Using tree-ring crossdating techniques to validate annual growth increments in long-lived fishes

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Abstract: We applied crossdating, a dendrochronology (tree-ring analysis) age validation technique, to growth increment widths of 50 *Sebastes diploproa* otoliths ranging from 30 to 84 years in age. Synchronous growth patterns were matched by the following: (*i*) checking the dates of conspicuously narrow growth increments for agreement among samples and (*ii*) statistically verifying that growth patterns correlated among samples. To statistically verify pattern matching, we fit each time series of otolith measurements with a spline, and all measurements were divided by the values predicted by the curve. This standardized each time series to a mean of 1, removing the effects of age on growth and homogenizing variance. Each time series was then correlated with the average growth patterns of all other series, yielding an average correlation coefficient (r) of 0.53. Average growth of all 50 samples was significantly correlated with an upwelling index (r = 0.40, p = 0.002), the Pacific Decadal Oscillation (r = –0.29, p = 0.007), and the Northern Oscillation Index (r = 0.51, p = 0.0001), corroborating accuracy. We believe this approach to age validation will be applicable to a wide range of long-lived marine and freshwater species.

Résumé : Nous avons utilisé la datation croisée, une technique de validation de l'âge en dendrochronologie (analyse des anneaux des arbres), pour étudier les largeurs des incréments de croissance des otolithes de 50 *Sebastes diploproa*, âgés de 30 à 84 ans. Les patrons de croissance synchronisée ont été corroborés (*i*) en nous assurant que les dates d'incréments particulièrement étroits correspondent dans les échantillons et (*ii*) en vérifiant statistiquement que les patrons de croissance sont en corrélation dans les différents échantillons. Pour vérifier statistiquement la correspondance des patrons, chaque série chronologique de mesures d'otolithes est ajustée à une spline et toutes les mesures sont divisées par les valeurs prédites par la courbe. Cette opération standardise chaque série chronologique autour d'une moyenne de 1, éliminant les effets de l'âge sur la croissance et rendant la variance homogène. Chaque série chronologique est alors mise en corrélation avec le patron de croissance moyen des autres séries, ce qui génère un coefficient de corrélation (r) moyen de 0,53. La croissance moyenne de l'ensemble des 50 échantillons est en corrélation significative avec l'indice d'affleurement (upwelling) (r = 0,40, p = 0,002), l'oscillation décennale du Pacifique (r = –0,29, p = 0,007) et l'indice d'oscillation boréale (r = 0,51, p = 0,0001), ce qui confirme sa précision. Nous croyons que cette méthode de validation de l'âge pourra s'appliquer à une variété d'espèces de mer et d'eau douce à grande longévité.

[Traduit par la Rédaction]

Introduction

Counts of annual growth increments formed in otoliths provide a relatively quick, convenient method for estimating fish age. Age is estimated from hundreds of thousands of otoliths each year, with a minimum of over 1 million fish aged either by scales or otoliths in 1999 alone (Campana and Thorrold 2001). These data are of critical importance in the assessment of fish stocks, as well as in estimates of growth and mortality rates. Yet despite their importance in fisheries management, significant errors may occur (Boehlert and Yoklavich 1984). Complications may arise from the asymmetric form of the otolith and the tendency of numbers and widths of increments to vary among different regions of the otolith. Also, boundaries of the increments may be diffuse and difficult to identify. Consequently, considerable error may occur in the interpretation of otoliths, and age estimates may vary among readers and laboratories (Beamish 1979; Boehlert and Yoklavich 1984). In most cases, ageing errors depart from the actual age of the fish by 1 or 2 years, but more extreme errors are not uncommon, especially in longer-lived fish (Wilson and Boehlert 1990). Management policies based on inaccurate data could lead to the overexploitation of fish populations.

