CLIMATE AND FISHERIES IN THE PACIFIC NORTHWEST: HISTORICAL PERSPECTIVES FROM GEODUCKS AND EARLY EXPLORERS

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INTRODUCTION

There has been growing awareness among fisheries biologists in recent years that climate can be a key factor in structuring marine ecosystems. This has led to a renewed focus on questions that have been debated periodically for over a century: To what extent does climate determine the productivity of commercially important fish and shellfish populations? Are there predictable relationships between climate variables and species abundance? How can the effects of climate on marine ecosystems be disentangled from those imposed by human actions? (Ljungman 1880, Hjort 1914, Hubbs 1948, Francis and Hare 1994). Despite recent advances in understanding climate processes and fish population dynamics, the main obstacle to effectively answering any of these questions remains an acute lack of historical data. In the Pacific Northwest, continuous measurements of key climate variables such as sea surface temperature are rare, and extend at best to the 1920s and 1930s. Trawl surveys provide indices of fish abundance going back to the late 1940s for some areas, but with the exception of salmon, we know very little about which species flourished in these waters even as recently as the late 1800s (Miller, Moulton and Stadler 1991). There is increasing evidence, however, that the ocean has remained anything but constant since the first explorers arrived in the Pacific Northwest (Hubbs 1948, Baumgartner et al. 1992, Finney et al. 2000).

To explore linkages between climate and marine productivity requires longer historical datasets than are currently available. During the 20th century, climate over the Northeast Pacific Ocean shifted abruptly on at least three separate occasions (Mantua et al. 1997). With each shift specific groups of marine organisms found favorable conditions and grew in abundance while others underwent severe population declines. Between 1947 and 1976 conditions were favorable for Pacific Northwest salmon, but poor for Alaskan salmon. After 1976 the situation reversed. Record returns of salmon in Alaska coincided with disastrous returns to the south (Hare and Francis 1995, Mantua et al. 1997). King crab (*Paralithodes camtschaticus*) and Alaska pink shrimp (*Pandalus eous*) were abundant in the Gulf of Alaska prior to the 1976 climate shift, but nearly disappeared afterwards (Anderson and Piatt 1999). Quantifiable relationships between climate and marine productivity may exist, but before we can confidently predict which marine species will find favorable conditions as climatic conditions and ocean environments change, we will first need to reconstruct a history of the ocean and its inhabitants. Fitting time-series models to datasets that span only a few decades' results in too much uncertainty given that new climate regimes can persist for 20-30 years (Mantua et al. 1997).

Reconstructing a history of the Pacific Northwest marine environment requires data from a wide array of sources. This thesis is focused on two pieces of the puzzle: temperature reconstruction using growth rings in the shells of geoduck clams (*Panopea abrupta*), and historical research documenting periodic occurrences of Pacific sardine (*Sardinops sagax*) in the Pacific Northwest over the last two centuries.

Chapter 1 provides background information on bivalve shell growth and examines the various factors that may have been responsible for limiting accretion of shell material in geoduck clams at the primary study site near Protection Island in the Strait of Juan de Fuca. This chapter also describes an exploratory growth study that was conducted to determine if either temperature or food could be identified as the primary factor controlling geoduck shell growth.

Chapter 2 describes a new method to reconstruct sea-surface temperatures using annual ring widths recorded in the shells of geoduck clams. This study was conducted to determine if geoduck growth rings could be used as the marine equivalent of tree-rings to reconstruct climate. Previous studies have reconstructed Pacific Northwest temperatures from tree-rings, but no ocean temperature reconstructions for this region have yet been derived from organisms living in direct contact with the marine environment.

Chapter 3 integrates results from the geoduck derived climate reconstruction with new research intended to document historical sardine occurrences in Pacific Northwest waters. Early explorers and naturalists visiting the Pacific Northwest often wrote about the marine species they encountered, but no comprehensive effort has yet been made to compile and analyse this observational data. Since sardines appear to be a climate sensitive species, this research can serve as a source of historical context and, given enough supporting evidence, an independent source of verification for the climate reconstruction.

Chapter 1

DOES TEMPERATURE LIMIT THE GROWTH OF GEODUCK SHELLS NEAR PROTECTION ISLAND?

1.1 Introduction

There has been extensive research conducted over the years to determine how trees used for climate reconstruction respond to environmental stimulus. By contrast, very little is known about the factors responsible for geoduck shell growth. Trees are normally sampled from sites where a climate variable of interest, such as precipitation or temperature, is known to limit growth (Fritts 1976). Limiting factors for geoducks are also likely to be site specific, but identification of those factors is complicated by a lack of long-term data and by inter-relationships between variables. Bureau et al. (2002) found that growth of geoduck shells varied greatly between locations, and that shells at northern sites grew slower than at southern sites. Noakes and Campbell (1992) suggested that temperature could be a factor in determining growth variation of geoducks over time. Hoffman et al. (2000) found that geoduck growth was highest at sites with intermediate tidal flow and favourable substrate. Goodwin and Pease (1991) suggested that shell growth in geoducks was related to food abundance and temperature. They found that sites where tidal currents were moderate, temperatures were higher, and local productivity of phytoplankton was spread out over a longer time-period provided the best combination. Because geoducks are filter feeders that subsist primarily on phytoplankton (Goodwin and Pease 1991), areas with moderate currents were judged to be more likely to provide both suitable substrate and a continuous flow of food-rich currents.

Food abundance, temperature, or a combination of the two, may serve as limiting factors for shell growth in geoducks. McFarlane and Beamish (2001) suggested that in a climate-regime context the species composition of phytoplankton blooms should also be considered when modelling the response of marine species to varying environmental regimes. Geoducks may be sensitive to such shifts in species composition, but without long-term data to quantify how the ecology and dynamics of phytoplankton in this region has changed over time it is difficult to identify the immediate causes of variability in growth. Two approaches to the question of what governs geoduck shell growth were investigated in this study. The first was to conduct a controlled experiment in which juvenile geoducks were subjected to varying levels of food and temperature. The second was to assemble physical and biological data that could provide insight into how the marine environment around Protection Island may have changed in recent years. Though neither approach provided definitive answers, the results did suggest possible hypotheses.

1.2 Growth Study

To investigate whether temperature could be identified as a more important factor than food abundance in controlling geoduck growth, an exploratory study was conducted at the Point Whitney Shellfish Laboratory in Brinnon, Washington. The experiment subjected juvenile geoducks to four treatments with different combinations of food and temperature. Juvenile geoducks were used because their fast growth rates enabled the study to be conducted within the short time frame available. The experimental design was a full factorial set of treatments with two levels of food and temperature. Temperature levels were maintained at 15-16 ^{0}C and 10-11 ^{0}C. Food abundance was maintained at 45k and 15k cells/ml. The food consisted of three algal strains: *Chaetocerus mulleri*, and two varieties of *Thalasiosira pseudonana*. The treatment combinations were: high-temp/high-food, high-temp/low-food, low-temp/low-food, and low-temp/high-food. There were three replicate trays for each treatment and 100 geoducks in each tray. The trays were 30 cm. square, lined with a permeable fabric and filled with sand. The trays were submerged in a hatchery raceway where water flow could be carefully controlled.

The experiment was allowed to run for 30 days. Shell lengths of geoducks in each tray were measured before and after the experiment. Due to time constraints it was not practical to identify each geoduck individually and to pair the before and after measurements. Instead, the mean growth for each tray was calculated.

It was assumed that increases in shell length were related to increases in shell thickness. This assumption was based on the results of Valasquez (1992), who found that shell length was significantly correlated with shell thickness in juvenile geoducks. Velasquez (1992) also speculated that temperature might be a factor in increased calcification rates, leading to thicker shells in some of the juveniles. Storr et al. (1982) had previously found that calcification rates in the littleneck clam *Mercenaria mercenaria* were directly related to temperature between 4.4 ^{0}C and 13 ^{0}C. At temperatures above 15.6 ^{0}C calcification rates declined.

Food concentrations, flow rates, and temperatures were monitored throughout the experiment to assure consistency within treatments. None of the geoducks died over the course of the experiment. The clams displayed normal behaviour and quickly burrowed into the sand.

ANOVA results showed that the increase in shell length was detectable and that mean growth differed significantly between the treatments (p=0.0037). The high-temp/high-food trays showed consistently higher growth (fig. 1). There was no significant difference between the three remaining treatments however. Mean growth was 1.63 mm for the high-temp/high-food treatment and averaged 0.63 mm for the rest.

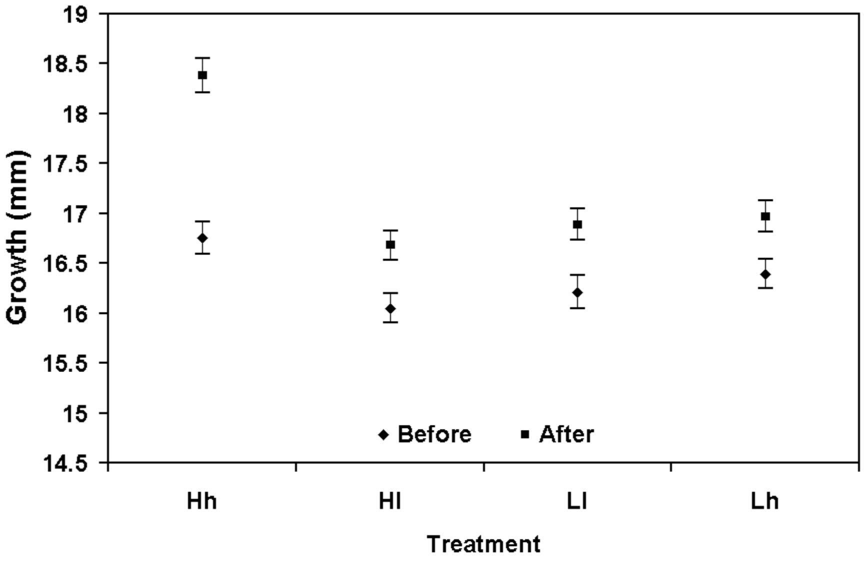

Fig. 1. Growth of juvenile geoducks exposed to four different treatment combinations of high and low temperature (H, L), and high and low food concentrations (h, l). The average lengths for each set of three replicates are plotted prior to the treatments (diamonds) and after the treatments (squares). Error bars represent 95% confidence intervals.

