

Establishing highly accurate production-age data using the tree-ring technique of crossdating: a case study for Pacific geoduck (*Panopea abrupta*)

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Abstract: We apply the tree-ring technique of crossdating to generate highly accurate age data and evaluate error in annual growth increment (annual growth zone) counts for long-lived Pacific geoduck (*Panopea abrupta*) in the Tree Nob Islands, northern British Columbia, Canada. Crossdating is the most fundamental procedure of tree-ring analysis and is based on the tendency of environmental variability to synchronize the growth of all individuals at a given site. By cross-matching these synchronous growth “bar codes”, all growth increments can be correctly identified and assigned the correct calendar year, including the innermost year of recruitment. In this analysis, a total of 432 geoduck individuals were aged using crossdating methods as well as annual growth increment counts. The entire crossdating process was completed using visual techniques, requiring no additional equipment beyond a microscope or microprojector. When compared with cross-dated ages, growth increment counts consistently underaged Pacific geoduck, particularly in the oldest individuals. These inaccuracies obscured major recruitment pulses and underestimated the rarity of strong recruitment events. To date, cross-dating has been used to develop growth chronologies in a variety of marine and freshwater bivalve and fish species, but no study has demonstrated how the technique can be used to dramatically and economically improve accuracy in age data.

Résumé : Nous utilisons une technique d’interdatation servant à l’étude des anneaux de croissance des arbres pour produire des données très précises de détermination de l’âge et pour évaluer l’erreur du dénombrement des incréments annuels de croissance (zone de croissance annuelle) chez la panope du Pacifique (*Panopea abrupta*), un mollusque à forte longévité, aux îles Tree Nob, nord de la Colombie-Britannique, Canada. L’interdatation est la technique la plus fondamentale de l’analyse des anneaux des arbres et elle se base sur la tendance qu’a la variabilité environnementale à synchroniser la croissance de tous les individus à un site donné. Par l’appariement croisé de ces « codes à barres » de croissance synchronisée, il est possible d’identifier correctement tous les incréments de croissance et d’assigner la bonne année du calendrier, même à l’année la plus ancienne de recrutement. Dans notre analyse, nous avons déterminé l’âge de 432 panopes à l’aide de méthodes d’interdatation et de dénombrement des incréments annuels de croissance. Tout le processus d’interdatation a pu être complété à l’aide de techniques visuelles, ne nécessitant aucun équipement autre qu’un microscope ou qu’un microprojecteur. Par rapport à la détermination de l’âge par interdatation, le dénombrement des incréments de croissance sous-estime systématiquement l’âge des panopes du Pacifique, particulièrement chez les individus plus âgés. Ces imprécisions masquent les principales périodes de recrutement plus intenses et sous-estiment la rareté des événements de fort recrutement. À ce jour, l’interdatation a servi à élaborer des chronologies de croissance chez une variété d’espèces de bivalves et de poissons marins et d’eau douce, mais aucune étude n’avait démontré comment la technique peut être utilisée pour améliorer de façon spectaculaire et économique la précision des données de détermination de l’âge.

[Traduit par la Rédaction]

Introduction

In fisheries management, accurate estimates of fish age are required to establish population growth and mortality rates, recruitment patterns, and the effects of human activities and natural environmental variability on fish populations. Consequently, hundreds of thousands of fish and

shellfish ages are estimated each year, typically by counting annual growth increments (i.e., annual growth zones or annuli) in scales, otoliths, shells, or other hard structures (Campana and Thorrold 2001; Valero et al. 2004). These age estimates often involve widely agreed upon criteria for interpreting annual growth increments, as well as any blind areas, checks, or other irregular patterns. Yet they may still contain considerable error, especially for longer-lived species (Beamish and McFarlane 1983; Boehlert and Yoklavich 1984).