A number of age-validation techniques have been developed to reduce this error, several of which only roughly estimate the lifespan of long-lived individuals. One of the most common of these methods is bomb radiocarbon, which uses as a time-specific marker the sudden increase of ^{14}C in the marine environment that occurred following nuclear testing in the 1950s and 1960s (Kalish 1993; Campana et al. 2001). Levels of ^{14}C in otolith cores should correspond to time-

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specific increases in marine ^{14}C. In comparison with known ^{14}C chronologies for the region, over-ageing would shift the otolith ^{14}C chronology to earlier years and under-ageing would shift the otolith ^{14}C chronology to later years (Kalish 1993; Campana et al. 2001). Thus, ageing errors can be corrected by aligning otolith ^{14}C with marine ^{14}C values. In a related technique, decay rates of radioisotopes are used as a chronometer for estimating otolith age. Half-lives serve as an indicator of time elapsed since the radioisotopes were incorporated into the otolith. A frequently applied technique for older fish is calculating the ratio of ^{210}Pb to ^{226}Ra in the core of the otolith, which is useful for time scales up to approximately 120 years (Bennett et al. 1982; Burton et al. 1999; Andrews et al. 2002). Though radioisotopes and bomb carbon are used to confirm longevity of very old fish, they lack the annual resolution necessary to validate an exact age or exact number of growth increments.

On a finer scale, other techniques have been developed to precisely validate the annual nature of ring formation and assign the correct calendar year to each growth increment. Most of these techniques require an event at a known date that imparts a unique, identifiable mark on a bony structure of the fish. To date, these studies have largely used chemical or isotopic signatures in bony structures, particularly otoliths. For example, one of the most rigorous approaches is the release and recapture of marked fish of a known age. At the time of release, the fish may be injected with a compound such as oxytetracycline, which distinctly fluoresces when exposed to ultraviolet light. When the fish is recaptured, the number of otolith increments is checked against the time elapsed since release (Beamish and Chilton 1982; Leaman and Nagtegaal 1987; Heifetz et al. 1998). Presently, mark–recapture studies are considered to be the most precise and accurate means of age validation (Beamish and McFarlane 1983; Campana 2001). Yet they are best applied over relatively short periods because the probability of recapturing a fish declines over time.

Though much less thoroughly explored than the use of chemical and isotopic signatures for age validation, morphological variations within an otolith could also be used as time-specific markers for age validation. Growth increment width integrates many potential time-specific markers. It reflects the overall physiological condition of the fish, which in turn is a function of competition, access to food, and the physiological and developmental status (age, size, vigor, phase in life cycle) of the fish over time. More importantly, otolith growth can reflect conditions of the physical environment, such as sea surface temperature, or other physical factors affecting prey availability or physiological condition. Indeed, strong El Niño events, such as that which occurred in 1983, appear to have reduced the growth increment width in yellowtail and widow rockfish (Woodbury 1999). Also, Pacific whiting, splitnose rockfish, and canary rockfish increment-width chronologies were significantly influenced by a variety of physical variables, including sea surface temperature and upwelling (Boehlert et al. 1989; Dorn 1992). In freshwater systems, ring-width chronologies of calcified growth structures were significantly correlated with climatic variables, as demonstrated for the freshwater drum in Minnesota, rock bass in streams of the Ozark Mountains, and lake sturgeon in the Great Lakes region (Guyette and Rabeni 1995; Pereira et al. 1995; LeBreton and Beamish 2000). Finally, thermally induced marks on otoliths of young fish produce “bar codes” that can later be used to estimate fish age (Volk et al. 1994). In recommending appropriate validation techniques in fish ageing, Beamish and McFarlane (1983, p. 741) suggested that “It may be possible to find some ‘natural’ mark on a structure that identifies a particular year class, but such marks appear to be very rare.” However, these natural markers may be much more common than originally thought.

It is this correspondence between growth increment and physical environment that we use as the basis for dating each annual increment, and ultimately, for age validation. We apply a technique from dendrochronology (tree-ring analysis) called crossdating, which is used to cross-match growth patterns among samples to assign the correct calendar year to each growth increment. Data sets with properly dated growth increments can be used to generate high-resolution growth chronologies, as well as to determine the exact age of each tree. Crossdating is based on the assumptions that growth increments form at regular intervals (in this case, annually), growth increment width is limited by some aspect of climate, and the intesity of this climatic variable fluctuates over time. If these assumptions hold true in marine systems, climate will induce synchronous, time-specific growth patterns in otolith increment widths, much as it does in tree rings. To ensure that each growth increment is properly dated, growth patterns are visually matched by checking that the calendar years of conspicuously narrow or wide growth increments tend to correspond among samples. For statistical verification, climate-induced growth patterns are isolated from each time series and cross-correlated with the growth patterns of other specimens. High correlations indicate a high degree of precision among the otolith time series, while low correlations suggest ageing errors. We then correlate otolith growth patterns with climate records to corroborate accuracy, thus verifying that the correct calendar year is assigned to each growth increment. If otolith growth patterns correlate strongly among fish and with records of the physical environment, each growth increment should be assigned the correct calendar year and age estimates of each fish should therefore be correct.

