all other detrended measurement time series.

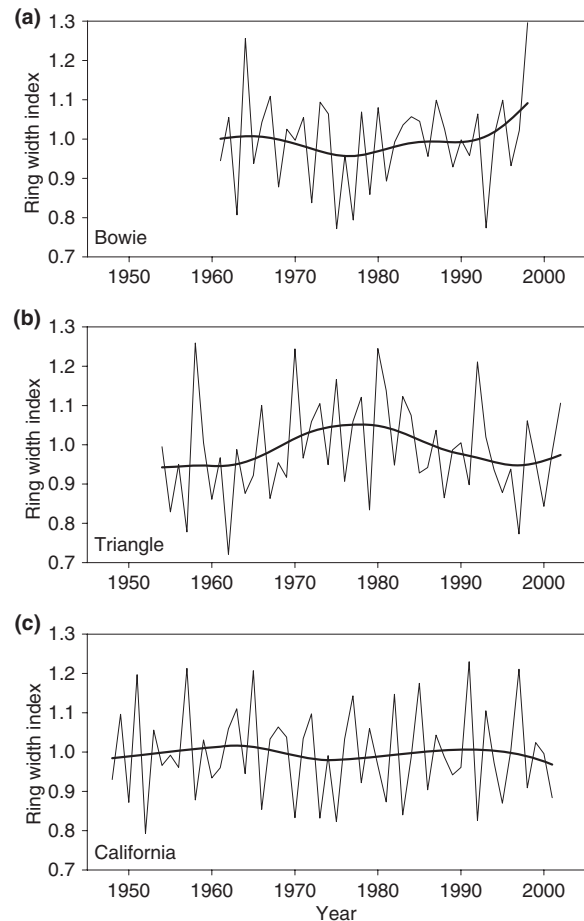
Table 1. Yelloweye rockfish chronology properties.

For those portions that were measured, interseries correlation, an indicator of growth synchrony among samples, was highest within Bowie ($r = 0.68$) and Triangle ($r = 0.65$). In both datasets, every otolith correlated significantly with the average growth pattern of all the others ($P < 0.05$). Although the mean interseries correlation for California was somewhat lower ($r = 0.54$), all correlations in the dataset were still statistically significant ($P < 0.05$) with the exception of only two samples (Table 1). Visual inspection of these otoliths confirmed that they were cross-dated correctly, but the measurement time series were relatively short in length (mean of 25.7 yr), which may in part explain why they failed to correlate as strongly.

All portions of the final chronologies were generated using a minimum of eight measurement time series. This sample size was sufficient to capture the synchronous growth pattern, as indicated by EPSs that consistently exceeded values of 0.85. Also, mean sensitivity, an index of high frequency (year-to-year) variability, was consistent among the three sites at 0.20, a level that is considered high in tree-ring studies (Fritts, 1976). In addition, the California chronology contained the highest levels of autocorrelation, which could indicate long-term growth patterns in the dataset (Table 1). As for relationships among chronologies, California and Triangle were negatively correlated with one another ($r = -0.56$; $P = 0.0003$), as were California and Bowie ($r = -0.29$; $P = 0.15$). However, Triangle and Bowie showed almost no relationship to one another, with a correlation of $r = -0.06$ ($P = 0.78$). With respect to lower-frequency variability, both the California and Bowie chronologies exhibited slower growth from approximately 1965 through 1985, whereas the opposite occurred in the Triangle chronology (Fig. 2). The Bowie and Triangle chronologies exhibited faster growth from the mid 1990s to the present, though California experienced slower growth during that same period (Fig. 2).

Multiple climatic variables were highly significantly ($P < 0.01$) correlated with all three yelloweye rockfish chronologies (Fig. 3). In general, all three chronologies were sensitive to environmental variability during the prior fall and current winter. The California chronology and, to a lesser extent, the Bowie chronology also were sensitive to environmental variability during the current fall, yet the signs of these climate-growth correlations were reversed in comparison with those earlier in the year (Fig. 3a,c). For example, the California chronology positively correlated with NOI and upwelling in January and February, but negatively correlated with these same variables in

Figure 2. Master chronologies of yelloweye rockfish for three locations in the northeast Pacific. Heavy lines are 22-yr cubic splines to emphasize low-frequency trends.