To address this issue, a number of validation techniques have been developed to assess the accuracy of age estimates (Campana 2001). In one approach, fish or shellfish are physically or chemically tagged, released, and recaptured at a later date to verify the periodicity of growth increment formation over the time elapsed (Beamish and Chilton 1982; Heifetz et al. 1998). More specific to long-lived species, the absolute age of material in the core of calcified structures

Received 5 December 2007. Accepted 18 June 2008. Published on the NRC Research Press Web site at cjfas.nrc.ca on 13 November 2008.
J20301

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can be determined using the decay of naturally occurring radioisotopes (Turekian et al. 1975; Shaul and Goodwin 1982; Turekian et al. 1982) or the sudden pulse of marine ^{14}C that followed nuclear testing in the 1950s and 1960s (Kalish 1993; Campana 1997; Ebert and Souton 2003). Any disagreements between age estimates from annual growth increment counts and radiometric techniques would indicate biases in ageing criteria. A number of other age validation techniques are also available for fish or shellfish, each with its own set of advantages, limitations, and ranges in accuracy and precision (Campana 2001).

Borrowing from tree-ring science (dendrochronology), crossdating offers an additional validation tool that could provide high levels of ageing accuracy, particularly for long-lived species (Black et al. 2005). The procedure is based on the tendency of environmental variability to synchronize growth such that the calendar years of relatively narrow or wide growth increments correspond among individuals from a given site. By crossmatching these synchronous growth "bar codes", all growth increments can be correctly identified and thus assigned the correct calendar year. For ageing purposes, crossdating is an entirely visual process and requires no measurements or statistical analysis. The technique is similar to annual growth increment counting with the additional step of checking that growth patterns align with those in other individuals. If an increment has been missed or falsely added, the growth pattern will be offset by a year relative to that in other samples, and the point where the offset begins indicates the location of the error. In this manner, an accurate age may be obtained by working from the known year of capture at the margin through the innermost year of recruitment.

To date, crossdating has been demonstrated in a variety of aquatic species, including Pacific rockfish, freshwater mussels, and marine bivalves, including Pacific geoduck, and has been primarily used to build annually resolved chronologies for reconstructing climate or assessing the effects of climate on growth (Strom et al. 2004; Black et al. 2005; Helama et al. 2006). Yet its potential as an age validation tool has been much less thoroughly explored, even though crossdating could provide highly accurate age estimates for a large number of individuals and with no additional equipment requirements beyond a microscope. This is in contrast with most other age validation techniques, which can only accommodate small samples sizes. Under such circumstances, growth increment interpretation is validated only for a specific group of age readers in a specific group of specimens. Error could occur as the ageing criteria are employed by new age readers or applied to new samples (Beamish and McFarlane 1983; Campana 2001). Crossdating, however, validates the age estimate for each individual to which the procedure has been applied, potentially yielding large volumes of validated age data to develop high-resolution estimates of population age structure and recruitment patterns.

In this analysis, we demonstrate how crossdating can be implemented on a production-ageing level using Pacific geoduck (*Panopea abrupta*), a marine bivalve mollusk that can live in excess of 150 years and supports a multimillion dollar fishery along the Washington, British Columbia, and southeast Alaska coasts (Goodwin and Pease 1991; Orensanz et al. 2004; Strom et al. 2004). Our objective is to dem-

onstrate the accuracy and utility of crossdating by (i) ageing 432 geoduck individuals via crossdating, (ii) statistically verifying crossdating accuracy and quantifying the strength of the synchronous growth pattern, (iii) evaluating the accuracy of growth increment counts versus crossdated ages, (iv) estimating crossdating precision by comparing geoduck ages independently crossdated by two readers, and finally (v) developing a highly accurate recruitment history using the crossdated data set. This study represents the first application of crossdating to generate age data, the first comparison of crossdating with growth increment count data and, to our knowledge, the first highly accurate and fully validated ageing data set for any fish or shellfish species.

