Bomb-produced radiocarbon validation of growth-increment crossdating allows marine paleoclimate reconstruction

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ABSTRACT

The bivalve Pacific geoduck (Panopea generosa) has been used in the eastern North Pacific Ocean to create proxies for environmental factors such as temperature and oceanographic conditions. This type of research depends upon accurate age determination of Pacific geoducks, which historically was based on shell growth-increment counts. A recent study comparing age estimates generated by the dendrochronology (tree-ring science) procedure of crossdating to those estimated from growth-increment counts found a significant difference between the methods for geoduck older than 30 years. Compared to the traditional age determination method of counting growth increments, the crossdating method estimates a greater longevity in this species, with some individuals living in excess of 150 years. In the present study, the accuracy of each method was independently assessed using bomb-produced radiocarbon (^{14}C) techniques. Specimens whose birth years were estimated to be within the era of the bomb-produced marine ^{14}C increase and where the differences between ages estimated by the two methods were greatest were selected for ^{14}C analysis. The difference between age estimates from traditional growth-increment counts and those from crossdating was evaluated using their respective ^{14}C chronologies in comparisons to a reference chronology as a standard. The comparisons relied on Bayesian nonlinear models using Markov Chain Monte Carlo simulation. This method of analysis showed that with a 50% probability geoducks were aged correctly when using the crossdating method, compared to the growth increment counts which had a 50% probability of underestimating the age by 4 years. Therefore, the crossdated age estimates were found to be more accurate than increment counts. Furthermore, these results provide new confidence in using Pacific geoduck biochronologies for paleoclimate and paleoenvironmental reconstruction.

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1. Introduction

Biogenic calcified structures that form regular growth increments in marine organisms such as coral (Correge, 2006; Felis and Rimbu, 2010), bivalves (Schone et al., 2005), and fish (Elsdon and Gillanders, 2004; Kerr et al., 2007; Jones, 2008) represent an increasingly important archive for reconstructing past climate, environmental, or ecological information. Morphological, chemical, and isotopic properties of growth increments record a wide range of environmental parameters including temperature, upwelling, growth, and productivity (e.g., Killingley and Berger, 1979; Krantz et al., 1987; Marchitto et al., 2000; Goman et al., 2008; Correa et al., 2010). Thus, growth increments in long-lived species can yield valuable physical and biological indices for marine systems in which observational records may be relatively scarce and from a limited time span.

To maximize the quality of an environmental reconstruction, every growth increment in all structures must be assigned the correct calendar year of formation (dated). In recent years, the dendrochronology (tree-ring analysis) technique of crossdating has been successfully applied to exactly date annual growth increments in a wide range of marine and freshwater organisms (Helama et al., 2006; Black, 2009; Rypel et al., 2009; Butler et al., 2010; Matta et al., 2010). Crossdating is based on the assumptions that climate variability induces synchronous patterns in the growth-increment widths of individuals collected from a given species and region and that these growth increments are annual. Beginning at the outermost (marginal) increment formed during the known year of capture and proceeding back in time, crossdating is the

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process of cross-matching these shared growth patterns among samples. In the event of a "missing" or "false" growth increment in a sample, the growth pattern will be offset by a year relative to that in the other samples, indicating that an error has occurred. Once crossdating is complete, all growth increments will have been assigned an estimated calendar year of formation and can be used to develop high-resolution biochronologies or population age structures (birth dates). In the marine environment crossdating appears to work for fish in temperate climates (Black et al., 2005, 2008a), bivalves (Marchitto et al., 2000; Strom et al., 2004; Black et al., 2008b), and even tropical corals (Hendy et al., 2003). Moreover, historical samples with an unknown date of death may be crossdated against live-collected samples to extend chronologies further back in time (Butler et al., 2010).

Ultimately, the tendency for individuals from one location to exhibit synchronous growth patterns provides a strong corroboration that increments are formed annually and have been correctly dated (Black et al., 2008a, 2008b). However, shared growth patterns among individuals, or successful crossdating, may not necessarily yield accurate estimates of true age, or comprise an age validation (Kimura et al., 2006), considering that uniform dating inaccuracies (age determination bias) could occur had sub- or supra-annual growth increments formed in all members of the sample set. Correlations of growth-increment chronologies with records of climate indicators, such as sea surface temperature or upwelling intensity, can provide further evidence to suggest dating accuracy, but not necessarily a strong validation. A true age validation would instead require proof of a direct "cause-and-effect relationship" between the environmental indices and the apparent growth fluctuations. For many species, relationships between growth and environmental indices are logical, and conventional wisdom frequently accepts them as strongly linked (Noakes and Campbell, 1992; Searle et al., 2006; Nielsen et al., 2008). However, strong correlations do not necessarily indicate causation.

Pacific geoduck (*Panopea generosa*) has been used as a climate indicator for the North Pacific and also supports a multimillion dollar fishery along the coasts of Washington, British Columbia, and Alaska (Orensanz et al., 2004; Strom et al., 2004; Black et al., 2009). Thus, accurate dating of Pacific geoduck growth increments, (i.e., age determination) is critical not only for climate reconstructions, but also for fishery management, given that estimates of population age structure are a central component of stock assessment (Beamish and McFarlane, 1983; Campana, 2001). An earlier study of Pacific geoduck by Shaul and Goodwin (1982) proposed the use of basic growth-increment counts for age determination. Their study validated the ages determined by growth-increment counts using several methods, the best of which was evidence of a growth disturbance due to substrate dredging 26 years earlier. However, the difficulty of interpreting growth increments still exists and could result in bias from true age, especially for older specimens. Black et al. (2008b) compared Pacific geoduck age estimates generated from growth-increment counts to those generated by crossdating and found minimal bias among specimens aged 30 years or less. However, bias in specimens aged 30 years or older was often greater than 10 years and up to 34 years, and overall a bias existed in 72% of the specimens (Black et al., 2008b). While crossdating is generally thought to produce more accurate age estimates than counting growth increments, both methods have some level of uncertainty. Therefore, independent validation of growth-increment dating is critical. Crossdating has only rarely been independently tested (Marchitto et al., 2000), though it is increasingly used in marine settings to reconstruct climate, understand the effects of climate on fish growth, or generate population age data (e.g. Black et al., 2009; Matta et al., 2010).

Our goal was to use bomb-produced ^{14}C to independently validate crossdating in Pacific geoduck. Specifically, we tested the same specimens used by Black et al. (2008b) in the comparison of crossdating to growth-increment counts. A robust age validation using bomb-produced ^{14}C will more fully legitimize the use of crossdating to reconstruct climate indices and to generate population age data from Pacific geoduck growth increments.

Bomb-produced radiocarbon (^{14}C) is a valuable tool in age validation studies. This method relies on an observed increase of marine ^{14}C that occurred due to above-ground testing of atomic bombs during the 1950s and 1960s (Nydal, 1993). In calcified marine biological structures, including bivalve shells and fish otoliths, this increase can be measured and used as a time-specific signal (Kalish, 1993). Two data sets are required: first, a ^{14}C chronology from the specimens being validated (the test specimens), and second, a reference ^{14}C chronology to establish the exact time frame of the ^{14}C increase. A reference ^{14}C chronology is typically generated from ^{14}C levels in known-age samples, which are often otoliths of young or juvenile fish caught during the 1950s and 1960s (Piner and Wischniowski, 2004). The reference ^{14}C data are fit with a model to provide estimates of pre-bomb levels, the exact time and rate of increase, and the maximum level attained. The test sample is composed of adult specimens for which ^{14}C values have been measured in calcified material deposited early in life, often during the first year of growth. If sample material in each of the test specimens has been correctly dated (aged), the ^{14}C increase spanning the 1950s to 1960s observed in a series of test specimens should be in phase (in time) with that of the reference chronology. If the test ^{14}C chronology and the reference ^{14}C chronology are not synchronous, then the test specimens may not be dated (aged) correctly and it may be possible to estimate an average dating bias (Kastelle et al., 2008). Some researchers have estimated birth years for individual test specimens based on the relationship between measured ^{14}C in test specimens and the known timing of ^{14}C in a reference chronology (Andrews et al., 2005). Bomb-produced radiocarbon has been measured in a number of mollusks for various purposes including age validations (Weidman and Jones, 1993; Kilada et al., 2007). Two reference ^{14}C chronologies exist for the eastern North Pacific, one from Pacific halibut (*Hippoglossus stenolepis*) and a second from yelloweye rockfish (*Sebastes ruberrimus*) (Kerr et al., 2004; Piner and Wischniowski, 2004); these have been used in a number of successful fish age validations (Piner and Wischniowski, 2004; Kerr et al., 2005; Kastelle et al., 2008).