The low temperatures in the treatments were comparable to mean summer temperatures measured at the ADM002 sampling station by the Washington Dept. of Ecology (Newton et al 1998). The station is located 9 km. NE of Protection Island. Data on algal cell counts for the Protection Island area proved more difficult to obtain. It is possible, however, that food abundance in the treatments were considerably higher than what a geoduck would normally encounter at depth near Protection Island. Analysis of bottom water samples recently obtained from the Protection Island area suggests that cell counts seldom reach the levels maintained in the treatments.

Results of this study failed to indicate whether food or temperature was more important in controlling growth of the juvenile geoducks. A paired comparison of growth differences for each clam before and after the treatment may have provided clearer indications. Allowing the experiment to run longer, and including more levels of food and temperature may also have produced more definitive results. The experiment did show, however, that higher growth could be expected under conditions of increased temperature and algal abundance. Though a larger experiment would have been desirable, the design was largely opportunistic. Laboratory facilities were needed for other projects and the hatchery was ending production of geoduck seed.

1.3 Post-1989 Changes at Protection Island

A much larger, natural experiment has been underway at Protection Island over the last decade. Annual growth increments in geoduck shells sampled near Protection Island were unusually wide during the 1990s, and it was hoped that recent data sets might provide some indication of the factors responsible. Perhaps the most dramatic visible change has been the loss of nearby kelp beds. Extensive kelp forests along the north and northeast sides of the Island began disappearing in 1990 and were entirely gone by 1996 (Tom Mumford, Washington State Department of Natural Resources, cited by Nightingale 2000). The cause of this disappearance is unclear.

The Washington Dept. of Ecology has been monitoring water quality at the ADM002 site, near Protection Island, since 1988 (Newton et al. 1998). Sampling has been conducted on a near monthly basis since 1991. Light transmission at ADM002 decreased steadily during the 1990s. Decreased light transmission could be the result of either increased sediment load or increased phytoplankton in the water. Sea surface temperature (SST) measurements from both the Race Rocks Lighthouse near Victoria, British Columbia, and at ADM002 have trended upward since 1990. Unfortunately there were no usable data on phytoplankton abundance. Chlorophyll measurements were too sparse to be meaningful (Newton et al. 1998).

Additional quantitative data on physical and biological changes in the region come from Canadian research along the outer coast of Vancouver Island. Mackas et al. (2001) showed that the zooplankton community responded strongly to changing wind and current patterns after 1990. Species composition became more ‘southerly’ between 1990 and 1998 as northward moving winds and currents became more predominant. Copepods normally found off the central and northern California coast experienced order of magnitude increases in abundance, while more northerly species showed dramatic declines. Upwelling along Vancouver Island decreased during the same time period, and both nutrient concentrations in the upper ocean layers and total zooplankton biomass decreased (Mackas et al. 2001). Trends in spring temperature anomalies, the timing of zooplankton blooms, and data from seabird colonies also suggests that spring arrived earlier during the 1990s than during the two previous decades (Bertram et al. 2001). Piscivorous seabirds were found to breed earlier in the year as April temperatures became warmer, and the warming arrived earlier. Zooplankton productivity reached maximum values earlier in the year as well (Bertram et al. 2001).

Because productivity of zooplankton and of phytoplankton tends to be coupled (Strickland 1983) overall phytoplankton abundance may also have been lower along Vancouver Island during the 1990s. This is consistent with model results obtained by Robinson and Ware (1999) who estimated that production of diatoms along the southwestern coast of Vancouver Island declined by approximately one third between 1987 and 1998. Whether the same was true at the eastern end of the Juan de Fuca Strait at Protection Island is uncertain given the lack of local data. Due to the presence of sills and high currents, the water around Protection Island is generally cold, well mixed, and maintains high nutrient levels year around. Primary productivity is mostly light limited (Strickland 1983). If the physical changes that led to lower zooplankton productivity in offshore waters also reduced the abundance of phytoplankton around Protection Island, however, it would suggest that shell growth in geoducks is primarily driven by temperature. Years when both temperature and ocean productivity were high might have enhanced shell growth, but the main trends would have been driven by temperature. Zooplankton abundance in the Juan de Fuca eddy region, located just outside the western entrance to the Strait was below normal through most of the 1990s. The only significant exception was in 1995 (Mackas et al. 2001). Though shell growth increased dramatically throughout the period of low zooplankton abundance, the most exceptional increase in ring widths occurred during 1995 when both zooplankton productivity (Juan de Fuca eddy, fig 2) and local sea surface temperatures were above normal.

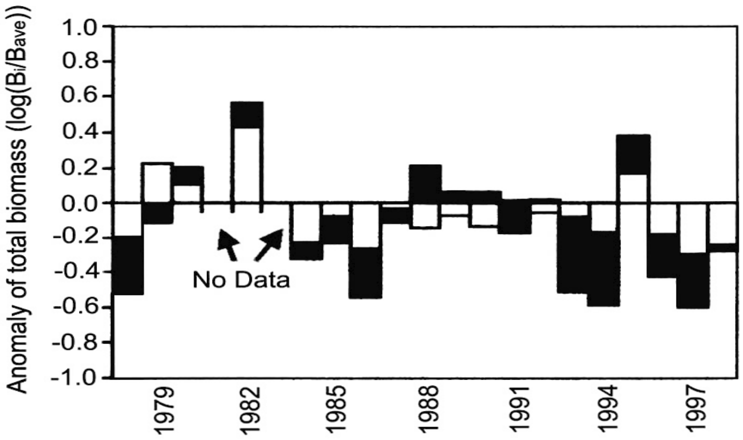

Fig 2. Annual anomalies of zooplankton biomass from the continental shelf and basin areas off the southwest coast of Vancouver Island (open bars), and in the Juan de Fuca eddy region (solid bars) located just outside the western entrance to the Strait of Juan de Fuca (Mackas et al. 2001).

1.4 Other Bivalve Growth Studies

Food abundance does not appear to be a prerequisite for shell growth in bivalves. Lewis and Cerrato (1997) found that shell growth in the eastern softshell clam *Mya arenaria* was positively correlated with oxygen consumption. Elevated temperatures led to higher metabolic activity and increased shell growth. Citing earlier studies (Pannella and MacClintock 1968, Thompson 1975), the authors claimed that shell growth in bivalves was never negative, and was detectable even in starving animals. Pannella and MacClintock (1968) found that shells of the littleneck clam *Mercenaria mercenaria* increased in thickness even after food had been withheld for several months and tissue growth was negative. Dramatically increased shell growth commonly occurred when bivalves were subjected to increased temperatures. Higher temperatures led to increased metabolic activity, greater oxygen consumption and rapid shell growth (Arnold and Holland 1976, Lewis and Cerrato 1997, Cerrato 2000).

The top panel in figure 3 (Cerrato 2000) indicates that shell growth was nearly a linear function of temperature in *Mya arenaria* within the range of 5-20° C. Tissue growth (middle panel) declined and became negative above 12° C, while oxygen consumption (bottom panel) increased, reaching an asymptote above 25° C. If shell growth in geoducks follows a similar pattern to that of the softshell clam *Mya arenaria* (Cerrato 2000)*,* or the littleneck clam *Mercenaria mercenaria* (Storr et al. 1982) then this would imply a linear or nearly linear dependence between temperature and shell accretion within the range of temperatures commonly encountered in the vicinity of Protection Island. Summer temperatures at the Protection Island sample site normally ranges from 10-12° C.

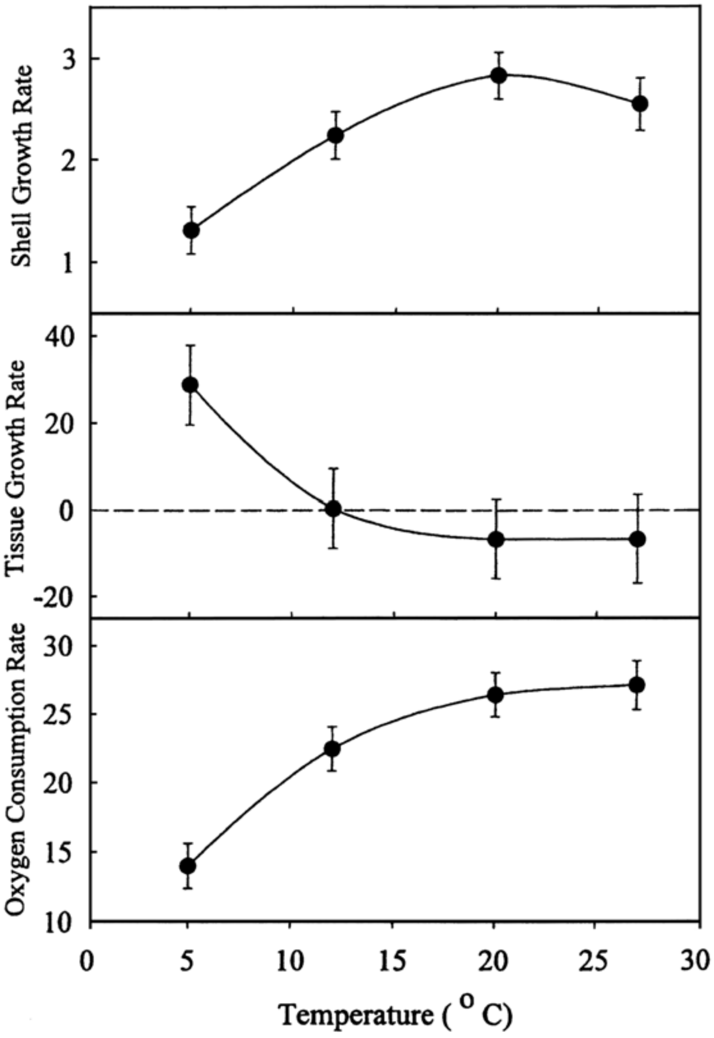

Fig 3. Shell growth rate (µm per tidal cycle), tissue growth rate (mg per tidal cycle), and oxygen consumption rate (mg O_2 per tidal cycle) vs. temperature for *Mya arenaria* held under semidiurnal conditions for 2-3 weeks on a fixed daily ration. Error bars represent 1 S.E. (data from Lewis and Cerrato 1997, figure from Cerrato 2000).