Materials and methods

Pacific geoduck (*P. abrupta*) range from Kodiak, Alaska, to southern California and can be found buried in ocean floor sediment from the lower intertidal to depths up to 100 m (Bernard 1983; Coan et al. 2000). For this study, we use geoduck harvested from three sites within the Tree Nob Islands, located west of Prince Rupert, British Columbia (site 1: $54^{\circ}12.587'\text{N}$, $130^{\circ}49.521'\text{W}$; site 2: $54^{\circ}13.042'\text{N}$, $130^{\circ}47.36'\text{W}$; and site 3: $54^{\circ}15.676'\text{N}$, $130^{\circ}48.609'\text{W}$). These samples were all live-collected during density surveys conducted by commercial geoduck harvesters in the summer of 2004. Sampling depths ranged from 6 to 20 m, and divers attempted to sample nonselectively from the entire range of geoduck sizes. For crossdating and chronology development, we analyzed the growth increments found in the hinge plate. The hinge plate (inner shell layer) grows at a rate proportional to that of the outer shell layer, but is protected from erosion and thus provides the most complete record. To prepare growth increments for analysis, a single shell from each geoduck specimen was cut along the height axis of the valve through the center of the hinge plate region 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 sandwiched between two glass slides and viewed either by a microprojector or a dissecting microscope, both using transmitted light.

All 432 acetate peels were first aged by annual growth increment counts as part of routine production ageing at the Fisheries and Oceans Canada Fish Ageing Laboratory, Nanaimo, British Columbia. Subsequently, visual crossdating was conducted for 167 of the peels at the Hatfield Marine Science Center in Newport, Oregon, and for 325 peels at Nanaimo. Sixty of the same peels were crossdated at both locations to evaluate crossdating precision. The process of visual crossdating involved matching the high-frequency, year-to-year variability that occurred among specimens (Stokes and Smiley 1996). Examining high-frequency variability allowed for much more exact placement of a sample in time than would be possible using low frequency, long-term trends and also removed age-related growth declines from consideration.

In this study, we applied the list year technique in which calendar years of conspicuously narrow and wide increments

were recorded from the marginal growth increment, formed at the known year of death (2004), to the origin (Yamaguchi 1991). The width of each growth increment was assessed relative to the widths of the two or three growth increments on either side of it. Thus, working from the margin toward the center, we noted the calendar year of each growth increment that was prominently narrow or prominently wide relative to its immediate neighbors. Applying such a narrow 5–7 year window ensured that we would record only high-frequency patterns of variability, filtering out age-related growth declines or any other low-frequency patterns.

The crossdating process was best accomplished by starting with the clearest individuals. As each new sample was processed, we checked that lists of calendar years corresponded among the other samples. If a growth increment had been missed or falsely added in the sample, recorded calendar years would be offset relative to those recorded for the other samples, and the point at which the shifting began indicated the location of the error. At no time, however, was a growth pattern forced on an individual. Dating was adjusted only when further visual inspection revealed that a growth increment had indeed been missed or falsely added. We found that we had sufficiently memorized the synchronous growth pattern after listing signature years for approximately 20 individuals and could visually crossdate the remaining samples from memory.

Of all the peels examined, 33 were particularly old and consistently clear, which we used for crossdating verification. Under the dissecting microscope and at 60 \times magnification, we took four to eight overlapping digital photographs with a Leica DC300 7.2 megapixel camera and used Image Pro Plus 6.0 to tile the photographs into a single panoramic image (Media Cybernetics Inc., Silver Spring, Maryland). Using Image Pro Plus 6.0, we measured growth increment widths along continuous transects that followed the axis of growth. Each growth increment was delineated at the end of the winter line and start of the new growing season. Two transects were measured on each hinge plate. To statistically validate crossdating, all 66 measurement time series were then imported into the International Tree-Ring Data Bank Dendrochronology Program Library program COFECHA written in 1982 by Richard Holmes of the Laboratory of Tree-Ring research at the University of Arizona (available through the University of Arizona Laboratory of Tree-Ring Research Web site www.ltrr.arizona.edu/software.html). In the first step of statistical validation, we used COFECHA to remove low-frequency variability in each geoduck measurement time series via the process of detrending. For this procedure, each geoduck measurement time series ($n = 66$) 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 whereby 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 and were therefore applied in this study to Pacific geoduck (Black et al. 2005). Once fitted, each geoduck measurement time series was then divided by the values predicted by the cubic spline, thereby removing low-frequency variability, homoge-

nizing variance, and equally weighting each set of measurements to a mean of one (Holmes 1983; Grissino-Mayer 2001). Detrended geoduck measurement time series were tested for any remaining autocorrelation, which if present was removed to ensure serial independence. Finally, each detrended measurement time series was correlated with the average of all other ($n = 65$) detrended measurement time series in the sample set. 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 pattern prevented spuriously high correlations among individuals and also mathematically mimicked the process of visual crossdating by eliminating low-frequency growth patterns.