August, September, and October (Fig. 3c). Although there were some similarities as to the time of year in which the chronologies were most sensitive to climate, correlation strengths and signs varied considerably among sites. Perhaps the most important difference was that correlations with the four variables in the California chronology were opposite in sign to those in the Bowie and Triangle chronologies (Fig. 4). Most notably, the Bowie and Triangle chronologies negatively correlated with NOI and upwelling during the late fall and winter of the current year, whereas the California chronology positively correlated with these same variables during the same time of the year (Fig. 3). Another difference was that SST and the PDO correlated most strongly and over the greatest number of months in the Triangle chronology. There were no significant correlations with the PDO in the Bowie chronology (Fig. 3a), and the only significant correlations in the California chronology occurred in

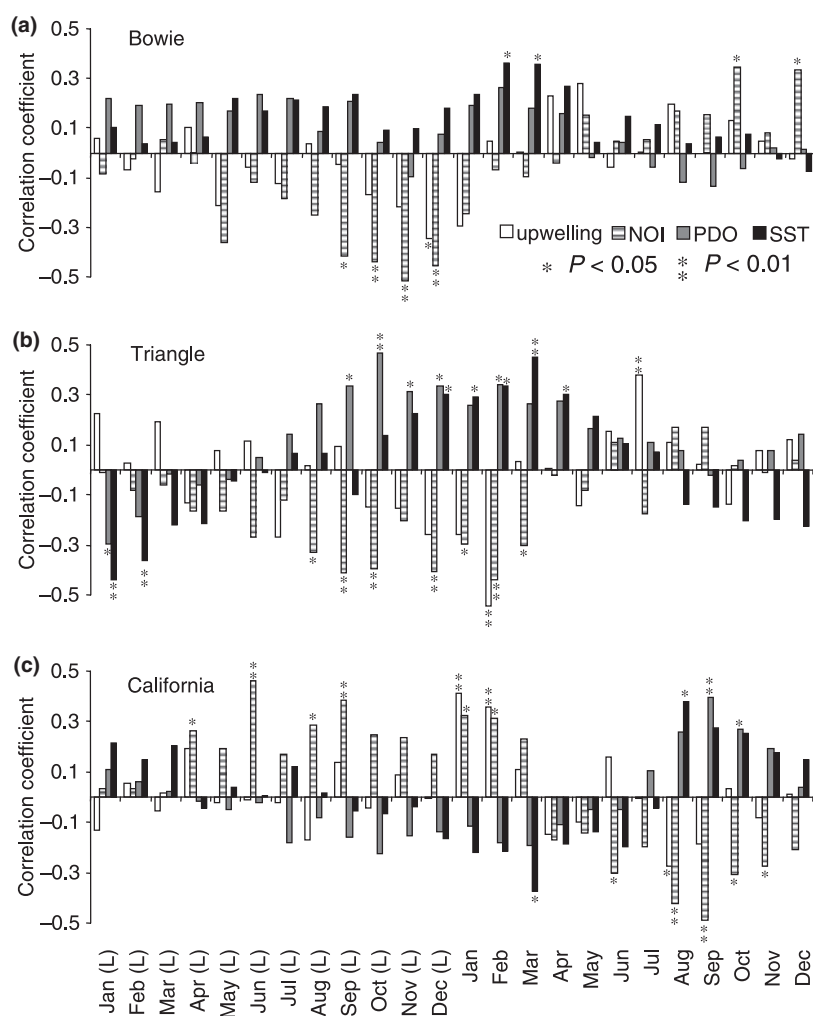


Figure 3. Correlations between climate variables and each of the three yellow-eye growth chronologies: (a) Bowie Seamount, (b) Triangle Island, and (c) California. Climate indices are upwelling index, the Northern Oscillation Index (NOI), the Pacific Decadal Oscillation (PDO) and sea surface temperatures (SST). Each chronology is correlated with monthly averages of each environmental variable for each month of the current year, as well as each month lagged (L) by 1 yr.

the current September and October (Fig. 3c). Finally, the Triangle chronology strongly and negatively correlated with SST in the prior January and February, though it positively correlated with this variable in the current January and February (Fig. 3b).