1.5 Conclusions

Though current data are insufficient to demonstrate exactly what has stimulated the unusually high shell growth at Protection Island evident in shell cross-sections during the 1990s, circumstantial evidence suggests that temperature is the primary factor. Evidence from the western end of the Juan de Fuca Strait suggests that food abundance may have declined during this period. Temperatures, however, increased both at the western end of the Straits and near Protection Island during the same period. If shell growth continues even when food is limited, then the increased sea-surface temperatures and earlier onset of spring (Bertram et al. 2001) recorded during the 1990s probably accounted for the difference. A reasonable working hypothesis is that this would have led to higher metabolic activity, a higher rate of shell accretion and more time during the year for shell accretion to occur.

Chapter 2

PACIFIC NORTHWEST CLIMATE RECONSTRUCTION USING GROWTH RINGS IN THE SHELLS OF GEODUCK CLAMS (*PANOPEA ABRUPTA* CONRAD, 1849)

2.1 Introduction

Bivalve shells have been investigated for a number of years as potential candidates for climate reconstruction. Just as annual growth rings in trees have proven to be exceptionally useful for recording terrestrial climate variability, growth rings and chemical properties contained within the shells of some bivalve species have proven to be sensitive recorders of environmental change in the marine realm. Unfortunately, several practical and technical difficulties have until recently limited their usefulness as climate proxies. Jones et al. (1989) found close correlation between growth rates of the littleneck clam *Mercenaria mercenaria* and mean annual water temperatures in Narragansett Bay, Rhode Island ($r = 0.88$, $P<0.01$). None of these clams exceeded 40 years in age, however, and would have been unsuitable for use as climate proxies. Exactly the opposite problem has prevented wider use of the ocean quahog, *Arctica islandica* for climate reconstruction. Despite great longevity, estimated as high as 221 years (Jones 1983), correlations between growth and climate variables have been disappointing (Thompson et al. 1980, Marchitto et al. 2000). Temperature reconstructions based on δO^{18} measurements in *Arctica islandica* shells have proven more successful, but isotopic analysis of the narrow growth bands is expensive, technically challenging, and only recently became possible with the development of computer guided micron-scale sampling tools, and accelerator mass spectroscopy (Weidman and Jones 1994).

Geoduck clams (*Panopea abrupta*) possess a combination of traits that make them good candidates for climate reconstruction while bypassing some of the limitations mentioned above. They are long-lived, they deposit annual growth bands in the shell each winter, shell growth in some areas appears to be correlated to temperature, and they normally add enough shell material each year that growth rings can be accurately measured using low to moderate magnification. (Shaul and Goodwin 1982, Noakes and Campbell 1992).

The maximum estimated age for geoducks was recently extended from 146 years (Harbo et al. 1983) to 168 years (Bureau et al. 2002). Canadian researchers conducted extensive geoduck aging between 1993 and 2000 to obtain growth parameters for stock assessment, and discovered that 100 year-old individuals were common at a number of sites along the coast of British Columbia. Several shells exceeded 160 years in age (Bureau et al. 2002).

Canadian researchers were also the first to suggest a potential link between climate and geoduck growth. Noakes and Campbell (1992) found evidence of a direct correlation between temperature and geoduck growth rates while studying the effects of environmental disturbance on growth of geoducks in Ladysmith Harbor on Vancouver Island, British Columbia. Shell accretion declined steeply after 1960, apparently in response to initiation of log storage in the harbor. For the period prior to 1960, however, their results indicated a direct relationship between growth increment widths and indices of air and sea-surface temperatures. They recommended further study to determine if geoduck shell growth could be used as a proxy to reconstruct climate.

Another advantage of geoducks is their relative abundance. They occur over a broad geographic area, from California to Alaska, and due to the existence of a large commercial fishery, shell samples can be obtained from a variety of sources and regions. They range in depth from intertidal to 100+ meters, and are abundant from Puget Sound to SE Alaska (Goodwin and Pease 1991). Geoducks attain a shell length of 1.5-2.0 mm after about a month of larval growth and then burrow into the substrate. They rapidly lose the ability to dig as they grow older and then become completely sedentary at a refuge depth of about one meter below the surface of the seabed (Goodwin and Pease 1991).

Shell growth is rapid during the first 10-15 years of life, but slows with age (Harbo et al. 1983). After age 15 the increase in shell length nearly ceases, though the shell continues to grow thicker and heavier at a gradually slowing rate (Harbo et al. 1983). The decline in shell accretion with age can be modeled using a modified negative exponential curve. Residuals about this curve can then be used to calculate indices that may reflect external factors controlling growth, such as temperature, food abundance or environmental disturbance (Noakes and Campbell 1992).

Accumulations of shells from dead geoducks can be found in many areas (Alex Bradbury, pers. comm.) and offer the potential of extending growth chronologies well beyond the age-span of any one individual using crossdating techniques. Crossdating is commonly used in tree-ring research to match distinctive patterns of growth in wood samples of known age with corresponding patterns of growth in older undated material. Given a sufficiently long period of overlapping growth the older material can then be accurately dated and added to the growth chronology (Cook and Kairiukstis 1990).

2.2 Materials

Geoduck shells were obtained from several locations in Puget Sound and the Strait of Juan de Fuca, but only one set of samples (from Protection Island in the Strait of Juan de Fuca) has currently been developed into a full growth chronology (fig 4). The Protection Island site was chosen for two reasons. 1) Growth rings from this site were more distinct than at other locations. 2) Alternating periods of wide and narrow growth bands were visible in cross-sections of the shell. This suggested that a common, possibly climate related forcing of shell growth was operating at the site. At other locations, such concurrence of growth patterns was less evident.

The Protection Island shells were obtained from three sources. The first set of 30 samples were surplus shells obtained from the Washington Department of Fish and Wildlife following a dive survey of the Protection Island tract conducted in September 1999. Over a hundred additional shells were obtained between May and September 2000 from members of the Jamestown S'Klallam tribe. These geoducks had been harvested for personal use, and the shells were kindly donated for this study. The remaining shells were obtained from the Washington Department of Health over the course of two years starting in April 2000. These shells were from geoducks that had been selected for toxicology testing. Several hundred shells were collected from the combined sources. Nearly all of the Protection Island geoducks were harvested within a depth range of 8-20 meters. In addition, Taylor Shellfish Farms, a commercial grower of geoducks located in South Puget Sound, donated five known age geoducks. These geoducks were grown from seed in Totten Inlet, and the shells were used to validate aging methods.

2.3 Methods

2.3.1 Sectioning Methods

The most reliable way to age geoducks is to section the shell and count internal growth lines. External growth lines become crowded and obscured after about age five as the shell approaches its maximum length and size (Shaul and Goodwin 1982). Because geoduck shells continue to grow heavier and thicker throughout life, internal growth lines can often be distinguished in even the oldest shells (Bureau et al. 2002).

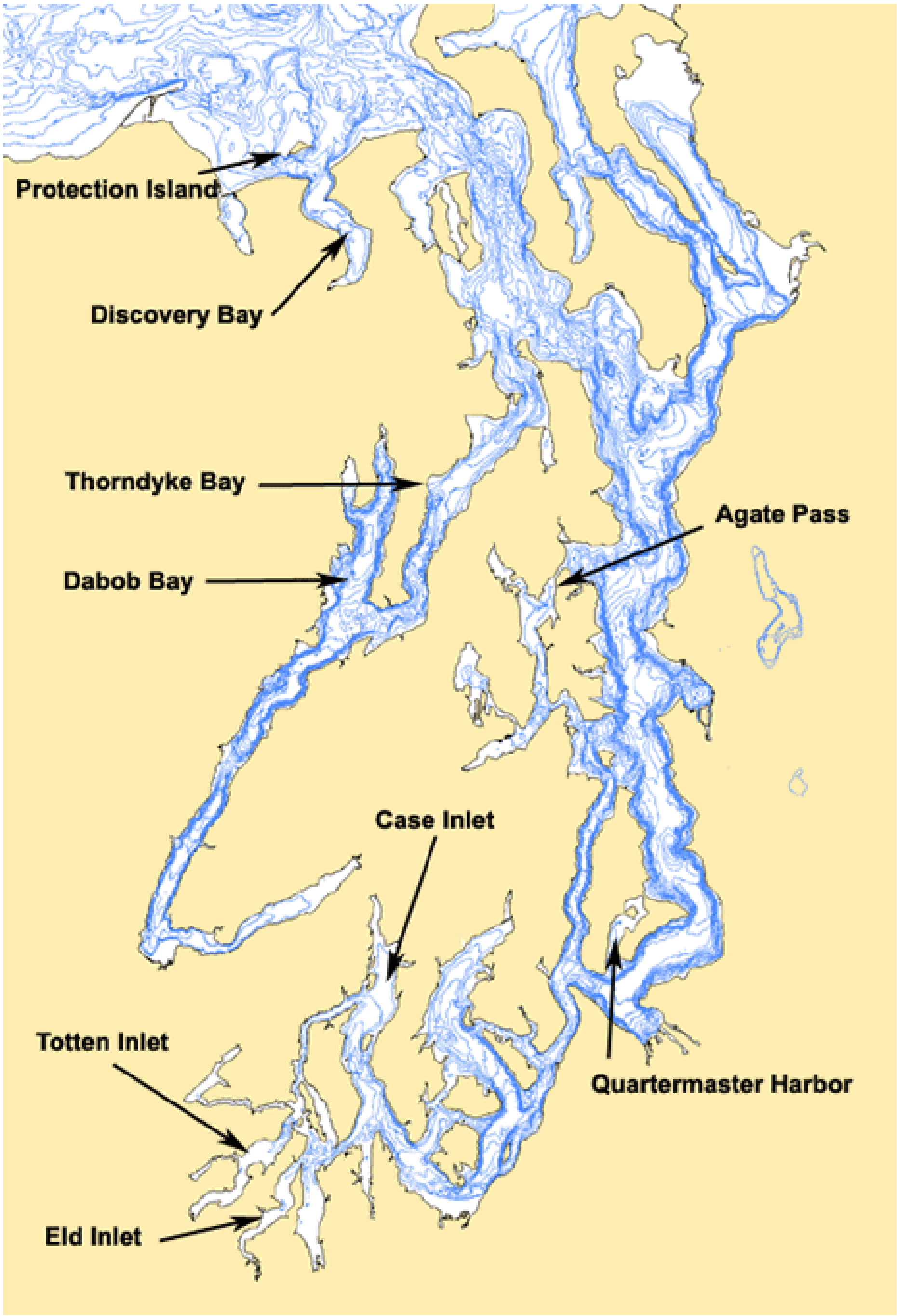

Fig. 4. Locations where geoduck samples were obtained in Puget Sound. Only the Protection Island site in the Strait of Juan de Fuca has currently been processed into a full chronology.