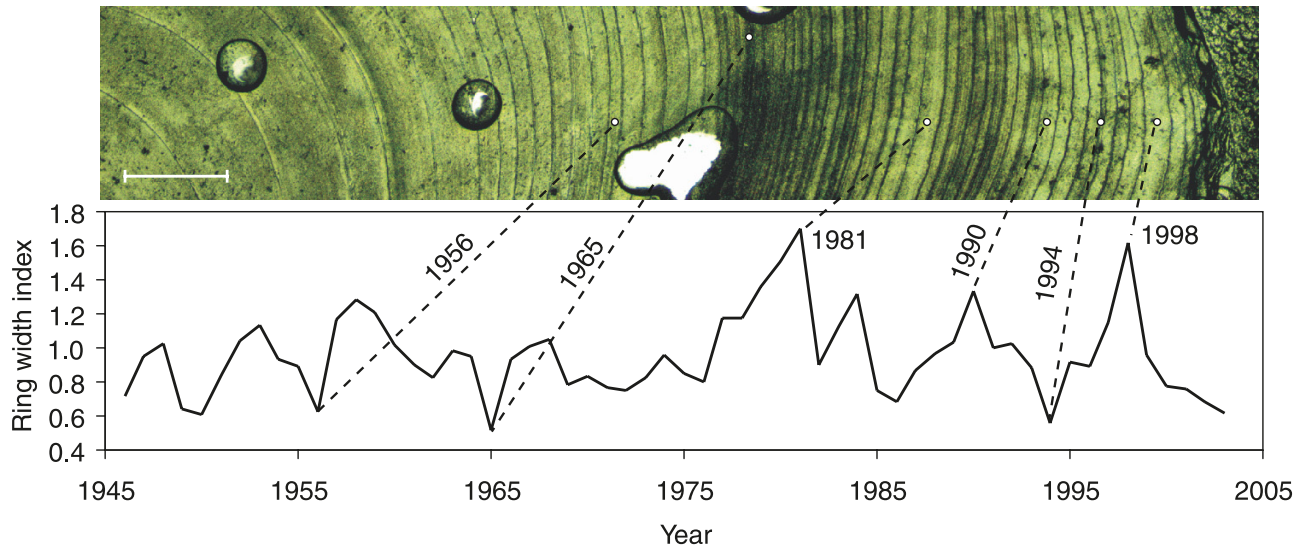
Results and discussion

Crossdating in geoduck

Geoduck samples exhibited a strong synchronous climate signal with several signature growth patterns that facilitated crossdating. For example, a conspicuously wide 1998 and narrow 1994 were distinctive as well as an extremely narrow 1965, a narrow 1956 (Fig. 1), a wide 1941 and narrow 1940, a narrow 1926 and 1933, a wide 1915, and a narrow 1904 and 1891. Thus at least one prominent signature year or pattern occurred approximately every decade, which allowed for frequent verification as we moved through the growth pattern. Somewhat less pronounced, yet consistently synchronous growth patterns guided crossdating between these highly visible marker years. At no time did we find a truly missing annual growth increment, though very small “micro” increments occurred in some samples, particularly in 1965. Checks, or nonannual growth zones that could be mistaken as annuli (winter zones), were much more common and quickly identified through visual crossdating. In addition to width, we used other morphological characteristics of the growth increments to aid in crossdating (Stokes and Smiley 1996; Hendy et al. 2003). For example, checks consistently occurred in 1940, and the combination of a wide 1941 and narrow 1940 with checks was highly distinctive. Once the synchronous growth pattern for the site was committed to memory, crossdating proceeded rapidly and we found we could crossdate approximately 15–20 individuals per hour.