Crossdating among samples is considered the most important step in any tree-ring analysis and serves as the principle on which modern dendrochronology was founded (Stokes and Smiley 1996). Assigning the correct calendar year to all growth increments is imperative if tree rings are to be used to date archaeological ruins or reliably reconstruct climate, forest dynamics, or forest age structure. Despite the parallels between the two fields, very few sclerochronology (analysis of growth increments in hard structures) studies have attempted to apply dendrochronology to otolith age validation and development of increment-width chronologies (Guyette and Rabeni 1995; Pereira et al. 1995; LeBreton and Beamish 2000). Thus, in this study we demonstrate that crossdating is possible for validating the ages of long-lived splitnose rockfish (*Sebastes diploproa*). This species serves as an example of a large number of rockfish species that live to ages in excess of 50 and even 100 years, to which this technique will likely apply (Munk 2001). The annual precision and accuracy afforded from crossdating could provide valuable age data for fishery management and complement the suite of age validation techniques already in use.

Methods

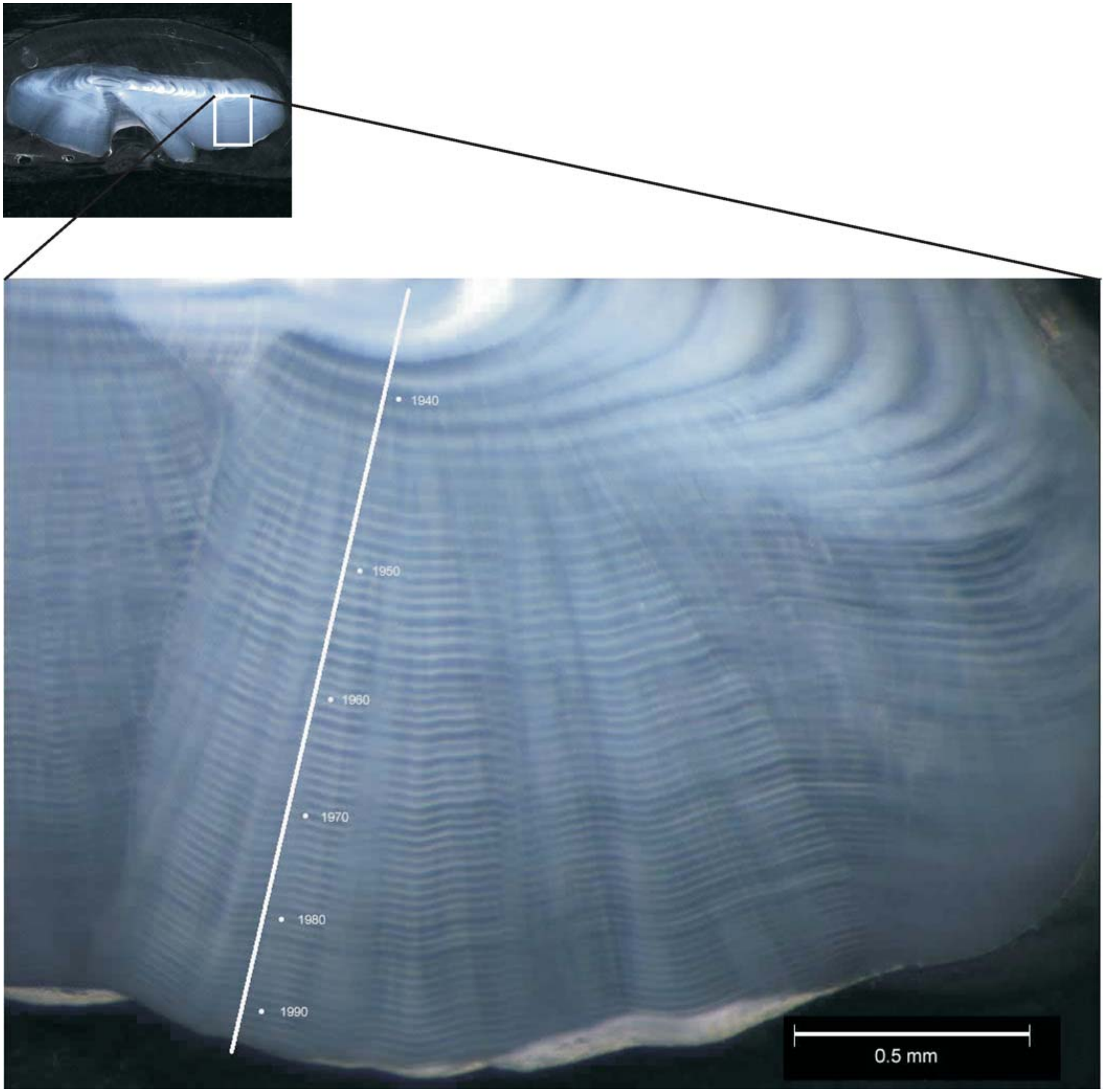
Sebastes diploproa otoliths were collected during rockfish surveys conducted by the Alaska Fisheries Science Center (NOAA Fisheries, Seattle, Washington, USA) in 1989 and 1995. All fish were collected from late June through mid-August off the west coast of the United States between 35°N and 40°N. At this time of year, *Sebastes* have typically completed a hyaline zone and have begun formation of an opaque zone with the onset of the new growing season (Pearson 1996; Woodbury 1999). Otoliths were embedded in resin and mounted on a diamond lapidary saw; thin sections approximately 0.4 mm in thickness were cut along a dorsal–ventral axis of the otolith. Cuts were perpendicular to the sulcus and passed through the focus of each otolith. Thin sections were then mounted on glass slides and polished by hand using 400- and 2000-grit sandpaper. Otolith age was preliminarily determined by counting annual growth increments along one continuous axis from the distal dorsal surface to the proximal dorsal surface. One increment consisted of an opaque summer growth zone and a translucent winter growth zone. All otoliths less than 30 years of age were omitted from further analysis so there would be an adequate number of degrees of freedom for subsequent correlation analyses. From the set of specimens at least 30 years in age, otoliths were selected in which increment borders were crisp and readily identifiable.