To reveal internal growth lines and prepare shells for aging, two methods were investigated; the acetate peel method and the thin-section method. While most geoduck aging studies to date have used the acetate peel method (Shaul and Goodwin 1982, Noakes and Campbell 1992, Bureau et al. 2002) the thin-section method was found to be more appropriate for this study. To make acetate peels, the cut and acid-etched surface of shell cross-sections are wetted in acetone, and thin sheets of acetate plastic film are applied. After the film dries it is peeled off, and an impression of the growth increments remains imprinted in the plastic (Shaul and Goodwin 1982). After several trials using this method, and after separate inspection of acetate peels made by Shaul and Goodwin (1982), it was determined that the acetate peel method would not provide the resolution needed to accurately measure the narrow growth increments found in many of the oldest geoducks. Although the thin-section method is more labor-intensive, it provides better resolution of ring structure, and allows for easier replication of age assessments. A series of thin sections can be cut along the length of the shell hinge. With more sections there is greater choice in selecting measurement locations and ample replication in ring counts to ensure that growth increments are accurately dated. This method was recently used to age Alaskan geoducks and was recommended by Peter Hagen of the Alaska Dept of Fish and Game (Peter Hagen, pers comm.).

2.3.2 Sample Preparation

To prepare geoduck shells for sectioning, a 5-cm. square segment of shell material encompassing the hinge plate area was removed from the right valve of each geoduck. If the right valve was missing, then the left valve was used. Shell segments were removed using a hand held circular cut-off tool with a standard 3-inch abrasive blade. Trimmed shell segments were then secured in the chuck of a low speed Struers Minitom saw equipped with a diamond blade. The chuck was custom built and padded to avoid shell breakage. At least three thin cross-sections were extracted from each shell. Thin-sections were obtained by making two parallel cuts perpendicular to the hinge axis, and approximately 0.35 mm. apart. The thin wafer that remained was then broken loose using light fingernail pressure. The first thin-section was extracted at the intersection of the umbo and the hinge plate—the location where shell growth originates (fig 5). The second section was cut halfway between the umbo and the widest part of the hinge plate, and the third section was cut at the widest part of the hinge. The hinge is the preferred location to section because it is normally the thickest part of the shell; it has the best resolution of growth lines; it includes the earliest years of growth, and is well protected from erosion.

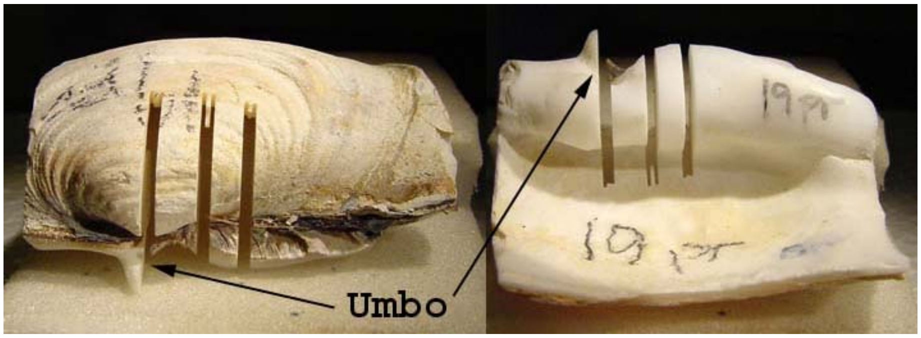

Fig 5. Locations along the shell hinge where thin-sections were cut and extracted. The image on the left shows the outside of the shell. The tooth is located near the origin of growth, also known as the umbo. The image on the right is an inside view of the same shell segment and shows the hinge.

Each group of three thin-sections was cleaned, dried, and mounted together on standard microscope slides using Cytoseal adhesive. After curing for 2 days, the sections were sanded and polished using a Struers variable speed grinding and polishing machine. Section thickness was reduced by wet grinding and polishing until all growth rings were visible using transmitted light microscopy. The final polishing was done using 2400 grit SiC discs. To enhance resolution of the growth rings under magnification, sections were etched in 1% HCl for approximately 60 seconds.

Etching created a distinct topography on section surfaces, causing magnified growth rings to appear as ridges of coarser, more crystalline material. This suggested that Scanning Electron Microscopy (SEM) would be a good alternative method to view and digitize growth rings. Sample preparation for the SEM consisted of cutting slightly thicker 1-mm. thick shell sections, in the same manner as above, grinding, polishing and removing all surface debris, etching, and finally mounting the sections on aluminum stubs specially manufactured for SEM use.

The most challenging part of this process was devising a method for removing the surface debris generated by grinding and polishing. SEM images were unusable unless the surfaces were completely free of all accumulated foreign material. The solution was to exploit the adhesive properties of acetate peels to pull debris off of section surfaces. As each peel was removed, surface debris would cling to the peel rather than the section. By looking at each peel under magnification it was possible to see if areas of debris were still present. After all debris was removed the sections were mounted and sputter coated in preparation for the SEM.

2.3.3 Digital Image Acquisition

Following sample preparation, a series of images were digitized from each section using either the SEM or a transmitted light microscope. Images were captured along a straight transect from the origin of growth to the outer edge. Transects were chosen to intersect growth increments as close as possible to perpendicular, and to avoid areas where rings were difficult to distinguish. Because growth increments were spaced anywhere from 700 μm. apart at age 1 to an average of 30 μm. apart after age 50, images along transects were digitized at three different magnifications. When images were digitized on the light microscope, 2.5x, 10x and 16x objectives were used in combination with a 10x eyepiece. SEM magnifications were similar, but less restricted to specific settings. The SEM used was a JEOL 840A. The best images were obtained with the accelerating voltage set at 2kv, the probe current at $1x10^{-10}$ amps, a bias of 2, and the working distance at 44mm. After images were captured, montages of transect images were assembled using Adobe Photoshop. Each transect montage would normally be composed of 20-30 individual images. Montages were filtered and enhanced using the 'levels' and 'unsharp mask' features in Photoshop.

Both the SEM and transmitted light microscope produced good images if the geoduck shell contained clear, well-defined growth rings. Though it was hoped that the SEM would be a good alternative method to acquire images of ring structure in geoducks that were difficult to see using light microscopy, this was seldom the case. If anything, SEM images tended to be harder to read when the underlying section contained poorly defined ring structure. Since the time required to prepare samples and acquire images was much greater for the SEM, this method was only used in special situations, such as when unusually opaque sections could not be polished thin enough to allow light transmission without destroying the sample.

2.3.4 Crossdating and Measuring

Fritts (1976) referred to crossdating as “perhaps the most crucial procedure in tree-ring analysis.” To reconstruct climate, dates assigned to growth rings must be exact. If any doubt exists then the growth series in question should not be used. Crossdating assured that each geoduck growth ring measurement was correctly dated, that false or missing annuli were properly identified, and that years producing unusual ring characteristics, such as abnormally narrow or wide growth rings, matched exactly from section to section. Geoduck growth series were rejected if the usable segment length for crossdating was too short (< 40 years), if ring counts did not agree among replicate sections, or if crossdating with other geoduck growth series was inconclusive.

Only geoducks with well-defined growth rings were selected for measuring and crossdating. Prior to measuring, transect images were displayed on a flat-screen computer monitor and growth rings were annotated with a thin line to mark the upper edge of the ring (fig. 6). This corresponded to the period right before growth commenced in late winter. Measurements were taken at an angle perpendicular to each growth ring axis using the Photoshop measuring tool. Distances were measured in pixels and calibrated to metric units using digitized micrometer images taken at identical settings.