Although crossdating procedures closely follow those developed for trees, a major difference for geoduck was that conspicuously wide signature years were just as reliable as conspicuously narrow signature years. Dendrochronologists typically rely most heavily on narrow signature years because tree growth tends to be most synchronized when climatic conditions are limiting. Almost all trees will be forced to produce a narrow ring during poor years, but growth during favorable years is often much more variable (Stokes and Smiley 1996). During a favorable year, the most competitive individuals grow vigorously while suppressed trees or those on poor microsites may fail to produce such a relatively robust increase in ring width. Such a range of growth rates often decreases synchrony during favorable years compared with that during poor climatic years. However, an analogous phenomenon is not apparent for geoduck at Tree Nob. Years with wide growth incre-

Fig. 1. Growth patterns in a geoduck (*Panopea abrupta*) hinge plate acetate peel compared with the average growth pattern for all geoducks from the Tree Nob sites, as calculated using the crossdating program COFECHA. The most common signature years (conspicuously narrow or wide growth increments relative to the two or three adjacent rings on either side) are highlighted. Note the close correspondence in growth patterns, including more subtle patterns of variability between major signature years. This geoduck specimen was harvested in the spring of 2004. Scale bar = 0.5 mm.



ments, such as 1998, 1941, and 1915, were often the most conspicuous and readily identifiable and were therefore treated the same importance as narrow years in the crossdating process. This also appears to be true in splitnose rockfish (*Sebastes diplopoa*), in which wide years were also highly useful for crossdating (Black et al. 2005).

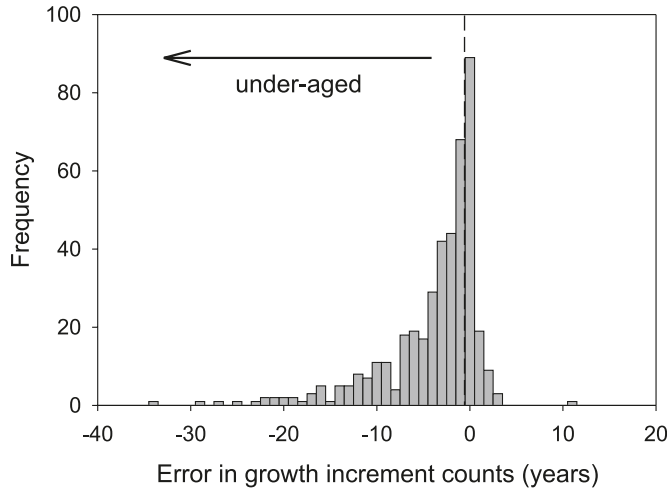
Statistical validation of crossdating verified that each growth increment had been assigned the correct calendar year and also quantified the strength of the synchronous growth pattern. Mean correlation between each set of detrended geoduck measurements and the average of all other detrended measurements (interseries correlation) was quite high at 0.735. All correlations were statistically significant ($p < 0.01$) with no segments flagged by COFECHA to check for potential errors. If, however, we simulate an error by intentionally skipping the narrow 1965 in sample No. 3a, the correlation between that sample and the average of all others drops from 0.81 (when correctly crossdated) to 0.22 (when omitting 1965), illustrating the power of this analysis. Overall, the strength of the synchronous growth pattern, as indicated by the interseries correlation, was higher than that found in mountain hemlock (*Tsuga mertensiana*) and Sitka spruce (*Picea sitchensis*) tree-ring data sets developed in the Gulf of Alaska region (Wiles et al. 1998; Gedalof and Smith 2001) and thus was at a level considered fully acceptable by dendrochronologists. The interseries correlation for geoduck was also higher than that found in Pacific rockfish (Black et al. 2005) and other marine and freshwater bivalves (Helama et al. 2006). As an additional check of accuracy, we correlated the geoduck master chronology generated by COFECHA with annual average sea surface temperature records (1941–1990) at the nearby Langara Lighthouse (54°9.0'N, 133°1.8'W). A correlation ($r = 0.72$; $p < 0.001$) was consistent with strong relationships found between geoduck growth increment width and sea surface temperatures in Puget Sound (Strom et al. 2004) and corroborated the an-

nual periodicity of growth increment formation and annual accuracy of the chronology. Indeed, the synchronous growth pattern in geoduck appeared to be remarkably strong and consistent, which was reflected by the ease with which crossdating could be performed in this sample set.