Crossdating was accomplished with the following two-step process: (*i*) a visual check of the dates of narrow and wide growth increments for general agreement among samples and (*ii*) statistical verification by cross-correlating growth increment measurements among samples. We began with the clearest otolith thin sections in which all growth increments were easily identified. Starting at the otolith margin, we proceeded toward the focus, noting the dates of conspicuously narrow or wide growth increments. This direction was opposite to that of most ageing procedures, which typically proceed from the focus to the margin. Yet this reversal was necessary so that we could tentatively date each growth increment by counting back from the partial increment formed at the margin during the year of capture. Growth increments were noted as conspicuously narrow (or wide) if they appeared to be noticeably reduced (or increased) in comparison with the immediate one to three neighbors on both sides. Many of these conspicuous growth increments, referred to by dendrochronologists as signature years, should be synchronous among samples (Yamaguchi 1991; Stokes and Smiley 1996). As we evaluated the otoliths, we found that the dates of many conspicuously narrow or wide growth increments corresponded among samples. These signature years occurred, on average, once per decade. For each otolith, we checked that the dates of conspicuously narrow or wide growth increments agreed with those in other samples. If a growth increment had been missed, tentative dates of narrow or wide increments would be shifted by a year, and the point at which the shifting began indicated the location of the error. Variability did occur among samples, yet the weight of evidence suggested all otoliths were properly aligned. We were careful not to impose changes in the calendar years of growth increments without first clearly identifying the missed or falsely added increment.

Measurement of the otolith growth increments was conducted using the program ImagePro Plus v. 5.0 (Media Cybernetics, Silver Spring, Maryland). Images were captured with a Leica DC300 7.2 megapixel digital camera attached a Leica MZ9$_5$ dissection scope with maximum magnification of 75×. Increments were measured from the dorsal proximal edge of the otolith to the focus, or as close to the focus as possible (Fig. 1). The axis of measurement was limited to radii in which all growth increments could be clearly discerned. Consequently, the location of the axis of measurement varied somewhat among otoliths. For consistency, our axis of measurement followed the axis of growth, which in most cases was a straight line. If the axis of growth curved, a curved measurement axis was used to ensure that all measurements followed a course parallel to the axis of growth (i.e., perpendicular to the axis of the increment boundaries). In some specimens, the boundaries of the youngest or oldest few increments were not clear enough to allow for measurement. For these otoliths, all other growth increments were measured, and we used the calendar years assigned to each increment by simple counts or visual crossdating.