2. Materials and methods

Pacific geoducks for ^{14}C analysis were obtained from a previous crossdating study (Black et al., 2008b) of 432 specimens live-collected during the summer of 2004 from three sites within the Tree Nob Islands, British Columbia, Canada. We selected 32 specimens whose birth years, as estimated by crossdating in Section 2.1, ranged from about 1950 to the mid-1970s (Table 1) to encompass the years of oceanic Δ^{14}C increase due to atomic bomb testing. We also selected specimens based on the difference between ages estimated by the growth-increment counting and crossdating methods. Because our goal was not to detect bias between the methods but to assess which method was in general more accurate, we purposely chose samples with the greatest difference in age estimates (Table 1). This nonrandom subsample does not represent the population at Tree Nob Islands, but was chosen to facilitate conclusive results in terms of the best method for future age estimation and paleoenvironmental reconstruction. Random sampling from the specimens whose estimated birth years were from about 1950 to the mid 1970s would have provided an average difference between methods too small to be tested with bomb-produced ^{14}C. In Black et al. (2008b), Pacific geoduck ages estimated by crossdating ranged from about 12 to over 150 years old; however, geoducks in our study ranged only between 27 and 56 years old to span the era of rapid increase in bomb-produced ^{14}C. Pacific geoduck growth-increment count and crossdating methods have been published elsewhere (Shaul and

Goodwin, 1982; Black et al., 2008b), and therefore we will provide only a brief summary of these methods in Section 2.1.

2.1. Growth-increment counts and crossdating in geoduck

In Pacific geoduck, the hinge plate grows at a rate proportional to that of the outer shell layer but is protected from erosion and thus provides the most complete growth record (Shaul and Goodwin, 1982). One valve from each geoduck specimen was cut through the umbo and hinge plate on the dorso-ventral axis using a diamond blade lapidary saw. The cut surface was polished with 600-grit sandpaper and then etched with 2% hydrochloric acid. An impression (acetate peel) was made by pressing the etched surface of the hinge plate against a piece of acetate film softened with a drop of acetone. The peel was placed between two glass slides and viewed using either a microprojector or a dissecting microscope, both using transmitted light. All 432 acetate peels were first aged by counting growth increments as part of routine age determination at the Fisheries and Oceans Canada Sclerochronology Laboratory, Nanaimo, British Columbia, as reported by Black et al. (2008b). The corresponding birth year estimates from are given in Table 1 for the chosen specimens ($n = 32$).

All specimen peels were visually crossdated (Black et al., 2008b). Crossdating consisted of matching the high-frequency, year-to-year variability that occurred among specimens (Yamaguchi, 1991; Stokes and Smiley, 1996). Working from the margin toward the center, the estimated calendar years for growth increments that were conspicuously

wide or conspicuously narrow relative to their neighbors were recorded (listed). These lists should agree among specimens if all increments were correctly identified. In this way, calendar years were assigned to all growth increments. Applying a narrow 5–7 year window, or in other words considering neighboring growth increments, ensured that only high frequency patterns of variability were identified, thereby filtering out age-related growth declines or any other low-frequency patterns. When a listed growth pattern for one specimen appeared to be offset from the others, corrections for missing or falsely added increments were made after visual re-inspection of the specimen. The birth years estimated based on crossdating are also given in Table 1.

After visual crossdating of the 32 specimens, growth increment widths were measured and crossdating was statistically verified, following the general methods of Black et al. (2008b). Using Image Pro Plus 6.0 software (Media Cybernetics) integrated with a Leica DC300 7.2 megapixel camera and Leica stereomicroscope (Leica Microsystems Inc.), growth increment widths were measured along continuous transects that followed the axis of growth. Each growth increment was delineated at the end of the winter line (translucent zone) and start of the new growing season (opaque zone) (Shaul and Goodwin, 1982). To statistically confirm visual crossdating, all 32 measurement time series were imported into the International Tree-Ring Data Bank Dendrochronology Program Library program COFECHA, written in 1982 by Richard Holmes (available through the University of Arizona Laboratory of Tree-Ring Research website: www.ltrr.arizona.edu/software.html). In the first step of growth increment width analysis, we used COFECHA to remove low-frequency

Table 1
Pacific geoduck (*Panopea generosa*) specimen birth year estimates based on the traditional growth-increment count and crossdating methods. Crossdating information: time span utilized in crossdating (calculated by crossdating), series correlation represents the correlation between each specimen and the average of all others, and calendar years spanned in material milled from hinge plates for ^{14}C analysis and mean milled calendar year. Radiocarbon results reported as fraction modern and $\Delta^{14}C‰$ with one standard deviation error (SD). The $\Delta^{14}C$ values were calculated using the mean milled calendar year as the time the exchange with the biosphere ceased and the fraction modern. Specimens were collected in 2004 at Tree Nob Islands, British Columbia, Canada, and analyzed in 2009.

Specimen ID	Birth year estimates by method		Results of crossdating				Radiocarbon results	
	Increment count	Crossdated	Crossdated time span	Series correlation	Milled hole span	Mean milled calendar year	Fraction modern (1 SD)	$\Delta^{14}C‰$ (1 SD) [a]
454	1960	1959	1961–2001	0.72	1961–1964	1962.4	0.9754 (0.0034)	−26.1 (3.4)
519	1966	1964	1967–2001	0.86	1964–1969	1966.6	1.0483 (0.0033)	46.2 (3.3)
520	1962	1961	1963–1999	0.69	1963–1965	1963.9	0.9747 (0.0044)	−26.9 (4.4)
521	1951	1950	1953–2001	0.81	1951–1955	1952.4	0.9039 (0.0035)	−96.4 (3.5)
535	1962	1957	1959–2003	0.57	1958–1961	1959.6	0.9308 (0.0049)	−70.3 (4.9)
550	1969	1969	1976–1995	0.73	1970–1972	1971.2	1.0483 (0.0042)	45.6 (4.2)
562	1965	1962	1964–2000	0.87	1963–1966	1964.3	1.0369 (0.0059)	35.1 (5.9)
581	1969	1969	1976–2001	0.69	1971–1974	1972.2	1.0647 (0.0053)	61.8 (5.3)
589	1962	1958	1962–2002	0.81	1959–1961	1960.2	0.9371 (0.0041)	−64.1 (4.1)
618	1969	1966	1968–2003	0.77	1967–1969	1968.2	1.0611 (0.0043)	58.8 (4.3)
636	1966	1967	1971–2002	0.71	1968–1970	1968.9	1.0653 (0.0044)	62.9 (4.4)
645	1967	1967	1972–2002	0.83	1969–1971	1970.2	1.0708 (0.0040)	68.2 (4.0)
653	1965	1957	1959–1998	0.78	1958–1960	1959.2	0.9063 (0.0038)	−94.7 (3.8)
654	1960	1960	1963–2002	0.72	1960–1962	1961.8	0.9408 (0.0050)	−60.5 (5.0)
664	1967	1966	1970–2002	0.62	1967–1969	1968.1	1.0647 (0.0115)	62.4 (11.5)
670	1962	1957	1962–2001	0.67	1958–1961	1958.9	0.9590 (0.0047)	−42.0 (4.7)
678	1973	1970	1975–2001	0.58	1972–1974	1973.1	1.0379 (0.0037)	35.0 (3.7)
695	1973	1971	1974–2002	0.73	1972–1974	1973.9	1.0528 (0.0040)	49.8 (4.0)
697	1957	1956	1959–2000	0.65	1958–1960	1959.0	0.9029 (0.0038)	−98.1 (3.8)
704	1974	1970	1974–2002	0.71	1971–1973	1971.7	1.0556 (0.0045)	52.8 (4.5)
717	1957	1953	1964–2002	0.74	1954–1956	1955.9	0.8831 (0.0041)	−117.5 (4.1)
718	1974	1972	1977–2003	0.85	1972–1974	1973.4	1.0621 (0.0037)	59.1 (3.7)
740	1963	1962	1968–2002	0.8	1964–1967	1966.0	1.0014 (0.0037)	−0.5 (3.8)
809	1963	1958	1963–2001	0.89	1959–1962	1960.8	0.9326 (0.0033)	−68.6 (3.3)
840	1979	1977	1980–2003	0.8	1979–1982	1980.7	1.0558 (0.0040)	51.9 (4.0)
861	1957	1954	1959–1995	0.82	1955–1959	1957.4	0.9000 (0.0044)	−100.8 (4.4)
879	1964	1961	1963–2001	0.92	1962–1966	1963.8	0.9780 (0.0039)	−23.6 (3.9)
884	1968	1967	1974–2000	0.63	1968–1974	1970.7	1.0497 (0.0044)	47.1 (4.4)
887	1960	1958	1960–2001	0.83	1959–1961	1959.9	0.9204 (0.0037)	−80.7 (3.7)
888	1962	1961	1967–2002	0.86	1963–1966	1964.3	1.0097 (0.0038)	8.0 (3.8)
890	1959	1952	1956–2003	0.87	1953–1955	1954.3	0.8699 (0.0039)	−130.6 (3.9)
894	1955	1948	1953–2003	0.81	1950–1952	1951.4	0.8979 (0.0035)	−102.3 (3.5)