Growth increment count ages vs. crossdated ages

When ages derived from growth increment counts were compared with crossdated ages, 89 of the 432 agreed. Among the remaining 343 individuals, 32 were over-aged by growth increment counting, while the other 311 were under-aged, in one case by 34 years (Fig. 2). The degree of underaging bias increased with geoduck age, such that growth increment count ages of the oldest individuals were the least reliable (Fig. 3a). This effect was particularly pronounced in geoducks that were more than 100 years in age (Fig. 3a). When expressed as number of underaging errors per decade, the error rate was not constant, but increased with geoduck age such that more growth increments were missed per decade in the oldest individuals than in their younger counterparts (Fig. 3b). This compounding error rate resulted in particularly low accuracy for older geoduck individuals. Such error could be partially explained by the fact that growth-increment width decreased with increasing age, particularly near the margin. These narrow increments were occasionally distorted, unclear, and therefore relatively difficult to interpret, leading to rapidly accumulating error. Furthermore, some hinge plates chipped during the cutting process, resulting in the loss of growth increments along the margin. The number of increments thus affected would have been greatest in older individuals, given the very slow growth rates they typically experienced late in life. During crossdating, however, missed annual growth increments or checks had the effect of offsetting the expected growth pattern and were therefore quickly identified. Even for those individuals with particularly troublesome margins, validation

Fig. 2. Frequency distribution of the difference between growth increment count ages and crossdated ages for 432 geoduck (*Panopea abrupta*) individuals. Negative values represent underageing in growth increment count data.



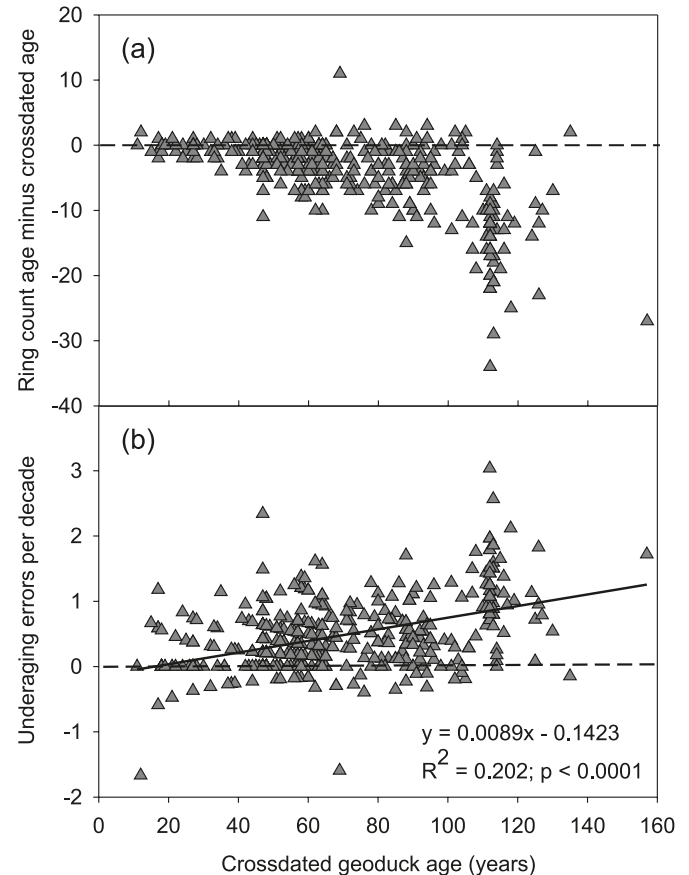
through crossdating was possible once the clear innermost growth increments were reached. In almost every sample, the inner increments formed during young, rapid growth (the first 30–50 years) were quite clear, allowing for crossdating to the origin.