Statistical validation of crossdating was performed by isolating the common climate signal from the time series of otolith measurements, and then cross-correlating these growth patterns among all samples. The first step in this process was to isolate climate-induced growth patterns by partitioning them from all other influences on the width of otolith growth increments. Other variables affecting increment width included age, competition, the physiological and developmental status of each fish, and any artifacts of otolith preparation. In tree rings, climatic effects can be distinguished from other influences by isolating high-frequency variability. Although climate varies on a range of time scales and causes long-term variations in growth increment, climate is unique in that it induces high-frequency (year-to-year) variation in growth increments (Fritts 1976). Indeed, this concept is the basis of using signature years to visually crossdate time series: extreme climate events less than a year in duration yield a conspicuous growth increment. In contrast, age and competition tend to create much more sustained variations in widths of annual growth increments. In trees, such age-related and other long-term trends are removed by fitting each time series of measurements with a mathematical function, and then dividing the observed measurements by the expected values predicted by that function. Negative exponential, power, or linear functions are most frequently used. Where more flexibility is necessary, a cubic spline may better fit the measurements. We applied all these functions to otolith measurements and chose the ones that yielded the highest R^2 value, or in the case of the spline, provided a much better fit upon visual inspection of the function superimposed on the measurements. Removal of the age-related trend was then accomplished by dividing measurements by expected values predicted from the best-fit function. However, after this process of detrending, time series may still contain autocorrelation that could mask the high-frequency variability used for crossdating or induce

Fig. 1. Magnification of *Sebastes diploproa* otolith cross section. Annual growth increments are dated with white dots and the axis of measurement is indicated by a white line.



spuriously high correlations among samples. Any remaining long-term trends were therefore eliminated by removing as much autocorrelation (persistence) as possible from each detrended otolith time series using the autoregressive modeling. The resulting residual time series should contain almost exclusively high-frequency variability.

Once the climate signal was isolated by detrending and removing any remaining autocorrelation, crossdating was statistically validated by cross-correlating all residual otolith time series. In this final step, residual otolith time series were averaged to form a master chronology of sample-wide growth. Then each residual otolith time series was correlated with the master chronology. Yet before each correlation was performed, the otolith time series was removed from the master chronology to avoid comparing the tested series against itself. Correlations were performed 50 times; once for each residual otolith time series and the master chronology containing the average of all other otolith time series. Residual otolith time series were broken into 50-year segments that overlapped by 25 years (i.e., 1925–1975, 1950–2000), and each segment was correlated with the master chronology. Splitting each chronology into segments helped identify whether errors occurred early or late in the time series. The program COFECHA was used to automate all

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phases of statistical crossdating. COFECHA was written in 1982 by Richard Holmes of the Laboratory of Tree-Ring research at the University of Arizona, and is available through the International Tree-Ring Data Bank Program Library (ITRDBL) at the University of Arizona Laboratory of Tree-Ring Research website (http://www.ltrr.arizona.edu/software.html) (Holmes 1983; Grissino-Mayer 2001). A final splitnose rockfish chronology was compiled by averaging all 50 residual chronologies into a master chronology.