[a] The $\Delta^{14}C‰$ values were calculated using the standard equation presented on the National Ocean Sciences Accelerator Mass Spectrometry Facility's website [http://www.whoi.edu/nosams/page.do?pid=44997] from the fraction modern and the mean milled calendar year.

variability in each geoduck measurement time series via the process of detrending. For this procedure, each geoduck measurement time series ($n=32$) was fit with a cubic spline set at a 50% frequency response of 22 years (Cook and Peters, 1981; Grissino-Mayer, 2001). The frequency response is analogous to the length of a window used in calculating a moving average where the flexibility of the function increases with decreasing window length (Grissino-Mayer, 2001). Cubic splines with a frequency response of 22 years provided optimal crossdating verification results in long-lived Pacific rockfish (Black et al., 2005) and were therefore applied in this study to Pacific geoduck. Once fitted, each value in a Pacific geoduck measurement time series was divided by the corresponding 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). Also in COFECHA, detrended Pacific geoduck measurement time series were tested for any remaining autocorrelation, which, if present, was removed to ensure serial independence. Finally, between each detrended measurement time series ($n=32$) a correlation with the average of all other detrended measurement time series was calculated (interseries correlation). In so doing, the high-frequency growth pattern of each individual was compared with the high-frequency growth pattern of all other individuals. Isolating only the high-frequency, serially independent growth patterns prevented spuriously high correlations among individuals and also mathematically mimicked the process of visual crossdating by eliminating low-frequency growth patterns.

2.2. Radiocarbon ($\Delta^{14}C$) analysis

Following growth-increment counting and crossdating, ^{14}C analysis was performed on the remaining valves in each of the 32 selected specimens. Sample material was extracted from each hinge plate to represent a time span as early in life as possible. Hinge plates of one-year-old Pacific geoducks are thickest about 2 mm posterior of the umbo toward the siphon end (C. Kastelle, personal observation). Therefore, two adjacent thin sections were taken dorso-ventrally with an IsoMet low speed saw (Buehler), where the first cut was at the umbo with two succeeding cuts made progressing toward the posterior end. This careful positioning of the cuts produced two thin sections, each about 2.2 mm thick, from the region of the hinge

plate with the least compressed growth increments. The thin sections were mounted on a slide and polished with a series of wet and dry sand papers (600 to 1200 grit) on a Buehler Ecomet 3 polisher. The thin sections were cleaned in an ultrasonic cleaner with distilled and deionized water. The locations of early growth increments were visually identified under a Leica stereomicroscope and in digital images taken with a 7.2 megapixel camera integrated with the microscope (Fig. 1). These early growth increments were sampled for ^{14}C as close as possible to the first apparent winter growth zone by drilling about 1.5 mm deep with a 1.0 mm diameter endmill. This produced 2.0 to 4.0 mg of shell material which was collected, weighed, and placed in acid-cleaned vials. Endmill bits were cleaned between specimens to prevent cross contamination. The sample material was sent to the National Ocean Sciences Accelerator Mass Spectrometry Facility at the Woods Hole Oceanographic Institution, Woods Hole, MA, for ^{14}C analysis in 2009. Each sample was treated with a routine acid hydrolysis procedure to produce a graphite target and analyzed using accelerator mass spectrometry. We report results as $\Delta^{14}C$ (Stuiver and Polach, 1977) that have been normalized to 1950, corrected for isotopic fractionation with measured $\delta^{13}C$, and normalized to a $\delta^{13}C_{VPDB}$ value of -25‰ (Table 1). We also report fraction modern, which was used to calculate the $\Delta^{14}C$ values with the equation presented on the National Ocean Sciences Accelerator Mass Spectrometry Facility's website [http://www.whoi.edu/nosams/page.do?pid=44997] based on the crossdated mean milled calendar year (see the following paragraph). The mean milled calendar year represents the point in time when exchange with the biosphere ceased (i.e., the year the material analyzed was accreted). Thus, the $\Delta^{14}C$ values were not based on the year of analysis or specimen capture.

Milling was not located exactly within the birth-year increment (Fig. 1), so the following procedure was used to correct both the growth-increment and crossdated age estimates. The post- and pre-milled images of each hinge plate cross section were digitally merged to delineate the exact growth-increment boundaries within the milled hole for $\Delta^{14}C$ analysis material (Fig. 1). The crossdated mean milled calendar year was calculated as the sum of each calendar year in the hole weighted by its proportion of the milled hole (e.g., crossdated mean milled calendar year $= (1959 \cdot 0.289) + (1960 \cdot 0.513) + (1961 \cdot 0.197) = 1959.9$). The crossdated mean milled calendar year was typically about 2 to 4 years later in time than the actual crossdated birth year. This
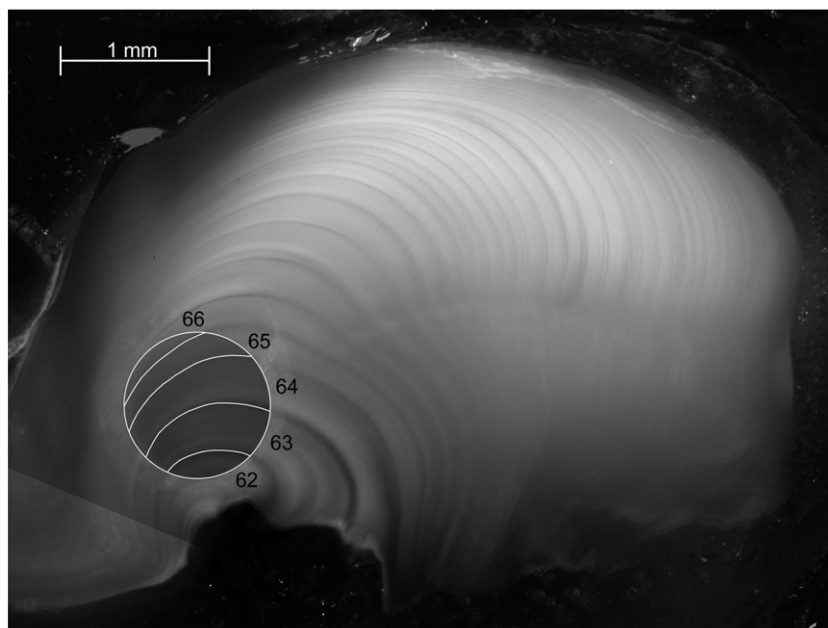
Fig. 1. Pacific geoduck (*Panopea generosa*) sample 879 U. Pre- and post- milled images are digitally merged and growth increment boundaries within the milled area are delineated. The milled area spans 1962 through 1966, and the mean calendar year (proportionally weighted by area) is 1963.8.

calculated difference was also applied to the growth-increment estimated birth year as a necessary correction prior to making comparisons to the reference chronology, described in Section 2.3. Thus, two test Δ^{14}C chronologies were generated for Pacific geoduck, one based on crossdated age estimates and the other based on growth-increment-count age estimates.