Once compiled, the crossdated geoduck ages revealed a highly episodic recruitment pattern with particularly strong events in 1892–1893 and 1957–1958 (Fig. 4a). Apart from these two major pulses, elevated levels of recruitment occurred during the 20-year period from 1940 through 1960, but remained low throughout the remainder of the chronology (Fig. 4a). Although the annual growth increment count data captured recruitment from 1940–1960 and 1957–1958, the entire 1892–1893 episode was lost. Instead, underageing of the oldest samples indicated a false pulse of recruitment from 1900 to 1910 (Fig. 4b). In general, annual growth increment count data underestimated the highly irregular nature of geoduck recruitment at the Tree Nob sites. Recruitment pulses were much stronger and more infrequent than the growth increment count data suggested with major recruitment events separated by more than 60 years. Others have noted the episodic nature of geoduck recruitment (Orensanz et al. 2004), yet these estimates have been based on annual growth increment count data. If the results from Tree Nob are an indicator, the rarity and intensity of recruitment pulses for this species is more pronounced than previously recognized. This is particularly relevant to the management of the British Columbia geoduck fishery, which is based on an age-structured yield model where the recruitment time series reconstructed from age data has a large effect on modeled harvest rates (Zhang and Hand 2006).

Remaining error

Although crossdating can substantially increase ageing accuracy beyond that possible with growth increment counts, some error may still occur, especially when interpreting the growth increments formed during the first few years of life. In the first possible source of error, age may be underestimated by a year or two if the hinge plate center, and

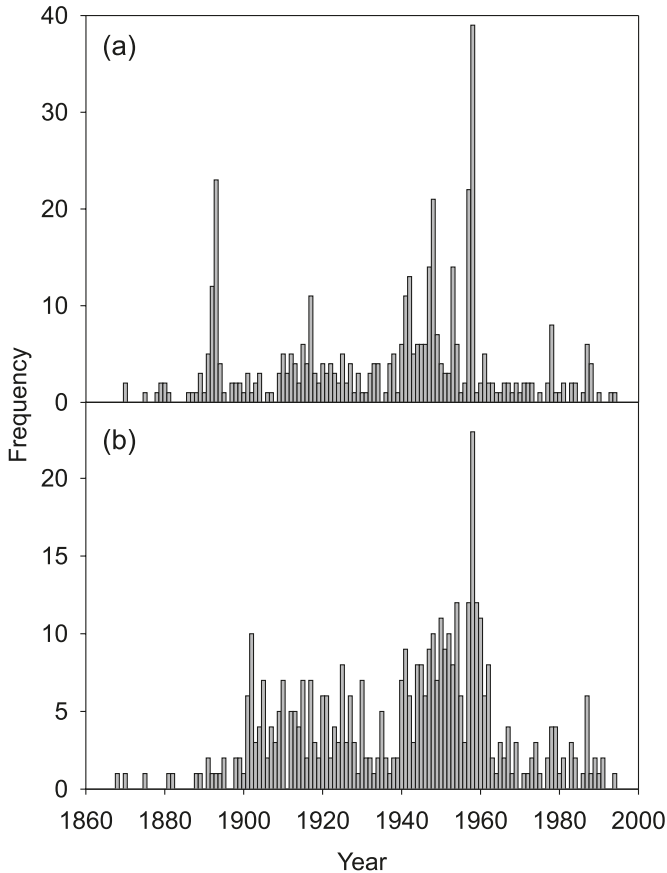
Fig. 3. (a) Difference between the growth increment (ring) count age and the crossdated age for each of the 432 geoduck (*Panopea abrupta*) individuals, plotted against crossdated geoduck age. Negative values represent underageing in growth increment count data; a value of zero (broken line) indicates no difference between growth increment count and crossdated ages. (b) Underageing errors per decade, calculated as crossdated age minus growth increment count age divided by crossdated age in decades (i.e., crossdated age divided by 10). A value of zero (broken line) indicates no difference between growth increment count and crossdated ages.



thus the innermost growth increment(s), was missed during the sectioning process. Similarly, underageing may also occur if the inner shell layer (hinge plate) underwent dissolution. We cannot quantify the degree of these error sources in our data set, but believe it to be relatively low.