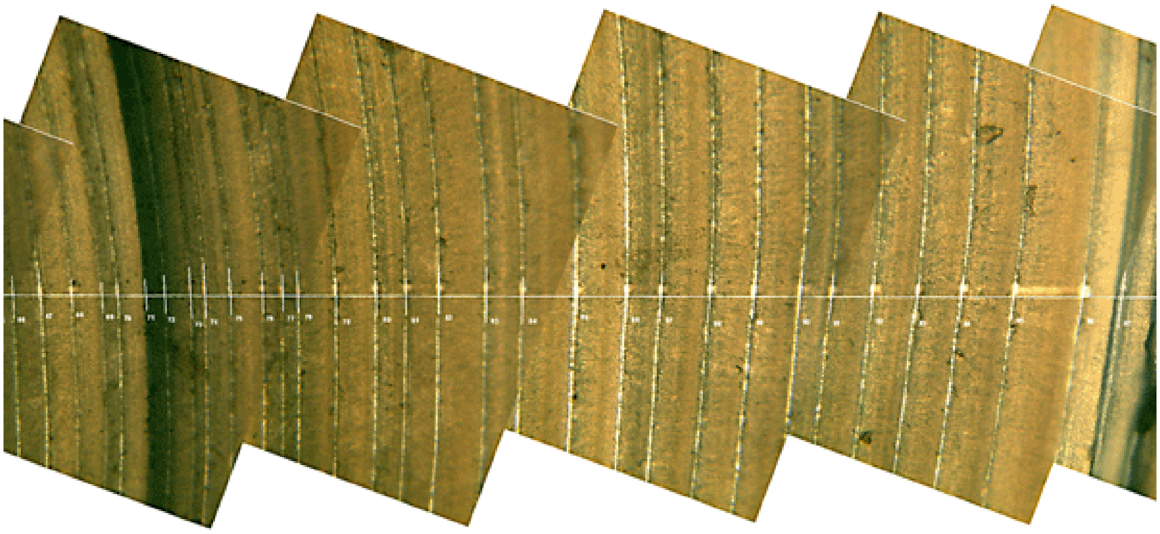

Fig 6. Digital image of a one magnified thin-section from a Protection Island geoduck shell. This montage spans from 1966-1997 and shows the straight transect used to define measurement locations. The widest growth ring on the right was deposited in 1995. The series of narrow rings on the left side of the image were deposited during the late 1960s and early 1970s.

Not all ring widths could be measured. In some cases the first few years of growth were missed because the straight axis used to standardize measurement locations could not follow the natural curvature in the section. On other occasions rings would be so poorly defined or compressed, especially in the very old geoducks, that only the earlier portion of the series was usable.

2.3.5 Validation of Aging Methods

Shaul and Goodwin (1982) conducted a series of experiments that verified internal growth lines in geoduck shells were deposited annually, normally between November and February each year. As an added check on these results, and to validate aging methods, five known age shells were obtained from Taylor Shellfish Farms, located in South Puget Sound. These shells had been grown from seed and were 4 ½ years old when harvested in December of 1998. Thin-sections were prepared for each shell following the methods described above and ages were determined by counting the growth rings.

Another way to validate aging methods was suggested by the results of Noakes and Campbell (1992) who found that geoduck shell growth appeared to be directly related to air and sea-surface temperatures. Given the *a priori* expectation that annual variability in growth should track annual changes in temperature, tests of correlations between growth and temperature were conducted to provide additional evidence that the geoducks were correctly aged. To test if the hypothesized relationships were significant, Pearson correlation coefficients were computed between the final geoduck growth chronology and temperature records from the Protection Island vicinity.

2.3.6 Standardization and Chronology Statistics

Before growth data from individual sections could be averaged together into a mean site chronology, the measurement series needed to be standardized. Standardization removes age-related growth trends and allows measurements to be converted to dimensionless indices. Several standardization methods were investigated, but only two yielded acceptable results. The best fit to measured growth series was obtained by using a modified exponential curve (Fritts 1976) of the form:

$$y_t = ae^{-bt} + k$$

where y_t is the expected growth in year t, e is the base of the natural log, and a, b, and k are parameters calculated for each growth curve. Standardized growth indices for each shell section were computed by dividing the actual growth in year t by the expected growth in year t (Fritts 1976). This also ensured that the variance was similar over the entire series. Indices were then averaged together using a biweight robust mean (Mosteller and Tukey, 1977 [cited in Cook and Kairiukstis 1990]) to construct the final site chronology.

For comparison purposes, a second chronology was constructed using the 'regional curve standardization' (RCS) method (Cook et al. 1995). Measurement series from all the sections were aligned by age and a modified exponential curve was fitted to the combined growth data. The premise behind the RCS method is that year-to-year variations in ring-widths will be averaged out by the age-based alignment, thereby allowing one empirical growth curve to be constructed that can be used to standardize all ring width series from a given site. This preserves low-frequency variability that might otherwise be lost using other methods (Cook et al. 1995). The RCS method appeared to be an attractive alternative given that the individual geoduck growth series were already fairly short in length.

The desire to preserve low-frequency variability was one reason that splines were rejected as a detrending option. The other reason was that they produced poor fits to all but a few of the ring-width series. Geoduck growth curves tend to be fairly stiff at either end. They have a sharp bend at around 15-30 years of age, as shell accretion rapidly diminishes, and after age 50 the growth curve becomes essentially linear (fig.7). Splines tended to be either too stiff to fit the curved portion, or so flexible that they removed much of the interdecadal variance.

Correlation methods recommended and described by Cook and Kairiukstis (1990) were used to assess the statistical quality of the resulting Protection Island chronology. The Expressed Population Signal (EPS) was calculated to quantify the chronology signal as a fraction of the total variance. The subsample signal strength statistic (SSS), a measure of the extent to which a *subsample* of growth indices approximates the signal in a full chronology, was calculated to determine the statistically acceptable length of the mean chronology (Cook and Kairiukstis 1990).

2.3.7 Calibration and Verification of Regression Models

Given the *a priori* expectation that geoduck growth was directly related to sea-surface temperature records (Noakes and Campbell 1992), a regression model was calibrated to reconstruct Race Rocks sea-surface temperatures. This was the longest continuous SST record available locally. Sea-surface temperature (SST) data were obtained from Fisheries and Oceans, Canada, for the Race Rocks (1921-1999), and Entrance Island (1937-1999) lighthouse stations, both located in British Columbia. Since there was strong correlation between the two SST records ($R^2 = 0.51$), the Entrance Island data served as an independent proxy for Race Rocks to validate the reconstruction.

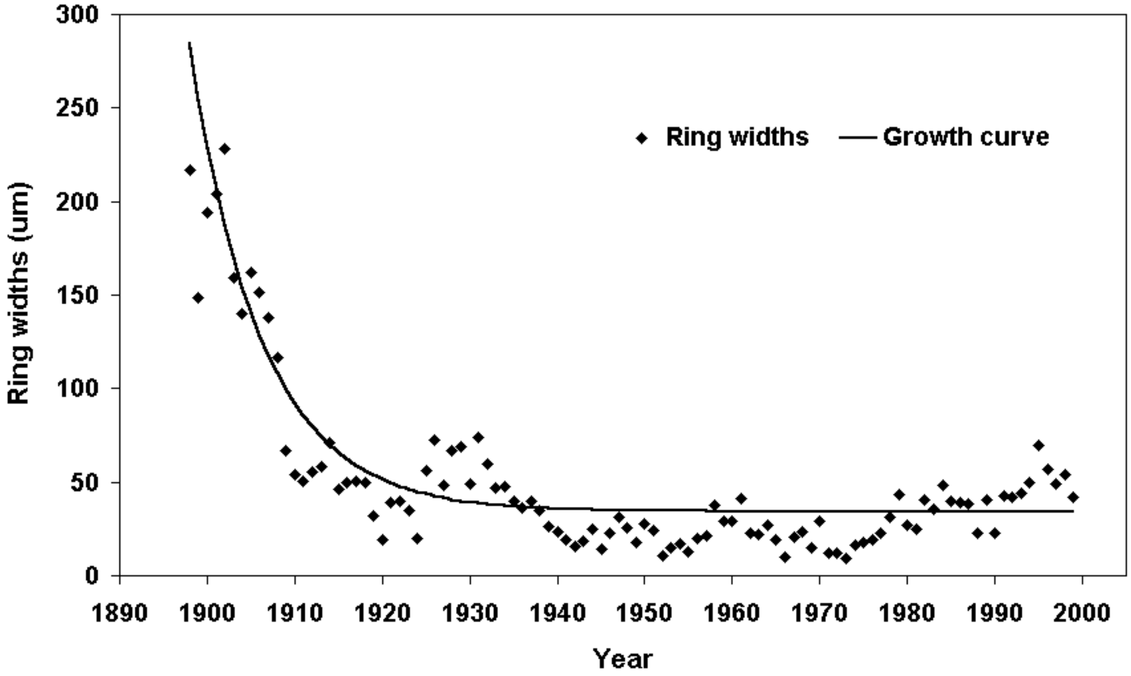

Fig. 7. Example of a modified exponential growth curve fitted to a ring width measurement series. In this example, widths were measured from age 8 (1898) to age 109 (1999). The exponential curve was best able to follow both the sharp curvature as growth slowed from the teens to middle age, and the nearly linear trend that followed.

An additional model was calibrated to reconstruct the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997). Though the PDO index is based on gridded temperature data over the entire Pacific Ocean north of 20 degrees latitude, there is evidence that continuous coastal sea-surface temperature records, even from a single location, can contain a significant amount of the variability seen in time-series covering much wider areas of the Pacific (McGowan et al. 1998). This suggested that a PDO reconstruction could be meaningful despite the fact that only one growth chronology from one site was used as a predictor. To reconstruct the PDO index, only the period from 1925-98 was used for calibrating the model. Biondi et al. (2001) suggested that undersampling of sea-surface temperature data prior to 1925 accounted for the disagreement they noted between tree-ring data and the instrumental PDO during the 1900-25 period. This also meant that the data withheld from model calibration could be used to validate the PDO reconstruction and test if the geoduck growth series diverged in a similar fashion to tree-rings between 1900-25.

Regression models were calibrated using the SAS AUTOREG procedure (SAS Institute 1993). Because Durbin-Watson tests indicated that correction for autocorrelation was needed, the ordinary least squares regression model was augmented with an autoregressive model to account for persistence in the errors. Autoregressive parameters were selected using a stepwise backwards elimination method, and the final model was estimated using the exact maximum likelihood option. The general form of the model is:

$$y_t = x_t'\beta + v_t$$

$$v_t = -\alpha_1 \nu_{t-1} - \ldots - \alpha_m \nu_{t-m} + \varepsilon_t$$

where:

$y_t =$ the response values

$x_t =$ the predictor values

$\beta =$ the structural parameters

$\alpha =$ the autocorrelation parameters

$\varepsilon_t =$ the normally distributed errors with a mean of 0 and variance σ^2

The stepwise selection method was programmed to estimate autoregressive error models out to 5 lags, but in each case only the first autoregressive parameter proved to be significant. Durbin-Watson tests were conducted following calibration of the models to verify that the remaining errors were independent after inclusion of the lag-one parameter.