2.3. Statistical methods

To evaluate the improvement in ageing accuracy of the crossdating-assisted method over the traditional growth-increment count method, we compared the Δ^{14}C chronologies derived from Pacific geoduck, one for each age determination method, with the Pacific halibut Δ^{14}C reference curve (Piner and Wischniowski, 2004). Comparisons of Δ^{14}C test sample data to reference Δ^{14}C curves have commonly been made across taxa, and while not optimal, using Pacific halibut to validate geoduck age estimates may be suitable because test and reference data were collected in the same area of the northeast Pacific Ocean (52°N–60°N). To facilitate comparison of the Pacific geoduck sample to halibut reference Δ^{14}C data, we fit these data using two common functional forms that have often been applied to Δ^{14}C chronologies for a wide range of species (Hamel et al., 2008): a logistic model which quantifies the rapid pulse in Δ^{14}C from atmospheric nuclear testing with no subsequent post-bomb decline (Piner and Wischniowski, 2004), and a coupled-function model that describes the same rapid increase of radiocarbon as a cumulative Gaussian function with a continuous exponential decay following the post-bomb peak (Hamel et al., 2008). In addition, we assumed that process error associated with the dependent variable (Δ^{14}C data) and measurement error associated with estimated birth year were both normally distributed and we incorporated these errors into the model. The logistic model was parameterized as:

$$\hat{y} = \lambda + \frac{k}{1 + \exp[\beta(\alpha - x)]} + \sigma_e^2$$

where $\hat{y}$ = estimated Δ^{14}C, x = birth year of the reference chronology or the test sample, with parameters λ = pre-bomb predicted Δ^{14}C value, α = birth year corresponding to midpoint of Δ^{14}C increase (or 50% estimated maximum), β = slope at α, k = the absolute increase of Δ^{14}C (predicted asymptote), and σ_e^2 = the error variance. The coupled-function model is written as:

$$\hat{y} = \lambda + k \exp\left[(\mu \cdot \gamma) + \frac{(\sigma_N \cdot \gamma)}{2}\right] \exp(-\gamma \cdot x) \Phi\left(x, \mu + \sigma_N^2 \gamma, \sigma_N\right) + \sigma_e^2$$

where Φ represents the cumulative normal function, μ = mean or peak year of radiocarbon Gaussian pulse curve, σ_N = standard deviation of the Gaussian pulse curve, γ = exponential decay rate (per year) of the post-peak decline, and $\hat{y}$, x, k, λ, and σ_e^2 are as above. Details of the coupled-function model and its derivation can be found in Hamel et al. (2008). The logistic parameter α is directly comparable to the coupled-function μ because the integral at the peak of the normal distribution is the inflection point. The difference (Δ) in any of these parameters, such as $\Delta(\alpha_R - \alpha_S)$, between the geoduck test sample (S) and halibut reference (R) Δ^{14}C curves can be quantified, and therefore in the case of α or μ is a measure of ageing bias for statistical comparison. In this way, the two age determination methods, crossdating and growth-increment counting, can be assessed by the relative size of the bias, as described below.

To fit these models to the Δ^{14}C data we developed a Bayesian model (Gelman et al., 2004) and used Markov Chain Monte Carlo (MCMC) simulation to estimate parameters and derive a statistical framework for hypothesis testing. Specifically, we were interested in answering the following three questions: 1) Which nonlinear model fits the data best, the logistic or the coupled-function model? 2) Among the two nonlinear functional forms, was age assignment

(dating) more accurate using the crossdating method or the traditional growth-increment counting method based on the halibut ^{14}C reference curve? 3) What is the probability of ageing bias if bias exists in either age assignment approach? The last two questions address the primary goal of this research. Given these objectives, Bayesian inference provides advantages over other inferential approaches because it 1) explicitly estimates uncertainty in model parameters and functions of those parameters, 2) provides a convenient framework for evaluating a suite of candidate models (Gelman et al., 2004), and 3) provides a probabilistic means of quantifying any ageing bias. Standard software using WinBUGS [Bayesian inference Using Gibbs Sampling (Lunn et al., 2000)] was used to fit the model to the data and evaluate convergence of the simulation. The Bayesian model and MCMC simulation provided an estimate of parameters in a resulting "posterior density distribution". From this the highest posterior density (HPD) represented the point estimate and was the mode of the distribution of each parameter. The HPD interval is a measure of parameter estimation error and was calculated as 100(1−0.05)%. Using these distributions, statistical comparisons were further performed in two ways. First, a null hypothesis compared the geoduck growth-increment count and crossdating-assisted ageing methods to the Pacific halibut reference under the assumption that there were no differences in the models describing the Δ^{14}C data. Under the null hypothesis one curve described both the test and the reference data, with the logistic and coupled-function models having four and five fixed effect parameters, respectively, with a single error variance. An alternate hypothesis assumed a better fit was achieved by species-specific curves with the logistic and coupled-function models having eight and ten fixed effect parameters, respectively, with a single shared error variance. This provided an evaluation for ageing bias in each age determination method relative to the reference chronology. In this way, the two age determination methods were indirectly compared using the Pacific halibut as a common reference chronology. Second, the functional form (logistic or coupled-function model) describing the Δ^{14}C data for each species in a comparison was evaluated. Formal tests of hypotheses for competing models or ageing methods were conducted using a deviance information criterion (DIC) (Spiegelhalter et al., 2002) based on the posterior densities. A smaller DIC indicated a better fit to the data and a ΔDIC>5 between two competing options indicated substantive differences between the options.

3. Results

Crossdating in the subset of 32 Tree Nob geoducks was identical to crossdating in the full collection of 432 samples (Black et al., 2008b). Growth patterns in the shell hinge plate were strongly conserved among individuals, had visually conspicuous narrow increments in 1965, 1982, and 1994, and had conspicuously wide increments in 1981, 1990, and 1998 (Fig. 2). Given this level of agreement among samples, interseries correlations were highly significant ($p<0.01$), and ranged from $r=0.57$ to 0.89 with a mean of $r=0.76$ (Table 1). Crossdated age estimates were in general agreement with growth-increment count age estimates, though growth-increment count estimates averaged 1.5 years lower (Table 1).

The MCMC simulation using the Gibbs sampler was computationally efficient, yielding 2000 samples with which to compute summary statistics and develop a framework for hypothesis tests. Initial testing of the MCMC simulation showed burn-in was achieved after 1000 samples, and between-sample autocorrelation of estimated parameters was non-significant after a lag of 10 sample parameter sets. While not shown, trace plots for all parameters showed good mixing and reasonable evidence that the chain had converged to a stationary distribution.

According to DIC values, the crossdating method was superior to growth-increment counting when compared to the common Pacific
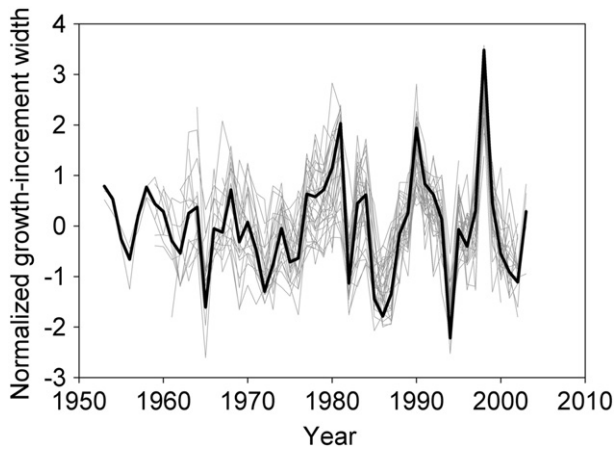
Fig. 2. Normalized growth increment width for all ^{14}C Pacific geoduck (*Panopea generosa*) individuals ($n = 32$) after removing low-frequency trends with cubic splines. Each gray line is an individual and the heavy black line is the mean. Note the high degree of growth synchrony, reflected in the strong series correlations (see data table).

halibut reference chronology. Further, the fits of the logistic and coupled-function were not always similar. The logistic and coupled-function models fit the Δ^{14}C data equally well with the exception of the comparison between functions using species-specific Δ^{14}C curves based on geoduck age estimates from increment counting (Table 2). Weight of evidence against the simpler logistic model for the Pacific halibut–Pacific geoduck growth-increment count comparison ($\Delta DIC_{L-C} = 14.8$) was three times the recommended limit of five and roughly five times larger than other comparisons. These results indicated that a post-peak decline in Δ^{14}C for the Pacific halibut data did not warrant the addition of an exponential decay parameter, while a post-peak decline was more evident for Pacific geoducks aged using the growth-increment count method. Since the weight of evidence in favor of the simpler logistic model was equivocal, hypothesis tests comparing Pacific geoduck ages estimated by the two methods to the halibut reference were conducted with both functional forms. Results were, however, not equivocal with regard to whether the null or alternate hypothesis was favored in comparing the two geoduck age determination methods to the halibut reference. The alternate hypothesis, two separate Δ^{14}C curves for the test specimens and the reference chronology, was highly preferred over the null hypothesis for the Pacific geoduck growth-increment count method in

Table 2

Statistical comparisons between Pacific geoduck (*Panopea generosa*) ^{14}C chronologies based on growth-increment counts or crossdating and the Pacific halibut (*Hippoglossus stenolepis*) reference ^{14}C chronology. Evaluation of null hypothesis (assumes a single model is fit to halibut and geoduck data) and alternate hypothesis (assumes a better fit is achieved by species-specific curves) by model, logistic or nonlinear coupled-function. Based on Bayesian multi-level nonlinear models fit to data using Markov Chain Monte Carlo simulation. Deviance information criterion (DIC) shown for each model fit takes into account model complexity based on the effective number of parameters. Comparisons between models made using ΔDIC. A smaller DIC indicates a better fit to the data and $\Delta DIC > 5$ constitutes substantive differences. Subscripts $L-C$ refers to comparisons between logistic and coupled-function and $A-N$ refers to alternate and null hypothesis.