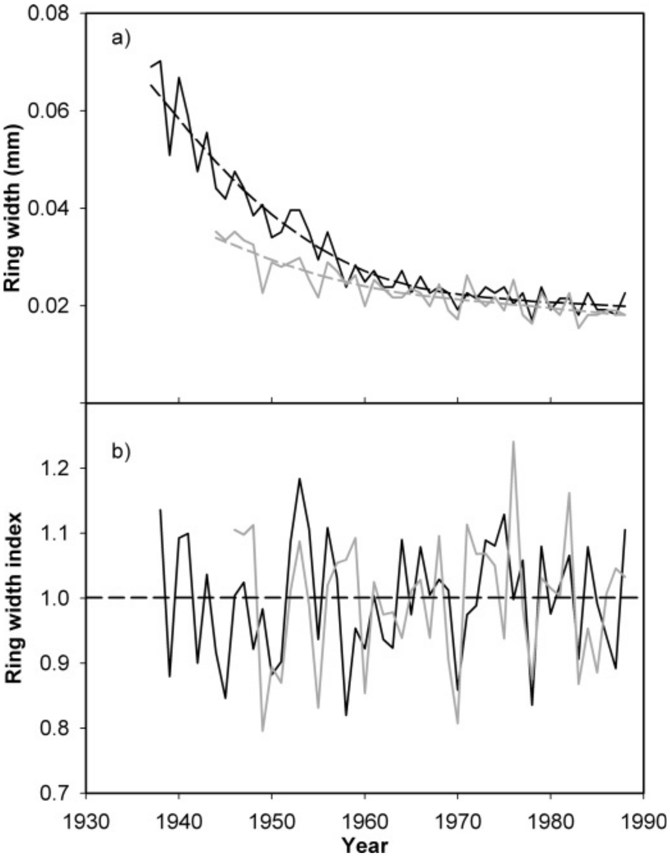
We correlated three climatic variables with the resulting splitnose rockfish biochronology: the Northern Oscillation Index (NOI), the Pacific Decadal Oscillation (PDO), and an upwelling index. The NOI and upwelling index were obtained through the Pacific Fisheries Environmental Laboratory website (http://www.pfeg.noaa.gov/). The upwelling index is calculated as wind stress divided by Coriolis parameter, in which positive values indicate upwelling and negative values indicate downwelling (PFEL 2004). NOI is the difference in sea level pressure anomalies between the North Pacific High (at 35°N, 135°W) and Darwin, Australia. The NOI provides a direct link to the North Pacific, unlike the more traditionally used Southern Oscillation Index (SOI), which calculates pressure differences between Darwin, Australia and Tahiti. Negative values of the NOI imply El Niño events, while positive values imply La Niña events (PFEL 2004). PDO values were obtained from the NOAA (National Oceanographic and Atmospheric Administration) and the University of Washington Joint Institute for the Study of the Atmosphere and the Ocean website (http://www.jisao.washington.edu/pdo/). Positive PDO values indicate warm phases, while negative values indicate cool PDO phases (Mantua et al. 1997).

Results and discussion

Signature years were evident in the growth increments of the splitnose otoliths. Narrow signature years included 1983, 1978, 1954, 1936, and to a lesser extent, 1988, 1970, and 1958, while 1971 was consistently wide. Not every signature year occurred in each otolith, and the prominence of the signature years varied among samples. Yet all otoliths did exhibit some combination of these signature years, which allowed for crossdating. The strongest example of a signature year was the 1983 increment, which was consistently narrow in almost all samples. Signature years crossdated in most otoliths on the first attempt of counting back from the outermost increment. In some cases, an increment would be missed, and the tentative dates of signature years offset. However, these unclear growth increments could be readily discerned on closer inspection. We did not reassign calendar years to growth increments without clearly identifying the initial error. In no case did we discover a year in which a fish did not form an increment, even in 1983. The same signature years were common to fish of all ages, and among otoliths collected in 1989 and 1995.

As in tree-ring measurements, the width of a growth increment decreased as the fish aged (Fig. 2*a*). This age-related decline is due to the changing geometry of the otolith and asymptotic growth of the fish. Though simple age-related declines occurred in the otolith time series, negative linear, negative exponential, or power functions did not fit these data. Cubic splines fit the decreasing increment-width trends much more closely, so we chose these functions to detrend otolith measurements (Fig. 2). As an additional step to this analysis, we attempted to identify the ideal spline rigidity necessary to maximize the power of crossdating in this data set. Spline rigidity can range from following every third growth increment at its most flexible to a straight line at its most rigid. Rigidity of a spline is typically expressed in terms of the wavelength at which 50% of the variance is removed. The shorter the set wavelength, the more flexible the spline will be. In dendrochronological applications, crossdating is typically optimized with a spline rigidity of 32 years (Holmes 1983). For otoliths, we began with a 32-year spline, and then experimented with a number of rigidity values. The optimum rigidity will be the one in which the average correlation among standardized series is the highest, which indicates that undesirable signals have been removed, and the common, sample-wide signal is maximized. After testing rigidities from 10 to 70 years, we found that 22 years yielded the highest average correlations among each otolith time series and the master chronology. Thus, we applied a spline with a rigidity of 22 years to all crossdating procedures. Prior to dividing by the spline (detrending), growth increments and variance were much greater in the younger