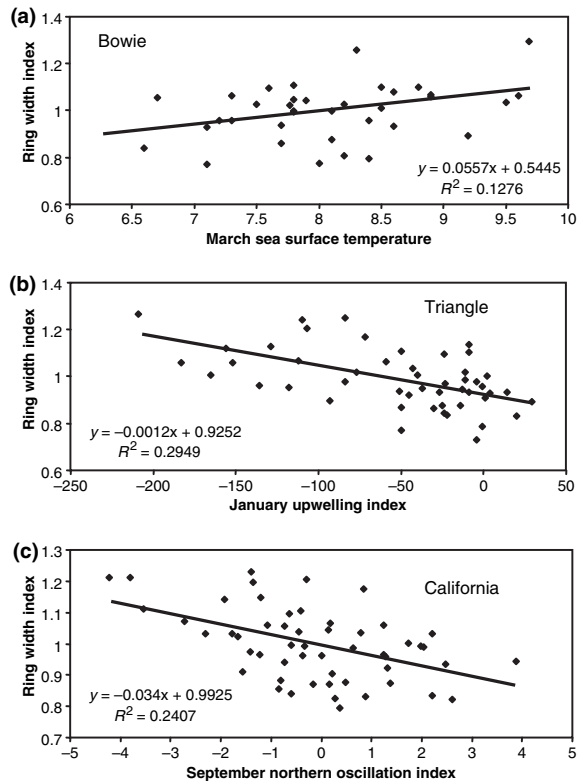
Overall, climate–growth relationships were better approximated by linear functions than by non-linear functions. For example, there was a linear relationship between September NOI and the California chronology, January upwelling index and the Triangle chronology, and March sea surface temperatures and the Bowie chronology, representative of the other climate–growth relationships in the dataset (Fig. 4).

DISCUSSION

Synchronous growth patterns in the otolith ring widths allowed for exact cross-dating and construction of high-resolution chronologies using a tree-ring-based approach. Indeed the average interseries correlations

(ISC) in these chronologies are comparable to those in tree-ring chronologies throughout the Pacific Northwest. As typical examples, the ISC of a noble fir (*Abies procera*) chronology in the central Coast Range of Oregon was $r = 0.65$, whereas that of a ponderosa pine (*Pinus ponderosa*) chronology east of the Oregon Cascades was $r = 0.55$ (Pohl *et al.*, 2002; B.A. Black, unpublished data). Mean sensitivity is also comparable to that found in tree-ring studies (Fritts, 1976), as is the expressed population signal (i.e., >0.85). Thus, by the standards of dendrochronology, the degree of growth synchrony is suitable for cross-dating, developing annually resolved chronologies, and establishing the effects of climate on growth. However, one irregularity is that although mean sensitivity is equivalent among all three sites, the ISC is somewhat lower for California (Table 1). In other words, the degree of interannual variability for California is comparable to that in the other two chronologies, but the synchrony of that variability is relatively low. This may be

Figure 4. Relationships between various environmental variables and yelloweye rockfish chronologies at (a) Bowie Seamount, (b) Triangle Island, and (c) California. Regression lines and equations are shown to highlight the linear nature of the relationships.



because California sampling occurred over a relatively large area and included fish from slightly different climate regimes, thereby resulting in lower synchrony. The same may be true for the splitnose rockfish chronology developed in the same study area, which has a comparable ISC of 0.52 (Black *et al.*, 2005).

Within each chronology, correlations with all four environmental variables reflected consistent climate-growth relationships, considering that PDO and SST are negatively related to NOI and upwelling. More specifically, high (low) values of PDO and SST (NOI and upwelling) indicate warm (cool) ocean conditions. Also, high (low) NOI values occur during La Niña (El Niño) years, and are associated with cool (warm) waters in the northeast Pacific (Schwing *et al.*, 2002). Thus, from correlations from the California chronology, yelloweye rockfish growth is favored in cool ocean conditions, at least through the current fall. In contrast, relatively warm ocean conditions favor strong yelloweye rockfish growth farther north. This inverse relationship between the California

chronology and that of the Triangle and Bowie chronologies is consistent with broad-scale productivity patterns in the northeast Pacific, which is generally divided into three (Ware and McFarlane, 1989) major domains: the Coastal Upwelling California Current system along the California, Oregon, Washington, and Vancouver Island coast, a Transition Zone to the Alaska border, and a Coastal Downwelling system from southeast Alaska through the Aleutian Islands. In the Upwelling California Current system, cool ocean regimes are associated with upwelling and high levels of primary and secondary productivity (Roemmich and McGowan, 1995; Hooff and Peterson, 2006), whereas farther north, productivity is associated with warm ocean regimes and downwelling (McFarlane and Beamish, 1992; Brodeur *et al.*, 1996). Considering that the California growth chronology falls within the Upwelling Zone, the Triangle Island chronology falls within the Transition Zone, and the Bowie Seamount chronology falls within the Downwelling Zone, yelloweye rockfish growth appears to coincide with these trends in primary and secondary productivity.