Model	Alternate hypothesis		Null hypothesis		ΔDIC_{A-N}
	Parameters	DIC	Parameters	DIC	
Crossdating					
Logistic	9	594.8	5	598.6	3.8
Coupled-function	11	591.9	6	596.2	4.3
	ΔDIC_{L-C}	2.9		2.4	
Growth-increment count					
Logistic	9	640.6	5	676.5	35.9
Coupled-function	11	625.8	6	672.7	46.9
	ΔDIC_{L-C}	14.8		3.8	

both functional forms. The Pacific geoduck growth-increment count Δ^{14}C curve differed from the halibut reference curve as shown by ΔDIC_{A-N} values of over 35 (Table 2). This suggested that Pacific geoduck age determination with the assistance of crossdating produced age interpretations (i.e., birth years) that were much more consistent with Δ^{14}C data from the Pacific halibut reference curve. These results are shown graphically in Fig. 3 and demonstrate that when ages are estimated by growth-increment counting the associated Δ^{14}C curves differ from the reference chronology in timing and asymptotic level of Δ^{14}C. However, when the ages are estimated with crossdating, the curves are similar in timing (Fig. 3). Direct comparisons of ΔDIC values between age determination methods were not made; our comparisons were made only to the Pacific halibut Δ^{14}C reference chronology because that is the essence of this age validation method.

In further addressing bias in either age determination method, the parameters of primary interest were the logistic model parameter α and coupled-function model parameter μ, both of which describe the birth year at approximately 50% rise in Δ^{14}C. Parameters estimated for Pacific geoduck Δ^{14}C curves based on crossdating were consistent with the Pacific halibut reference curve parameters, while those estimated from growth-increment counting were less similar. This provides evidence for the null hypothesis when crossdating is used (Fig. 3). With the logistic model, the HPD estimate for the Pacific halibut timing of 50% increase was $\alpha = 1962.6$ (HPD interval 1961.7–1962.9) compared to $\alpha = 1962.1$ (HPD interval 1961.3–1963.0) for crossdated Pacific geoduck ages. In contrast, for the Pacific geoduck growth-increment count method the fitted curves were more right-shifted ($\alpha = 1965.5$, HPD interval 1964.0–1966.5) relative to the halibut reference (as specified above) (Fig. 3). While not presented here in detail, the coupled-function model yielded very similar estimates of μ with the notable exception that the HPD intervals were broader than in the logistic model.

The differences in the geoduck Δ^{14}C curves relative to the halibut reference illustrate the relative ability of each method to accurately estimate true age and the extent of potential bias between the different age determination approaches. Bayesian analysis provided a distribution of these differences (Fig. 4). This was quantified by the difference in model parameter estimates, such as $\Delta(\alpha_R - \alpha_S)$ or $\Delta(\mu_R - \mu_S)$, which showed that Pacific geoducks aged 27–54 years old using the traditional growth-increment count method were under-aged by nearly 4 years overall. In contrast, for the comparison between the crossdating-assisted Pacific geoduck and Pacific halibut the difference was centered on about 0 years (Fig. 4A). This analysis also provided a calculated cumulative probability of either under- or over-ageing, which showed that with 50% probability the crossdating-assisted Pacific geoduck age estimates were biased by about 0 years (Fig. 4B). However, traditional growth-increment counts had a 50% probability of underestimating the date of growth-increment formation (age) by nearly 4 years, and on average a 10% probability of underestimating the date of growth-increment formation by 6 years (Fig. 4B).

4. Discussion

This study verified that crossdating should be used to improve the accuracy of dating (age determination) in Pacific geoduck. Indeed, traditional growth-increment counts had a substantial probability of underestimating the date of growth-increment formation by several years (Fig. 4). However, crossdating almost completely eliminated dating error, as illustrated by posterior density distributions of $\Delta(\alpha_R - \alpha_S)$ and $\Delta(\mu_R - \mu_S)$ in which the measure of overall bias was centered on 0 years (Fig. 4). These findings in Pacific geoduck lend credibility to the use of crossdating in other marine organisms.

Additionally, this study was the first to successfully apply the bomb-produced ^{14}C method of age validation to a bivalve species in the North Pacific Ocean. This highlights the versatility of the technique and adds to
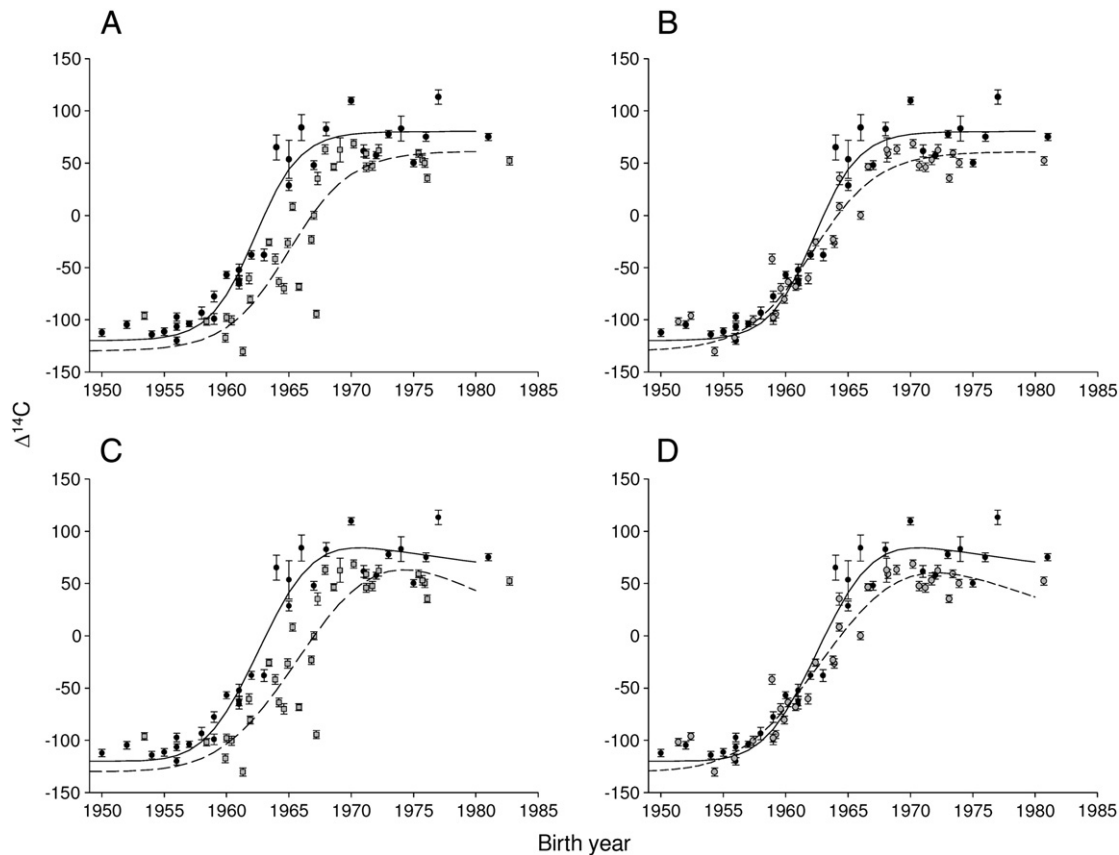
Fig. 3. Fits of species-specific logistic (A and B) and coupled-function (C and D) models to Pacific halibut (*Hippoglossus stenolepis*) reference $\Delta^{14}C$ (●) and Pacific geoduck (*Panopea generosa*) $\Delta^{14}C$ data with ages interpreted using growth-increment count method (□) in A and C and crossdating (○) in B and D.

an increasing list of species and marine areas in which it has been implemented.