Fig. 2. (*a*) Time series of growth increment widths of two otoliths, along with best-fit 22-year spline curves (broken lines). (*b*) Standardized increment-width indices in which measurements were divided by spline curve values. Both standardized otolith time series have a mean of 1 and homogenous variance. Note the synchrony in high-frequency growth patterns.



portions of each otolith time series (Fig. 2*a*). Detrending with the spline resulted in a series of dimensionless increment-width indices with a mean value of 1 and relatively homogenous variance along the length of each time series (Fig. 2*b*).

For all 50 otoliths, the average correlation between each standardized otolith time series and the master chronology (interseries correlation) was 0.523. Seven otoliths had 50-year segments that did not significantly ($\alpha = 0.05$) correlate with the master chronology, suggesting potential problems. To further verify crossdating and help identify potential errors in specimens with low correlations, each 50-year segment in each otolith time series was lagged between plus or minus 1–10 years to determine whether shifting the series yielded a higher correlation with the master chronology. A higher correlation with a lagged year would indicate missed or added increments and that the otolith time series should be reexamined. To better illustrate this concept, we introduced an error into one of the otolith time series that had a correlation with the master chronology of 0.62. We simulated missing the narrow 1983 growth increment by combining its width with that of 1982. In so doing, all measurements were shifted 1 year from their true dates of formation. This error substantially reduced correlation to the master chronology ($r = -0.11$). More importantly, lagging the otolith time series by 1 year improved the correlation coefficient ($r = 0.42$). Such a difference between the position of zero lag and 1 year of lag clearly indicated that an increment was missed. Correlations for the seven potentially problematic otolith time series were not as dramatic as that in the above example, and in all otoliths, the average correlation was positive (ranging from 0.184 to 0.277). In five otoliths, lagging would increase correlations with the master chronology. However, these correlations are almost certainly spurious, since the lags were 5–8 years, and the correlations were only negligibly higher. Inspection of problematic otoliths indicated that, in some regions, boundaries between increments were relatively unclear, which likely accounted for the low correlation with the master chronology. Though COFECHA indicates relatively low correlations in these samples, we did not feel correlations were low enough to question the overall crossdating. Visual crossdating was strong, and some individuals may experience different environmental conditions or respond differently to environmental variability.

For perspective on the strength of the otolith results, interseries correlations of splitnose rockfish are comparable with those of late successional tree species growing in closed, temperate forests. Eastern hemlock (*Tsuga candensis*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*) typically crossdate with interseries correlations between 0.5 and 0.6. Though interseries correlations are higher for species growing in environments in which climate is severely limiting, such as in deserts or tree-line forests, tree-ring data from closed, temperate forests significantly crossdate and correlate with climate variables (Cook and Cole 1991; Graumlich 1993; Tardif et al. 2001). The synchronous climate signal in eastern hemlock has even been used as proxy data for climate reconstructions (Cook and Cole 1991). Therefore, interseries correlations with the master chronology for splitnose rockfish are at levels considered fully acceptable by the dendrochronological community. This strongly suggests that climate induces a common signal in splitnose growth increments, and that increment widths can be used to validate age of splitnose rockfish with a high degree of precision.