In another source of error, accuracy may be reduced if the innermost growth increments are unclear or ambiguous. As the origin is approached, fewer and fewer increments are available to verify the synchronous growth pattern, and consequently a mistake in these “early” growth increments cannot be readily identified through crossdating. Because of this second source of error, 23% (14 of 60) geoduck specimens independently crossdated by two readers disagreed. However, these differences were relatively minor, with 11 ages disagreeing by 1 year, two ages disagreeing by 2 years, and one age disagreeing by 3 years. The majority of this error was probably due to one reader’s inexperience in interpreting the innermost growth increments. Finally, when the number of samples becomes very small (<5), as is the case

Fig. 4. Comparison between the (a) recruitment pattern based on crossdated ages of 432 geoduck (*Panopea abrupta*) individuals and (b) recruitment pattern based on growth increment count ages for the same individuals.



for the earliest growth increments in the oldest specimens, there are fewer individuals with which to correctly distinguish a true increment from a particularly convincing check or microgrowth increment. In such a circumstance, the chances of missing or falsely adding a growth increment to all samples are highest. Yet even with these sources of error, all of which would also occur in annual growth increment count data, crossdating provides a substantial improvement in accuracy as well as precision. For growth increment count data, agreement between readers in the Tree Nob data set was 19% to the same age and 48% plus or minus 1 year. By implementing crossdating, precision increased to 77% agreement to the same age and 95% plus or minus 1 year, underscoring the method's repeatability.

Applications and future directions

In conclusion, crossdating can be applied to develop highly accurate and replicable age data. The procedure has fewer requirements for specimen quality than annual growth increment count assessments and provides an objective means by which to account for all growth increments. Accurate ages can be derived even if the annual increments at the margin are missing or if there are periods of suppressed or distorted growth elsewhere in the specimen. Additional time must be invested in identifying and learning the synchronous growth pattern for the site, yet once this growth

pattern is committed to memory, crossdating proceeds quickly. It can be completed more rapidly than annual growth increment counts and with greater accuracy, especially in older specimens. Crossdating also provides objective feedback for learning to correctly distinguish annual growth increments, thereby increasing the speed and ease of crossdating over time. Finally, no additional equipment beyond a microscope or microprojector is required for crossdating. The synchronous growth pattern can be described entirely through the list year technique or a related method known as skeleton plotting, both of which require no measurements (Stokes and Smiley 1996). Measurements of geoduck growth increments were completed in this study for additional verification of crossdating and as a way to quantify the strength of the synchronous growth pattern. Yet even when these statistical analyses are conducted, correlations are only a guide, and the ultimate decision as to whether a sample is correctly crossdated should be based on a visual assessment (Grissino-Mayer 2001). Computer software may help to better automate the process in the future, though technologies for pattern recognition or accurately delineating growth increments are not yet that advanced.

In future studies, a given geoduck chronology could be used to crossdate samples collected from the site at a later date or to re-evaluate historical samples. It may also be relevant for crossdating samples collected from nearby sites, particularly if the sites share a similar climate regime. Although not important at Tree Nob, visual cues other than growth increment width may also be useful to consider in future crossdating studies. For example, in X-ray exposures of coral cross sections, luminance profiles proved extremely useful in crossmatching growth patterns (Hendy et al. 2003). Analogous morphological attributes in geoduck might include prominent winter zones (annuli), uniquely transparent or opaque zones, or the presence of distinctive checks, all of which could facilitate crossdating if they occur synchronously in a given sample set. As crossdating is applied over a wider geographic range, spatial patterns in recruitment will be better resolved, as will the environmental drivers of recruitment. Higher ageing accuracy will also allow for better estimations of the coherence of geoduck recruitment and better comparisons with annually resolved environmental indices, such as sea surface temperatures, the El Niño Southern Oscillation, or the Pacific Decadal Oscillation. Given the success of crossdating in other marine and freshwater fish and shellfish species (Black et al. 2005; Helama et al. 2006), the approach will almost certainly have relevance for ageing beyond Pacific geoduck.

Acknowledgements

We thank the Sclerochronology Group of the 16th North American Dendroecology Fieldweek for developing the initial geoduck chronology used in this analysis. We also thank Rose Kormanyos for her help in completing the Tree Nob chronology through the Research Experience for Undergraduates Program at the Hatfield Marine Science Center. Special thanks also go to three anonymous reviewers as well as Rose Kormanyos and Matthew Stuckey for their comments, which greatly improved the quality of this manuscript.

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