Our results are consistent with a previous study investigating the time scale of increment formation in Pacific geoduck shells (Shaul and Goodwin, 1982). For example, disturbance checks induced by substrate dredging 26 years earlier were used as time-specific markers to verify that growth increments were formed annually (Shaul and Goodwin, 1982). In another component of their study, Shaul and Goodwin (1982) verified the number of increments in three known-age geoducks, up to a maximum age of 8 years. By contrast, our study was unique in that it involved a much larger time span, ranging from 27 to 56 years. At these timescales, the differences between increment counts and crossdating become greater, providing more power to test differences between the two dating techniques (Black et al., 2008b).

The specimens analyzed in this study were not chosen randomly, but with the goal of maximizing the difference between crossdated and ring-count age estimates while capturing the period coinciding with the bomb-produced ^{14}C pulse in marine systems (Table 1). If the 32 specimens were chosen randomly, the results would likely have been less definitive. Our research objective was not to determine whether a bias between methods exists; that question has already been answered by Black et al. (2008b). Instead, we wanted to assess the *relative* accuracy of each method with regard to estimating true age, as demonstrated by the ^{14}C chronologies. In many specimens, especially younger ones, there is not a difference between ages estimated by the two methods (Black et al., 2008b). Therefore, the nonrandom choice of specimens from the given age range represents larger than average differences between the growth-increment count and crossdating methods but adds to the strength of our conclusions, i.e., that crossdating is in general more accurate than growth-increment counting. Because we chose specimens where the differences between ages from

the two methods were larger, we may be able to cautiously apply our results to older specimens where the differences were increased. We do not suggest unrestrained extrapolation of our results to older specimens, but the fact remains that the difference between the methods (i.e., bias) became larger with age (Black et al., 2008a, 2008b). Therefore, the choice of specimens with larger age differences may be useful. Our results suggest that crossdating is the more appropriate method of age determination, especially for older individuals, and that therefore paleoenvironmental reconstructions are best done with the crossdating method. Yet due to the limitations imposed by the timing of the bomb ^{14}C pulse, individuals in this study only ranged between approximately 27 to 56 years. Extending the validation to older individuals should be done with caution (Campana, 2001). However, the degree of synchrony among individuals in growth-increment width and the strength (correlations) of climate (local sea surface temperature records) to growth relationships do not diminish in older specimens, suggesting that crossdating is useful over the full lifespan of Pacific geoduck (Black et al., 2008b).

The bomb-produced ^{14}C age validation method relies on the assumption that the reference chronology is biologically and environmentally representative of the species to be tested (Campana and Jones, 1998; Piner et al., 2005). This means that without age determination error, the magnitude and timing of the ^{14}C increase should be similar in the test and reference species. A conspecific reference chronology is ideal but has only been available on rare occasions (Campana, 1997; Piner and Wischniowski, 2004); comparisons between diverse taxa such as Pacific geoduck and Pacific halibut could cause complications.

The $\Delta^{14}C$ in Pacific geoduck may be different from that in the Pacific halibut reference chronology due to factors other than age bias. The predicted values of *k*, the asymptote, for Pacific geoduck appeared to be different from those for Pacific halibut, and the
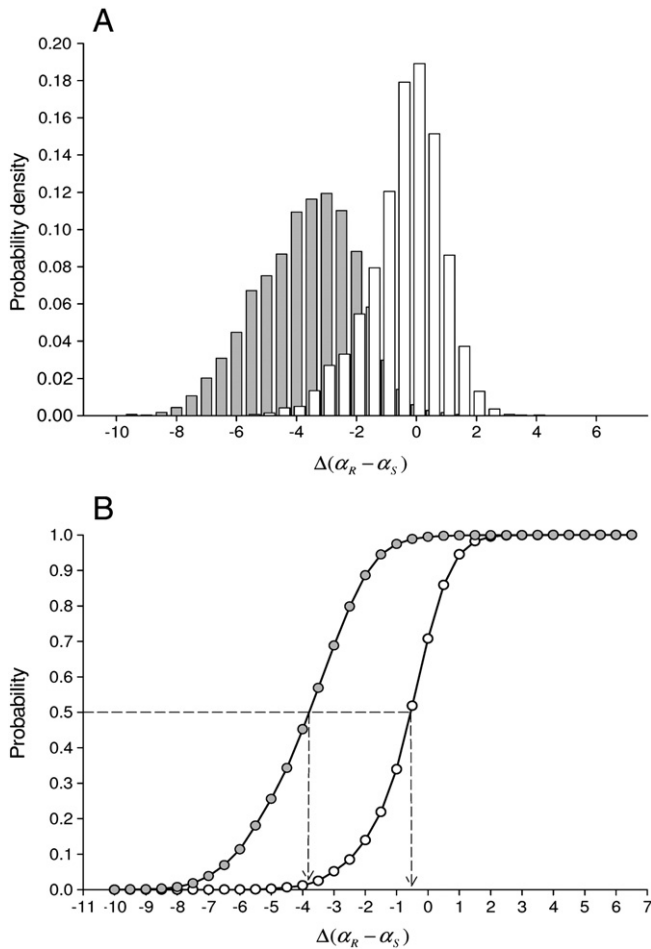
Fig. 4. Measurement of age determination bias based on an example given for estimated parameter α, the inflection point in the nonlinear logistic model, fit to Pacific halibut (*Hippoglossus stenolepis*) reference and Pacific geoduck (*Panopea generosa*) Δ^{14}C data. Bayesian nonlinear models were fit to data using Markov Chain Monte Carlo simulation with point estimates and estimation errors based on 2000 samples of the posterior distribution. Bias is measured as $\Delta(\alpha_R - \alpha_S)$ either interpreted by growth-increment counts (gray bars/circles) or the crossdating-assisted method (open bars/circles). The top graph (A) shows the marginal posterior distributions in $\Delta(\alpha_R - \alpha_S)$ and the bottom graph (B) shows the calculated probability of either under- or over-ageing. For example, age interpretation based on growth-increment counts has a 50% probability of under-ageing the sample by almost 4 years, while the crossdating-assisted method has 50% probability of under-ageing by less than 0.5 years.

range of post-peak Δ^{14}C values in both species was more variable (Fig. 3). This difference in asymptotes could be due to a violation of the assumption that the test and reference species are biologically and environmentally comparable. Unfortunately, because of the post-peak variability in Δ^{14}C values, true differences in k estimated for the reference chronology and Pacific geoducks could not be demonstrated statistically. There are two potential causes of unique asymptotic ranges in Δ^{14}C or increased variability in post-peak values: 1) a biological difference in the source of ^{14}C, or 2) a regional difference in the ^{14}C mixing rate or in its dilution rate, even at a small scale down to the individual specimen level. Regardless, differences in asymptote do not change the fact that the timing of bomb-produced ^{14}C increase strongly agreed between the crossdating-based test sample and reference chronology, providing evidence of dating accuracy.

Even though the comparisons made here were between widely disparate taxa, there is reason to believe that the biological sources of ^{14}C were generally similar. As juveniles, Pacific halibut reside at less than 40 m depth and prefer sand or sand mixed with gravel and mud (Norcross et al., 1995). The Pacific geoducks in this study

were captured in a similar depth range, about 6 to 20 m (Black et al., 2008b), and typically prefer bottom substrates similar to those of Pacific halibut (Goodwin and Pease, 1989; Campbell et al., 2004). The source of the ^{14}C, either directly from dissolved inorganic carbon in the water or from food, may be the same for fish and mollusks. For example, the source of ^{14}C for the ocean quahog, *Arctica islandica*, is dissolved inorganic carbon (Erlenkeuser, 1976) and the source of ^{14}C for many fish species is estimated to be 70% from dissolved inorganic carbon (Kalish, 1993, 1995). Even if juvenile Pacific halibut obtain ^{14}C from their food, they consume small, short-lived organisms from the same well-mixed shallow region in which Pacific geoduck reside (Holladay and Norcross, 1995); the carbon in these prey items should be representative of that in the seawater (Kalish, 1995). Despite these general similarities, the apparent difference in asymptotes could easily be due to a species-specific accumulation or source of carbon.