One advantage of autoregressive models is that both the contemporary annual signal in the growth rings as well as the persistence structure contributes to the final regression model. Guiot (1990) found that such models often performed better in terms of validation statistics than other methods, but that they were most suitable in cases where only a small pool of predictors was used in the calibration. This concern did not apply to the geoduck-based reconstructions since only one predictor chronology was available.

Reconstructions were verified using the "leave-one-out" cross validation method (Blasing et al. 1981). This method was chosen instead of a split-sample validation scheme because the geoduck chronology was relatively short in length. Given the low-frequency variability inherent in time-series such as the PDO, a split-sample validation scheme may have been biased if the portions used for calibration and validation came primarily from different phases of the oscillation. The reduction of error statistic (RE), the sign test, and the correlation coefficient were computed to validate the reconstructions. These statistics are fully described in Cook and Kairiukstis (1990). Comparison of the reconstructed values with independent proxies for the instrumental predictand series served as an additional check to validate the reconstructions.

2.3.8 Spectral and Wavelet Analysis

Spectral and wavelet analysis was used to identify any significant periodicities in the reconstructed temperature series, and to determine how these periodicities were distributed through time. Wavelet analysis was conducted using software provided by Torrence and Compo (1998). Significance levels were set at 95%, and tests were conducted against a red-noise (lag 1 autocorrelation) background spectrum. Spectral analysis was conducted using the smoothed periodogram method (Bloomfield 2000). Significance tests were again set at the 95% level and tested against a highly smoothed version of the underlying spectrum. The null hypothesis was that the estimated spectrum was not significantly different than the highly smoothed spectrum (Bloomfield 2000). This method was used by Meko et al. (1985), and has been included in a set of Matlab tools available from the University of Arizona Tree-ring Lab, in Tucson, Arizona (http://tree.ltrr.arizona.edu/~dmeko/geos595e.html).

2.4 Results and Discussion

2.4.1 Validation of Aging Methods

Validation tests confirmed that one growth increment was deposited in the known age geoduck shells each year, and that the predicted correlation between annual growth and annual temperature for the Protection Island shells was significant. The geoducks obtained from Taylor Shellfish

Farms were 4½ years old when harvested and all sections displayed 4 distinct growth rings (fig.8). Two of the shells had disturbances checks that appeared to have been deposited early during the first year of growth; possibly at the time of planting, but these checks were missing in other replicate sections from the same shell, and were not visible in the remaining known age shells. Significance tests of correlations between the Protection Island growth chronology and local temperature records were all significant at the 99% level. The nearest air temperature records were from Port Townsend (17 km. east, r=0.57) and Olga Bay (56 km NNE, r=0.52). Air temperature data were obtained from the U.S. Historical Climatology Network (Karl et al. 1990). The nearest sea-surface temperature record was from Race Rocks Lighthouse (46 km NNW, r=0.66). Sample sizes were adjusted for autocorrelation in each of the three tests.

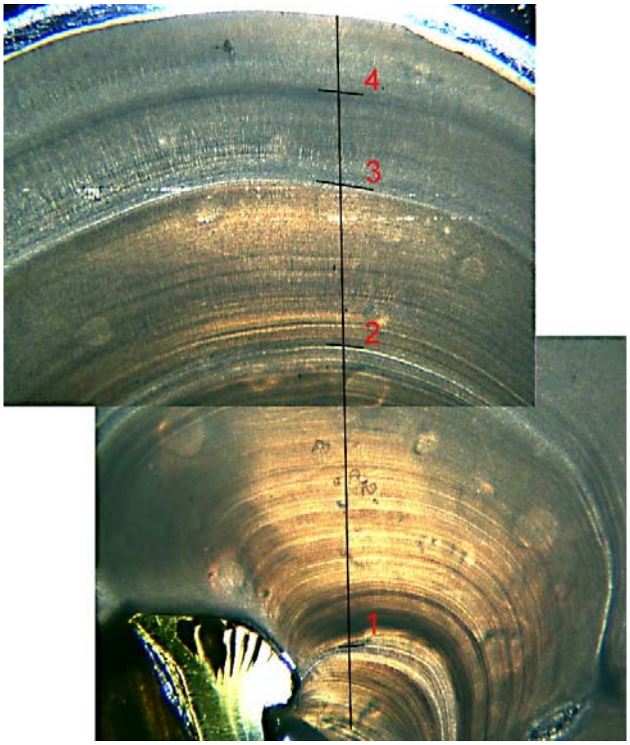

Fig. 8. Magnified section of known age geoduck obtained from Taylor Shellfish Farms. The geoducks were grown from seed and harvested at 4½ years of age. Four distinct growth increments are visible in the section. Annuli tend to be more translucent than surrounding shell material.

Evidence from the validation tests, combined with the mark-recapture results of Shaul and Goodwin (1982) left little doubt that growth rings in the Protection Island shells were deposited annually. Simple ring counts, however, would not have been sufficient to provide the absolute age assessments required for climate reconstruction. Without replication and careful crossdating, misidentification of growth rings would inevitably have led to inaccurate dating results. Though there were relatively few instances of misleading growth rings at the Protection Island site, this was not true for shell sections obtained from other sites. Samples obtained from Dabob Bay in Hood Canal, and from Case Inlet in South Puget Sound often displayed a bewildering array of indistinct and obscure growth rings that were impossible to crossdate. Results of this study illustrated the need for careful site selection. Shells that are to be used for climate reconstruction need to come from sites where distinct growth rings are produced, and where growth can be linked to climate variables of interest.

2.4.2 Factors Limiting Growth

The correlations between temperature and growth noted by Noakes and Campbell (1982) at Ladysmith Harbor, and in this study, at Protection Island, suggested that temperature, or another variable closely related to temperature, was the main factor limiting shell growth. This was not the case at all sites however. Crossdating patterns evident in Protection Island samples were conspicuously absent in shells obtained from Dungeness Bay, only one nautical mile to the south. Neither the narrow series of growth rings that characterized Protection Island shells during the early 1970s and 1990s, nor the exceptionally wide rings in 1995-98 could be detected in the Dungeness Bay samples. Hoffman et al. (2000) calculated growth parameters for geoducks at 11 sites in Puget Sound and the Strait of Juan de Fuca, and found that the slowest growing geoducks (as measured by the von Bertalanffy growth parameter *k*) were from Dallas Bank (*k*=0.1131), located on the north side of Protection Island. The fastest growth was found at Fishermans Point in Dabob Bay (k=0.2353) and Hunter Point in South Puget Sound (k=0.2283). Geoducks may be less sensitive to climatic factors at fast growth sites such as these where water temperatures are warmer and phytoplankton is more abundant (Goodwin and Pease 1991, Strickland 1983).

2.4.3 Comparison of Standardization Methods

The two detrending methods (RCS and negative exponential) used to construct Protection Island growth chronologies produced similar results for most years, but diverged noticeably during the period from 1865-1892. During this period the RCS method produced estimates of geoduck growth that were considerably higher than those produced by the negative exponential method, as illustrated in (Fig 9).

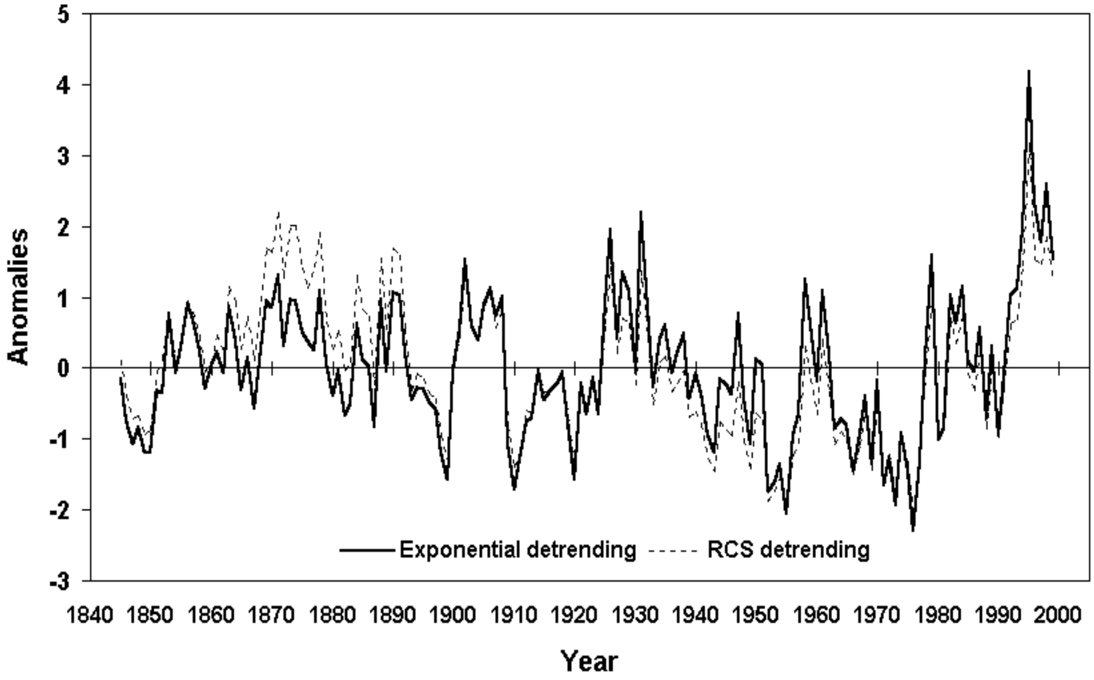

Fig. 9. Comparison of growth chronologies obtained using two different detrending methods: the regional curve standardization method (dashed line), and the modified exponential curve (solid line). Results diverged considerably between 1865 and 1892.