An opposing relationship between the California and Alaska Current domains has also been well documented in salmon (Hare *et al.*, 1999). In an analysis of catch data spanning the past 70 yr, abundance of chinook (*Oncorhynchus tshawytscha*) and coho salmon (*Oncorhynchus kisutch*) from the California Current region vary synchronously, but in a pattern opposite that of Alaska salmon. Salmon catch is high in Alaska and low in the California Current during warm regimes, with the inverse happening during cool regimes (Hare and Francis, 1995; Hare *et al.*, 1999). These patterns are identical to those observed in the yelloweye rockfish chronologies with the exception that salmon catch in the Transition Zone did not consistently follow an Alaska or California trend. Some stocks follow a southern pattern, whereas others follow a northern pattern (Hare *et al.*, 1999). However, the Triangle Island yelloweye rockfish chronology, located at the southern boundary of the Transition Zone, clearly follows a northern pattern with strongly positive correlations to warm ocean conditions.

The overall phenomenon of cool conditions leading to lower rockfish productivity in the north and higher rockfish productivity in the south is supported by other lines of evidence, mostly from the California Current system. For example, in the coastal waters of northern and central California, the strong 1983 El Niño significantly reduced the growth-increment width of widow (*Sebastes entomelas*) and yellowtail rockfish (*Sebastes flavidus*) (Woodbury, 1999).

Similarly, levels of visceral fat were much lower for yellowtail rockfish caught in 1983 than for those caught in 1980 (Lenarz and Wyllie Escheverria, 1986). Furthermore, an otolith growth-increment chronology for splitnose rockfish in northern California correlated negatively with the PDO and sea surface temperature but positively with upwelling and the NOI, as did the California yelloweye rockfish chronology in this study (Black *et al.*, 2005). These climate–growth relationships appear to be consistent with long-term recruitment patterns. From an analysis of marine bird diet spanning almost three decades, consumption of juvenile rockfish declined during warm years, particularly those with El Niño events (Miller and Sydeman, 2004). January and February upwelling was one of the most significant predictors of the occurrence of rockfish in seabird diet, especially during the cool phase of the PDO, which corresponds with our findings that winter upwelling is strongly positively correlated with yelloweye rockfish growth in California.

In contrast to these other rockfish climate–growth findings in the California Current, the California yelloweye rockfish chronology only has positive correlations with cool ocean conditions through the spring of the current year. Climate–growth relationships abruptly reverse for the late summer such that strong growth is instead associated with warm ocean regimes, including El Niño events and warm phases of the PDO. We attempted to determine whether this relationship could be an artifact of the analysis. The California yelloweye rockfish chronology does contain significant first-order autocorrelation, which could simply reflect the inherent, significant autocorrelation of the climate variables that are driving growth. Alternatively, the autocorrelation could be due to climate effects on growth carrying into subsequent years. For example, an extreme El Niño event may have effects that linger into the second or even third year, and such lagging could ‘smear’ and potentially alter the climate–growth relationships. To address this issue, we removed all significant autocorrelation from the California chronology using the program ARSTAN. Yet when we re-ran the correlation analyses using this residual chronology, the overall effect was only to slightly reduce correlation coefficients with almost no change to the overall correlation patterns. Thus the reverse in climate–growth relationships appears to be a genuine phenomenon. However, the mechanisms behind this reversal are unclear. Perhaps warm ocean conditions late in the summer or the early onset of an El Niño can temporarily increase productivity, extending the yelloweye rockfish growing season. Alternatively,

cool ocean conditions extending late into the summer may prematurely truncate the growing season. Hints of climate–growth reversals also are apparent during the prior winter for Triangle and the current summer at Bowie, so this reversal in climate–growth relationships may be a pattern for yelloweye rockfish throughout the study area.

Considering that, in terms of oceanography, the PDO signal is strongest in the North Pacific and the ENSO signal is strongest in the South Pacific (Mantua *et al.*, 1997), we expected correlations with PDO to be strongest in northern chronologies and correlations with NOI to be strongest in the California chronology. Instead, NOI was consistently and strongly correlated with all three chronologies, whereas the PDO was only weakly correlated with growth, even in the northernmost Bowie chronology. Thus, ENSO appears to affect yelloweye rockfish growth more strongly throughout the study region. Alternatively, the 25–45 yr spanned by each chronology may not be sufficiently long to fully address the impacts of the PDO. An analysis across multiple PDO cycles may be necessary to adequately evaluate its effects on growth, which may be possible if these chronologies are extended using additional samples at some point in the future. Another conspicuous irregularity is that upwelling did not strongly correlate with growth in the Bowie chronology. However, this could be because these fish were sampled offshore on a seamount where upwelling is expected to be a less influential driver of productivity.