Another important consideration is that the geographic regions represented by the two data sets were different. The Pacific geoducks were from one very confined location, the Tree Nob Islands in British Columbia (Black et al., 2008b). Conversely, the Pacific halibut were from throughout the Gulf of Alaska (Piner and Wischniowski, 2004). Any regional difference in oceanographic processes, such as upwelling or freshwater runoff from continental land masses, affects the bomb-produced ^{14}C level. Upwelling provides a source of carbon that is depleted in ^{14}C, so the mixed surface water in an upwelling area will have a lower (i.e., diluted) level of ^{14}C (Broecker et al., 1985). In general, the coastal Gulf of Alaska is predominately a downwelling region with some freshwater river input (Stabeno et al., 2004). However, depending on prevailing current patterns, intermittent upwelling also occurs (Stabeno et al., 2004; Mundy and Olsson, 2005). South of the Gulf of Alaska, generally at latitudes less than 48°, summer upwelling increases and thereby moderates the increase of bomb-produced ^{14}C (Nydal, 1993; Kalish, 1995; Bograd et al., 2009). Conversely, continental freshwater is considered to have a closer link to the atmosphere; hence, an influx of freshwater will regionally increase the marine bomb-produced ^{14}C (Campana and Jones, 1998). Given these considerations, it should not be surprising that the two species have different asymptotic levels, as the Pacific geoducks may have been in an area that has a regionally unique level of bomb-produced ^{14}C.

5. Conclusions

Growth increments in Pacific geoducks are generally well-defined and readily interpreted, yet even in this species, dating error can accumulate in the absence of crossdating, as evidenced by comparisons with increment-count data (Strom et al., 2004; Black et al., 2008b). Clearly, the crossdating method takes into account an arena of information not utilized when individuals are aged solely by growth-increment counting. The end result without crossdating is larger error in estimates of population age structure, and from the perspective of growth-increment chronologies and climate reconstructions, attenuation of the population-wide growth pattern. In a simulation using tree-ring data, even a modest dating error rate quickly reduced the quality of the master chronology by "smearing" high-frequency growth patterns (Fritts and Swetnam, 1989). This concept applies to environmental reconstructions based on any growth-increment property, whether morphological, chemical, or isotopic in nature. Careful dating is of critical importance for maximizing the quality of a climate reconstruction or a stock assessment, and crossdating is an important way of increasing age determination accuracy and annual dating resolution. Our nonrandom choice of specimens allowed these conclusions, but did not allow consideration of average population-wide ageing errors.

As in geoduck, many other marine and freshwater species exhibit synchronous growth among individuals, relationships with climate

records, and even significant correlations among chronologies representing diverse taxa and ecosystems (Guyette and Rabeni, 1995; Black, 2009; Rypel et al., 2009; Matta et al., 2010). In combination with adequate crossdating sample size and rigorous calibration and verification with target climate variables, crossdating should provide a level of age determination accuracy and signal strength in marine-based climate reconstructions comparable to that in tree-ring chronologies (Strom et al., 2004; Black et al., 2008b; Black et al., 2009). In the future, more validation studies will increase confidence in crossdating across other marine species and systems. For now, bomb-produced ^{14}C age validation in Pacific geoduck provides compelling evidence that crossdating is an effective technique for marine systems.

Acknowledgments

References

Andrews, A.H., Burton, E.J., Kerr, L.A., Cailliet, G.M., Coale, K.H., Lundstrom, C.C., Brown, T.A., 2005. Bomb radiocarbon and lead-radium disequilibria in otoliths of bocaccio rockfish (*Sebastes paucispinis*): a determination of age and longevity for a difficult-to-age fish. Mar. Freshw. Res. 56, 517–528.

Beamish, R.J., McFarlane, G.A., 1983. The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112, 735–743.

Black, B.A., 2009. Climate-driven synchrony across tree, bivalve, and rockfish growth-increment chronologies of the northeast Pacific. Mar. Ecol. Prog. Ser. 378, 37–46.

Black, B.A., Boehlert, G.W., Yoklavich, M.M., 2005. Using tree-ring crossdating techniques to validate annual growth increments in long-lived fishes. Can. J. Fish. Aquat. Sci. 62, 2277–2284.

Black, B.A., Boehlert, G.W., Yoklavich, M.M., 2008a. Establishing climate-growth relationships for yelloweye rockfish (*Sebastes ruberrimus*) in the northeast Pacific using a dendrochronological approach. Fish. Oceanogr. 17, 368–379.

Black, B.A., Gillespie, D.C., MacLellan, S.E., Hand, C.M., 2008b. Establishing highly accurate production-age data using the tree-ring technique of crossdating: a case study for Pacific geoduck (*Panopea abrupta*). Can. J. Fish. Aquat. Sci. 65, 2572–2578.

Black, B.A., Copenheaver, C.A., Frank, D.C., Stuckey, M.J., Kormanyos, R.E., 2009. Multi-proxy reconstructions of northeastern Pacific sea surface temperature data from trees and Pacific geoduck. Palaeogeogr. Palaeoclimatol. Palaeoecol. 278, 40–47.

Bograd, S.J., Schroeder, I., Sarkar, N., Qiu, X.M., Sydeman, W.J., Schwing, F.B., 2009. Phenology of coastal upwelling in the California Current. Geophys. Res. Lett. 36, L01602.

Broecker, W.S., Peng, T.H., Ostlund, G., Stuiver, M., 1985. The distribution of bomb radiocarbon in the ocean. J. Geophys. Res. 90, 6953–6970.

Butler, P.G., Richardson, C.A., Scourse, J.D., Wanamaker Jr., A.D., Shammon, T.M., Bennell, J.D., 2010. Marine climate in the Irish Sea: analysis of a 489-year marine master chronology derived from growth increments in the shell of the clam *Arctica islandica*. Quat. Sci. Rev. 29, 1614–1632.

Campana, S.E., 1997. Use of radiocarbon from nuclear fallout as a dated marker in the otoliths of haddock *Melanogrammus aeglefinus*. Mar. Ecol. Prog. Ser. 150, 49–56.

Campana, S.E., 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. 59, 197–242.

Campana, S.E., Jones, C.M., 1998. Radiocarbon from nuclear testing applied to age validation of black drum, *Pogonias cromis*. Fish. Bull. 96, 185–192.

Campbell, A., Yeung, C.W., Dovey, G., Zhang, Z., 2004. Population biology of the Pacific geoduck clam, *Panopea abrupta*, in experimental plots, southern British Columbia, Canada. J. Shellfish. Res. 23, 661–673.

Cook, E.R., Peters, K., 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. Tree-Ring Bull. 47, 45–53.

Correa, M.L., Montagna, P., Vendrell-Simon, B., McCulloch, M., Taviani, M., 2010. Stable isotopes (δ^{18}O and delta δ^{13}C), trace and minor element compositions of recent scleractinians and last glacial bivalves at the Santa Maria di Leuca deep-water coral province, Ionian Sea. Deep Sea Res. II Top. Stud. Oceanogr. 57, 471–486.

Correge, T., 2006. Sea surface temperature and salinity reconstruction from coral geochemical tracers. Palaeogeogr. Palaeoclimatol. Palaeoecol. 232, 408–428.

Elsdon, T.S., Gillanders, B.M., 2004. Fish otolith chemistry influenced by exposure to multiple environmental variables. J. Exp. Mar. Biol. Ecol. 313, 269–284.

Erlenkeuser, H., 1976. C-14 and C-13 isotope concentration in modern marine mussels from sedimentary habitats. Naturwissenschaften 63, 338.

Felis, T., Rimbu, N., 2010. Mediterranean climate variability documented in oxygen isotope records from northern Red Sea corals—a review. Glob. Planet. Change 71, 232–241.

Fritts, H.C., Swetnam, T.W., 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. Adv. Ecol. Res. 19, 111–188.

Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. Bayesian Data Analysis, second ed. Chapman and Hall, New York.

Goman, M., Ingram, B.L., Strom, A., 2008. Composition of stable isotopes in geoduck (*Panopea abrupta*) shells: a preliminary assessment of annual and seasonal paleoceanographic changes in the northeast Pacific. Quat. Int. 188, 117–125.

Goodwin, C.L., Pease, B., 1989. Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Pacific Northwest)–Pacific Geoduck Clam. : U.S. Fish wildl. Serv. Biol. Rep., 82(11.120). U.S. Army Corps of Engineers. TR EL-82-4 ed. 14 pp.

Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Res. 57, 205–221.

Guyette, R.P., Rabeni, C.F., 1995. Climate response among growth increments of fish and trees. Oecologia 104, 272–279.