The difference in results may have been an artifact of lower sample size in the early part of the chronology, combined with a more moderate decline in the growth curves of two of the oldest shells during their first 50 years of growth. If this is true then the divergence should be resolved in favor of one or the other detrending methods as new geoduck series are added to the earliest portion of the chronology in the future. Though the RCS method may have preserved more of the low frequency variance, the chronology produced by the negative exponential method was chosen as a basis for the temperature reconstructions because it provided a better fit to the growth curves and produced slightly better correlations with local temperature records.

2.4.4 Chronology Statistics

Statistical tests indicated that the Protection Island chronology was suitable to be used for climate reconstruction and that the usable portion ranged from 1877 to 1998. The Expressed Population Signal (EPS) served as a gauge of statistical quality. Cook and Kairiukstis (1990) recommended an EPS value of 0.85 as a cutoff point below which chronologies should not be used. The Protection Island EPS was 0.95. Similarly, a Subsample Signal Strength (SSS) value of 0.85 was recommended as the lowest acceptable value for a *subsample* of indices within the chronology. A 0.85 cutoff value implied that any additional reconstruction error due to low sample size would be limited to 15% (Cook and Kairiukstis 1990). For the Protection Island site, this meant that portions of the chronology based on measurements from less than 6 shells should not be used for climate reconstruction (fig 10). To calibrate the regression models only the statistically acceptable portion from 1877 to 1998 was used.

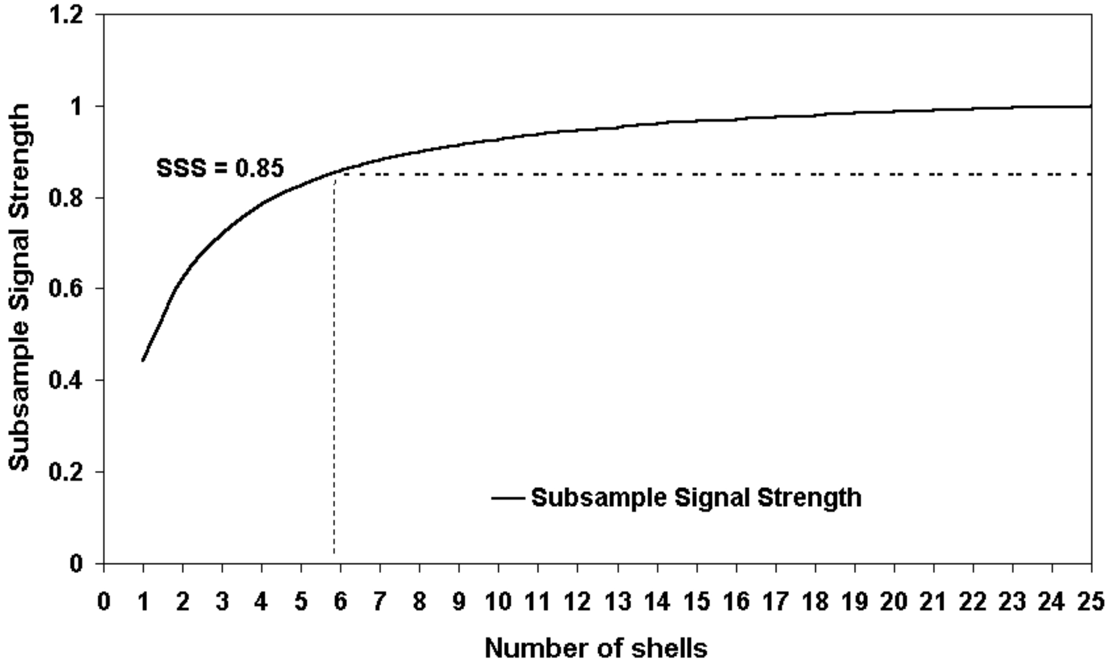

Fig. 10. Subsample signal strength (solid line) as a function of the number of shells in the chronology. To achieve an SSS value of 0.85 requires using at least six shells. Portions of the chronology with fewer shells should not be used to reconstruct climate.

2.4.5 Temperature Reconstructions

Analysis of the Protection Island chronology relative to seasonal temperature data showed that local March through October temperature records provided the strongest correlations with geoduck growth. This was consistent with the results of Shaul and Goodwin (1982) who found that the annual growth line was deposited during winter, from November through February, and that negligible shell growth occurred during this time. Though geoduck growth correlated strongest with growing season temperatures when local records were tested, more distant temperature series, including the PDO, correlated slightly better with annual values. This may have been because the annual averages were better suited to capture and integrate any differences in the timing or magnitude of distant versus local temperature signals.

To investigate whether the use of lagged predictors was justified an impulse response function for the relationship between Race Rocks SST and the growth series was computed. For this analysis the input SST series was prewhitened using an autoregressive AR10 model and the same model was used to filter the output growth series. Fig 11 indicates that the only significant relationship between the variables was at lag 0.

Cross-correlations between the same two variables prewhitened by separate AR1 models supported this conclusion. When autocorrelation was removed from both the Race Rocks series and the Protection Island growth series no positive lags were found to be significant at the 2 standard error level recommended by Meko (1981). There was a significant correlation at lag 0 (r=0.45), and one moderately significant negative correlation at lag –3 (r=0.31). Negative lag 3 models were difficult to justify from a physical standpoint, however, and were not considered for the reconstructions. As a result of this analysis it was determined that no added information would be gained by including lagged predictors. Any direct or indirect effects of temperature on growth were determined to be primarily contemporaneous. Consequently, the regression model to estimate Race Rocks temperatures was calibrated using Mar-Oct data, and the PDO reconstruction was calibrated using annual data.

Because the Protection Island geoducks were sampled less than 46 km. from the Race Rocks lighthouse, the Race Rocks SST reconstruction was expected to provide the strongest calibration statistics. Results showed this to be true (table 1). The estimated Mar-Oct Race Rocks SST series explained 57% of the variance in the instrumental record, while the reconstructed PDO index explained 36%. Durbin-Watson tests showed that no significant autocorrelation remained in the residuals after the lag-one autoregressive term was included in the models.

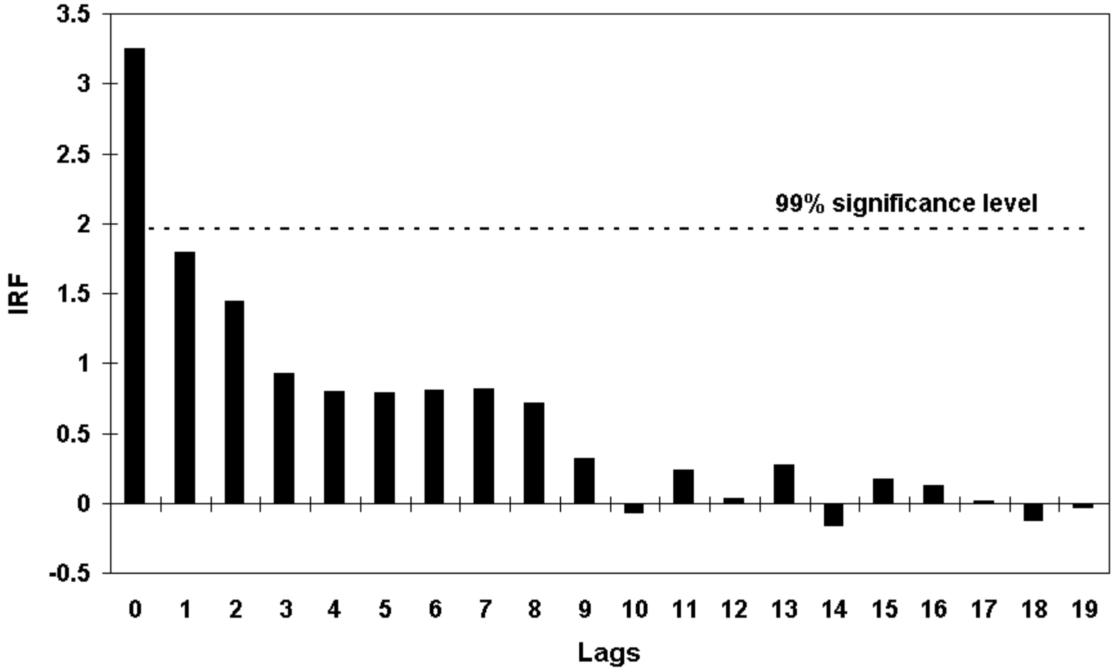

Fig 11. The estimated impulse response function plotted out to 19 lags. The bars indicate the output growth response as a function of an input temperature pulse. The significant weight at lag 0, and the lack of any significant weights at other lags indicated that most of the growth response was restricted to the current year. Significance was tested at the 99% level.

Validation tests also produced encouraging results (table 1). Correlations between the calibration and validation series were significant at the 99% level. The significance tests were adjusted for decreased sample size due to autocorrelation. The reduction of error statistic (*RE*) indicated that both of the regression models exhibited good predictive skill. The *RE* statistic is comparable to the calibration R^2. Any *RE* value above 0 indicates that the model has some skill, and values close to the calibration R^2 provide strong evidence of validation (Cook and Kairiukstis 1990). Differences between the calibration R^2 and the validation *RE* statistic were small in both cases. The Sign Test confirmed that the signs of positive and negative departures from the mean of the validation series were in agreement with the instrumental series more often than would be expected by chance (Cook and Kairiukstis 1990). Probabilities were less than 0.001 in both instances.

Table 1. Calibration and validation statistics for the geoduck ring-width reconstructions of Race Rocks SST and the PDO index. The r^2 adj. statistic is the coefficient of determination adjusted for loss of degrees of freedom. P r-1 is the Durbin-Watson test probability for no remaining autocorrelation in the residuals. Pearson correlation coefficients were calculated to test the relationship between the validation series and the instrumental series. The reduction of error (RE), and sign tests are diagnostics for the skill of the reconstruction.