As for rockfish management, understanding climate–growth relationships may help disentangle the effects of climate from those of harvesting on fish populations. Given their slow growth, extreme longevity, and late maturation, rockfish as a group are vulnerable to overfishing. Coincident with increased fishing pressure, many rockfish species, including yelloweye, have experienced substantial declines in biomass, recruitment, and density over the past 20 yr (Parker *et al.*, 2000; Love *et al.*, 2002; Tolimieri and Levin, 2005; Harvey *et al.*, 2006). Currently yelloweye rockfish is listed as overfished, and in the year 2000 stocks were only 7% of unfished levels in the waters off northern California, and 12% in the waters off Oregon (Love *et al.*, 2002; Harvey *et al.*, 2006). Our results indicate that in California, the shift to a warm regime in 1977 would have reduced growth, compounding declines associated with overharvesting, particularly during El Niño years. This observation is consistent with Tolimieri and Levin (2005) who assert that bocaccio rockfish (*Sebastes paucispinis*) populations have been negatively impacted not only by overfishing

but also by an unfavorably warm regime in the California Current system. In contrast, the warmer regime should have enhanced growth along coastal British Columbia and Alaska, and any recent declines are in spite of these favorable climate conditions. As for direct effects of fishing on growth, we could not identify any compelling growth signatures that might be due to the effects of overharvesting. One explanation is that surviving fish would experience compensatory growth in response to reduced competition. In their analysis of canary and splitnose rockfish growth increments, Boehlert *et al.* (1989) found a marked increase in growth rates after about 1970, which is consistent with compensatory growth. However, no such patterns are evident in the yelloweye rockfish chronologies.

Our comparisons of synchronous growth as part of cross-dating also provide clues as to the movements of yelloweye rockfish in the northeast Pacific. Overall, the high levels of synchrony within sites compared to that among sites indicate that yelloweye rockfish did not migrate long distances. If fish had migrated over large distances, we would expect that the growth patterns of those fish would not match with the rest of the population. For example, a fish from the Triangle region would fail to cross-date with those in the Bowie region given that these two chronologies share almost no synchronous growth patterns. In our analysis we found no outlier fish that failed to cross-date with the growth patterns in the others, suggesting that stocks did not mix over large areas. High interseries correlations for Bowie and Triangle, which were sampled over small areas, also suggest that the majority of movement occurs on fine spatial scales. If fish were moving from more distant locations, we would expect the interseries correlations to be comparable to that of the California chronology, which was sampled over a much wider area and therefore contained a greater diversity of growth patterns. In a study of telemetry data for blue rockfish (*Sebastes mystinus*) along the central California coast, fish movement was largely confined to a home range of approximately 9000 m². The majority of time was spent within an even smaller, core area (Jorgensen *et al.*, 2006). Greenspotted rockfish (*Sebastes chlorostictus*), which have a life history similar to that of yelloweye rockfish, showed very little vertical movement over a 3-month period in Monterey Bay. Although some fish traveled more than 3 km, horizontal movement was largely constrained to an area of less than 1.6 km² (Starr *et al.*, 2002). Additional chronologies would have to be developed to better address this issue in yelloweye rockfish, but the results from our study do suggest that these fish are not moving large distances.

In conclusion, we demonstrate that dendrochronology techniques can be applied to construct high-resolution growth chronologies from otolith growth increments, and that those chronologies can be used to describe growth variability across various spatial and temporal scales. Here we characterized growth chronologies for a single species, but as more chronologies are developed, growth patterns and climate-growth responses could be contrasted across multiple species to achieve a community-level perspective. Also, the interactions among recruitment and somatic growth could be evaluated by comparing otolith growth increment chronologies to records of recruitment, biomass, and catch data. Finally, master growth-increment chronologies also can be used as an age validation tool (Black *et al.*, 2005). Once a master chronology is established, the growth patterns of other fish caught in the region can be visually cross-dated to the innermost increment, thereby ensuring the correct estimate of recruitment dates. Given the wide-ranging use of these techniques in terrestrial ecology, we believe cross-dating and chronology development could prove equally useful for addressing analogous issues in fisheries ecology.

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