The master chronology generated by averaging residual chronologies of all 50 otoliths correlated with the upwelling index at 33°N, 119°W ($r = 0.33$, $p = 0.01$), the upwelling index at 36°N, 122°W ($r = 0.40$, $p = 0.002$), the PDO ($r = -0.29$, $p = 0.007$), and the NOI ($r = 0.51$, $p = 0.0001$). These results indicate that environmental variability strongly affected rockfish growth. More importantly for this study, they provide strong evidence that the correct calendar years were assigned to the chronology and crossdated growth increments. If fluctuations in the otolith growth patterns correspond to records of ocean variability, otolith increments should be properly dated. The relationship between environmental variability and growth response is not lagged, and ring width primarily reflects conditions of the current year. For example, others have noted in *Sebastes* that the 1983 El Niño substantially reduced growth in the 1983 increment (Pearson 1996; Woodbury 1999; Love et al. 2002). As we crossdated from the margin of the otolith toward the focus, we found the exact number of rings expected to the 1983 signature year, given the date of fish capture. For example, the 1983 signature year occurred six increments prior to the partial ring at the margin for fish caught in the summer of 1989. If a lag occurred between the event and growth response, we would expect to reach the signature year in fewer growth increments than expected. However, this was not the case. Furthermore, no significant ($\alpha = 0.05$) correlations occur between the splitnose rockfish chronology and environmental variables lagged by 1 or even 2 years. Thus, we believe the chronology has been accurately placed in time, and can therefore be used for age validation.

Our goal to correlate the splitnose rockfish master chronology with variables of the physical environment was to validate crossdating accuracy. However, these correlations also begin to reveal how climate has induced natural markers in the otolith time series. As indicated by a positive correlation with the NOI and upwelling and a negative correlation with the PDO, cool ocean conditions and high levels of upwelling positively affected splitnose growth. El Niño events, warm phases of the PDO, and downwelling led to narrow growth increments in splitnose rockfish. These responses to climate are consistent with other studies that suggest warmer water temperatures and reduced upwelling can reduce rockfish growth (Boehlert et al. 1989). For example, El Niño appears to have had negative effects on widow and yellowtail rockfish growth, causing narrow growth increments to form during the severe 1983 event (Pearson 1996; Woodbury 1999). Low levels of upwelling, such as those that occur during El Niño events, reduce productivity in the ocean and consequently reduce food supply and growth for rockfishes. As evidence of reduced food availability, levels of visceral fat in yellowtail rockfish collected in 1983 were much lower than those in 1980 (Lenarz and Wyllie Echeverria 1986). Apparently, warm ocean conditions indicate periods of low ocean productivity and reduced growth in splitnose rockfish. Conversely, cooler ocean conditions appear to indicate periods of enhanced productivity, which leads to increased growth in splitnose rockfish. Such climatic variability has induced short-term variations in growth, which in turn allowed for such strong crossdating.

In conclusion, crossdating is unique in that it uses natural markers induced by climate to validate the calendar year of each growth increment in long-lived fishes. Other methods that provide annual resolution, such as mark and recapture, are not as effective at such long time scales, nor can they be applied to large number of samples. Also, existing techniques for estimating longevity of long-lived fishes, such as bomb radiocarbon or radioisotopic analysis, are only accurate to within a few years. Thus, crossdating results in a higher level of accuracy and precision than other available techniques. While crossdating currently is limited to individuals greater than 30 years of age, this could be extended to younger fish if the synchronous growth pattern is strong. Very short-lived fish would provide too few degrees of freedom by which to fit trend curves to the growth increment series and to correlate the series with a master chronology. Also, crossdating is limited to individuals that form clear boundaries between increments, which may eliminate some long-lived fish species until improved preparation techniques enhance visibility of otolith structure. Fish with an unknown date of death may be crossdated as well, though a skeleton-plotting technique may be more effective for these samples than the “list year” approach we used in this study (Yamaguchi 1991; Stokes and Smiley 1996).

Future research will be necessary to evaluate other fish species for successful crossdating. Most likely, crossdating will be appropriate for other long-lived rockfish species and additional marine and freshwater fishes, given the clarity of their otolith cross sections (Guyette and Rabeni 1995; Pereira et al. 1995; LeBreton and Beamish 2000). The spatial extent over which otolith are collected must also be explored. This present study includes rockfish from a geographic area spanning five degrees of latitude. Yet spatial variability across larger areas may induce region-specific otolith growth patterns, which would reduce interseries correlations and the power of crossdating. Also, crossdating may be confounded if fish are migrating. But once the appropriate spatial scale for successful crossdating is established, master chronologies could be developed for each species and location and made available on the Internet. Individual otoliths could then be crossdated against the existing master chronology such that a large number of otoliths would not be necessary to generate a master chronology every time crossdating is applied. This would greatly expedite crossdating and would allow for age validation from small samples of otoliths. Overall, we believe that crossdating provides accurate estimates of fish ages that should have wide application to a variety of long-lived species in marine and freshwater systems.

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