Hamel, O.S., Piner, K.R., Wallace, J.R., 2008. A robust deterministic model describing the bomb radiocarbon signal for use in fish age validation. Trans. Am. Fish. Soc. 137, 852–859.

Helama, S., Schone, B.R., Black, B.A., Dunca, E., 2006. Constructing long-term proxy series for aquatic environments with absolute dating control using a sclerochronological approach: introduction and advanced applications. Mar. Freshw. Res. 57, 591–599.

Hendy, E.J., Gagan, M.K., Lough, J.M., 2003. Chronological control of coral records using luminescent lines and evidence for non-stationary ENSO teleconnections in northeast Australia. Holocene 13, 187–199.

Holladay, B.A., Norcross, B.L., 1995. August diet of age-0 Pacific halibut in nearshore waters of Kodiak Island, Alaska. Environ. Biol. Fishes 44, 403–416.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. 43, 69–78.

Jones, J.B., 2008. Stable oxygen isotope reconstruction of ambient temperature during the collapse of Eastern Scotian Shelf Cod (*Gadus morhua* L.). Dalhousie University, Halifax, Nova Scotia, Canada. Masters Thesis

Kalish, J.M., 1993. Pre-bomb and post-bomb radiocarbon in fish otoliths. Earth Planet. Sci. Lett. 114, 549–554.

Kalish, J.M., 1995. Radiocarbon and fish biology. In: Secor, D.H., Dean, J.M., Campana, S.E. (Eds.), Recent Developments in Fish Otolith Research. University of South Carolina Press, Columbia, SC, pp. 637–653.

Kastelle, C.R., Kimura, D.K., Goetz, B.J., 2008. Bomb radiocarbon age validation of Pacific ocean perch (*Sebastes alutus*) using new statistical methods. Can. J. Fish. Aquat. Sci. 65, 1101–1112.

Kerr, L.A., Andrews, A.H., Frantz, B.R., Coale, K.H., Brown, T.A., Cailliet, G.M., 2004. Radiocarbon in otoliths of yelloweye rockfish (*Sebastes ruberrimus*): a reference time series for the coastal waters of southeast Alaska. Can. J. Fish. Aquat. Sci. 61, 443–451.

Kerr, L.A., Andrews, A.H., Munk, K., Coale, K.H., Frantz, B.R., Cailliet, G.M., Brown, T.A., 2005. Age validation of quillback rockfish (*Sebastes maliger*) using bomb radiocarbon. Fish. Bull. 103, 97–107.

Kerr, L.A., Secor, D.H., Kraus, R.T., 2007. Stable isotope (δC-13 and δO-18) and Sr/Ca composition of otoliths as proxies for environmental salinity experienced by an estuarine fish. Mar. Ecol. Prog. Ser. 349, 245–253.

Kilada, R.W., Campana, S.E., Roddick, D., 2007. Validated age, growth, and mortality estimates of the ocean quahog (*Arctica islandica*) in the western Atlantic. ICES J. Mar. Sci. 64, 31–38.

Killingley, J.S., Berger, W.H., 1979. Stable isotopes in a mollusk shell: detection of upwelling events. Science 205, 186–188.

Kimura, D.K., Kastelle, C.R., Goetz, B.J., Gburski, C.M., Buslov, A.V., 2006. Corroborating the ages of walleye pollock (*Theragra chalcogramma*). Mar. Freshw. Res. 57, 323–332.

Krantz, D.E., Williams, D.F., Jones, D.S., 1987. Ecological and paleoenvironmental information using stable isotope profiles from living and fossil mollusks. Palaeogeogr. Palaeoclimatol. Palaeoecol. 58, 249–266.

Lunn, D.J., Thomas, A., Best, N., Spiegelhalter, D., 2000. WinBUGS — a Bayesian modelling framework: concepts, structure, and extensibility. Stat. Comput. 10, 325–337.

Marchitto, T.M., Jones, G.A., Goodfriend, G.A., Weidman, C.R., 2000. Precise temporal correlation of Holocene mollusk shells using sclerochronology. Quat. Res. 53, 236–246.

Matta, M.E., Black, B.A., Wilderbuer, T.K., 2010. Climate-driven synchrony in otolith growth-increment chronologies for three Bering Sea flatfish species. Mar. Ecol. Prog. Ser. 413, 137–145.

Mundy, P.R., Olsson, P., 2005. Climate and weather. In: Mundy, P.R. (Ed.), The Gulf of Alaska Biology and Oceanography. Alaska Sea Grant College Program, University of Alaska Fairbanks, Fairbanks, AK, pp. 25–34.

Nielsen, J.K., Helama, S., Schone, B., 2008. Shell growth history of geoduck clam (*Panopea abrupta*) in parry passage, British Columbia, Canada: temporal variation in annuli and the Pacific Decadal Oscillation. J. Oceanogr. 64, 951–960.

Noakes, D.J., Campbell, A., 1992. Use of geoduck clams to indicate changes in the marine-environment of Ladysmith Harbor, British Columbia. Environmetrics 3, 81–97.

Norcross, B.L., Holladay, B.A., Muter, F.J., 1995. Nursery area characteristics of Pleuronectids in coastal Alaska, USA. Neth. J. Sea Res. 34, 161–175.

Nydal, R., 1993. Application of bomb ^{14}C as a tracer in the global carbon cycle. Trends Geophys. Res. 2, 355–364.

Orensanz, J.M., Hand, C.M., Parma, A.M., Valero, J., Hilborn, R., 2004. Precaution in the harvest of Methuselah's clams — the difficulty of getting timely feedback from slow-paced dynamics. Can. J. Fish. Aquat. Sci. 61, 1355–1372.

Piner, K.R., Wischniowski, S.G., 2004. Pacific halibut chronology of bomb radiocarbon in otoliths from 1944 to 1981 and a validation of ageing methods. J. Fish Biol. 64, 1060–1071.

Piner, K.R., Hamel, O.S., Menkel, J.L., Wallace, J.R., Hutchinson, C.E., 2005. Age validation of canary rockfish (*Sebastes pinniger*) from off the Oregon coast (USA) using the bomb radiocarbon method. Can. J. Fish. Aquat. Sci. 62, 1060–1066.

Rypel, A.L., Haag, W.R., Findlay, R.H., 2009. Pervasive hydrologic effects on freshwater mussels and riparian trees in southeastern floodplain ecosystems. Wetlands 29, 497–504.

Schone, B.R., Fiebig, J., Pfeiffer, M., Gless, R., Hickson, J., Johnson, A.L.A., Dreyer, W., Oschmann, W., 2005. Climate records from a bivalved Methuselah (*Arctica islandica*, Mollusca; Iceland). Palaeogeogr. Palaeoclimatol. Palaeoecol. 228, 130–148.

Searle, T., Roberts, R.D., Lokman, P.M., 2006. Effects of temperature on growth of juvenile blackfoot abalone, *Haliotis iris* Gmelin. Aquacult. Res. 37, 1441–1449.

Shaul, W., Goodwin, L., 1982. Geoduck (*Panope generosa*: Bivalvia) age as determined by internal growth lines in the shell. Can. J. Fish. Aquat. Sci. 39, 632–636.

Spiegelhalter, D.J., Best, N.G., Carlin, B.R., van der Linde, A., 2002. Bayesian measures of model complexity and fit. J. R. Stat. Soc. B 64, 583–616.

Stabeno, P.J., Bond, N.A., Hermann, A.J., Kachel, N.B., Mordy, C.W., Overland, J.E., 2004. Meteorology and oceanography of the northern Gulf of Alaska. Cont. Shelf Res. 24, 859–897.

Stokes, M.A., Smiley, T.L., 1996. An Introduction to Tree-Ring Dating. University of Arizona Press, Tucson, AZ.

Strom, A., Francis, R.C., Mantua, N.J., Miles, E.L., Peterson, D.L., 2004. North Pacific climate recorded in growth rings of geoduck clams: a new tool for paleoenvironmental reconstruction. Geophys. Res. Lett. 31, L06206.

Stuiver, M., Polach, H.A., 1977. Reporting of C-14 data — discussion. Radiocarbon 19, 355–363.

Weidman, C.R., Jones, G.A., 1993. A shell-derived time history of bomb C-14 on Georges Bank and its Labrador Sea implications. J. Geophys. Res. 98, 14577–14588.

Yamaguchi, D.K., 1991. A simple method for cross-dating increment cores from living trees. Can. J. For. Res. 21, 414–416.