		Calibration		Validation		
Reconstruction	**Period**	**r^2 adj**	**P r-1**	**Pearson corr.**	**RE**	**Sign Test**
Race Rocks SST	1921-1998	0.57	0.71	0.75 ($p<0.01$)	0.55	+62,-16 ($p< 0.001$)
PDO Index	1925-1998	0.36	0.37	0.59 ($p<0.01$)	0.35	+58,-16 ($p<0.001$)

Correlation tests between the reconstructed series and independent instrument-measured temperature records (again adjusted for decreased sample size) provided additional evidence of validation. The Race Rocks predicted series was significantly correlated with the Entrance Island series at the 99% level (table 2). It was also significantly correlated with the Scripps Pier SST series from La Jolla, California. This was consistent with the results of McGowan et al. (1998) who found that the Scripps data contained much of the variability present in North Pacific temperature records. The authors noted strong positive correlations between the Scripps series and gridded temperature data stretching from the Gulf of Alaska to Baja California, and similarly strong but negative correlations with temperatures in the Central Gyre.

Table 2. Correlation tests between temperature series reconstructed from geoduck ring widths and independent instrument-measured temperature records. Correlation tests were adjusted for decreased sample size due to autocorrelation.

Reconstructed series	Instrumental Series	Period	r-value	Significance
Race Rocks SST	Entrance Island SST	1937-1998	0.61	$p < 0.01$
Race Rocks SST	Scripps Pier SST	1917-1998	0.58	$p < 0.01$
PDO Index	Pre-1925 PDO	1900-1924	0.57	$p < 0.05$

A striking example of this long-distance coherence in Pacific Ocean temperature records was the fact that the correlation between the estimated Race Rocks SST and the measured Scripps

SST was nearly identical to the correlation between the estimated Race Rocks SST and measured Entrance Island SST, although the latter two stations were located less than 111 km. apart. When the same period of years was compared (1937-98) the correlation between Race Rocks and Scripps was actually stronger (r = 0.63) than between Race Rocks and Entrance Island (r = 0.61). This may have been because the Protection Island area is influenced to a greater extent by oceanic conditions than Entrance Island in the Strait of Georgia. The flow of water coming into the Strait of Juan de Fuca tends to stay close to the southern shore, largely as a result of the Coriolus effect, and pulses of oceanic water, driven east by weather events, often reach the Protection Island area (Harold Mofjeld, pers comm.). The reconstructed and instrumental series are plotted in figs. 12 and 13.

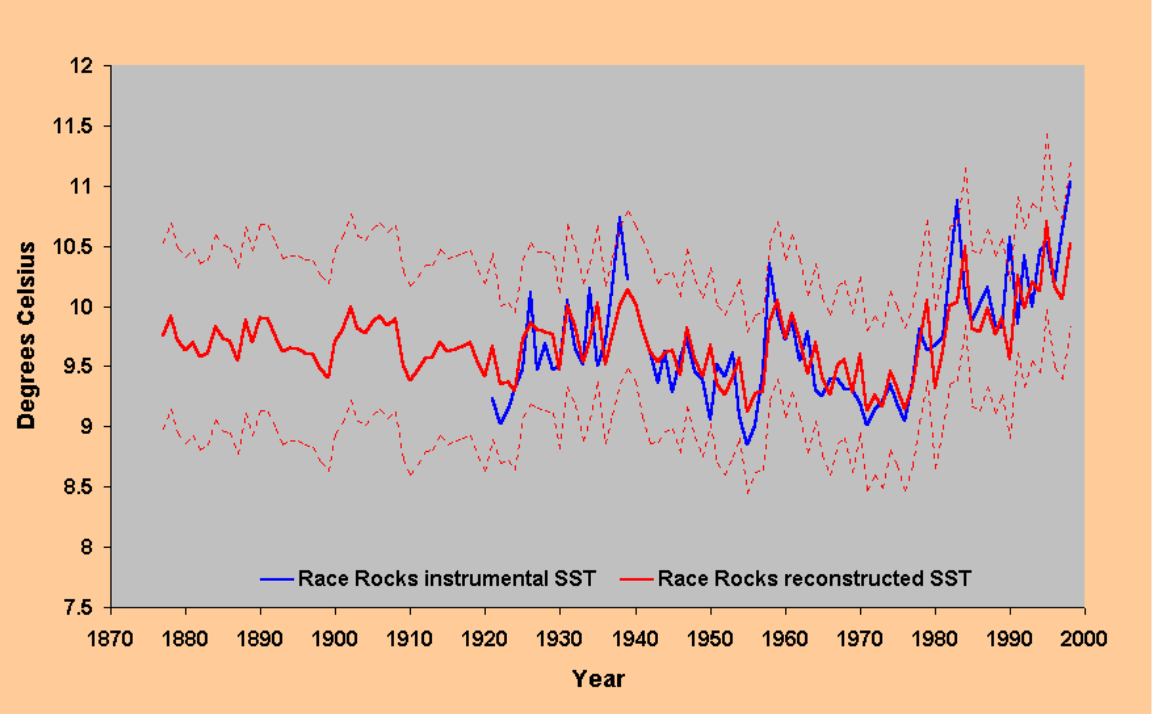

Fig. 12. Reconstructed Mar-Oct Race Rocks sea-surface temperatures (solid red line) and instrumental Mar-Oct Race Rocks SST (solid blue line), plotted with confidence intervals for the reconstructed series (dashed red line). Units are in degrees Celsius. Data are missing in the instrumental series for the years 1940 and 1941.

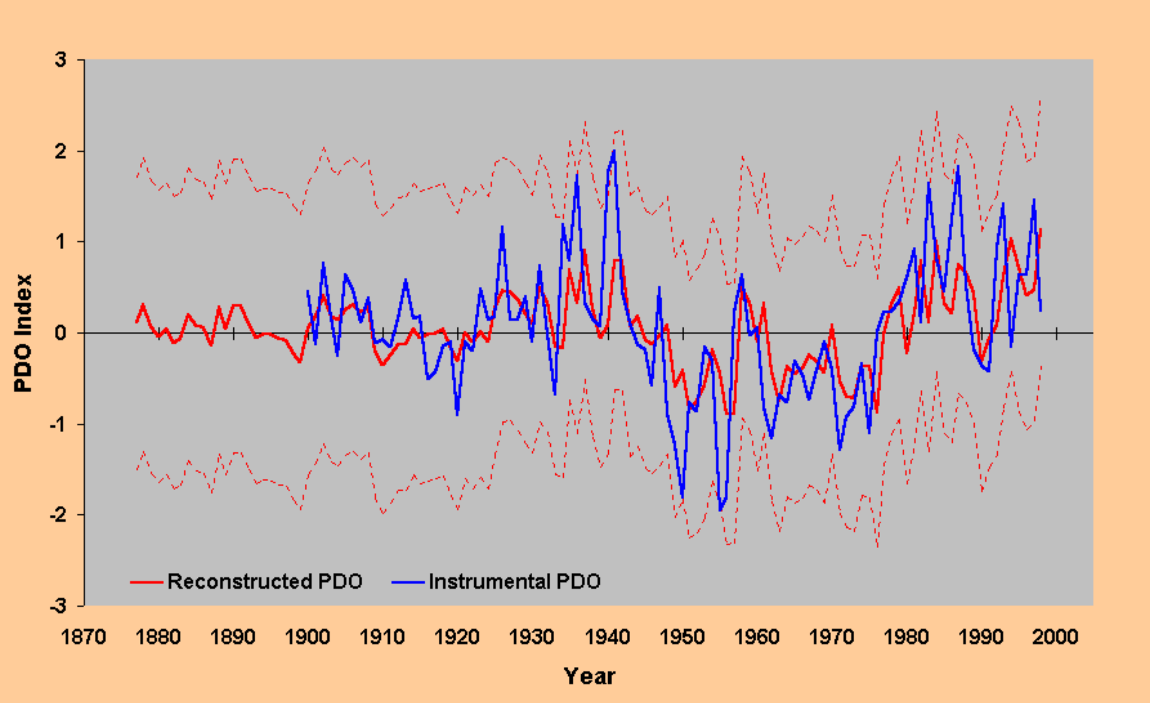

Fig. 13. Reconstructed PDO (solid red line) and instrumental PDO (solid blue line), plotted with upper and lower confidence intervals for the reconstructed PDO (dashed red line).

The only independent series available to test the PDO reconstruction was the short segment from 1900-24 that was not used in calibrating the regression model. This segment correlated with the annual predicted PDO at r=0.57, and was significant at the 95% level. By comparison, the Biondi et al. (2001) PDO reconstruction, based primarily on a network of precipitation sensitive tree-ring chronologies from Southern and Baja California, showed a slight negative correlation during the same 1900-24 period. Biondi et al. (2001) argued that the instrumental PDO during these years might not have reflected true conditions because insufficient SST data were available prior to 1925 to compose the index. Another possibility is that the relationship between the PDO and precipitation in the arid region where the trees were sampled was not the same between 1900 and 1920 as it was during other periods. El Niño events were more frequent and intense during the first decade of the 20th century than during the period from 1920 to 1960 (Mann et al. 1998, Urban et al. 2000) and may have altered “normal” patterns of rainfall. When the 1900-24 segment was excluded the Biondi et al. (2001) reconstruction explained a greater proportion of the instrumental PDO variance than the one derived from geoducks. The differences in results illustrate the need for developing the broadest possible collections of proxy climate records, including new sources of data from marine species such as geoducks. Using multi-proxy networks to reconstruct climate, and including chronologies from a variety of regions may provide the best opportunity for producing robust reconstructions that remain stable over extended time-periods.

The final parameters estimated by the autoregressive models to reconstruct the Race Rocks SST series and the PDO index were as follows:

Race Rocks: $\hat{y}_t = 8.9658 + .7355*\text{growth}_t + \nu_t$
$\nu_t = .5459\nu_{t-1} + \varepsilon_t$
Estimated variance (ε_t) = 0.10032

PDO Index: $\hat{y}_t = 0.521 + .2341*\text{growth}_t + \nu_t$
$\nu_t = .4744\nu_{t-1} + \varepsilon_t$
Estimated variance (ε_t) = 0.48311

One concern when using autoregressive models to predict climate is the possibility that standard errors and confidence intervals may be underestimated (Don Percival, pers comm., SAS Institute 1993). This is particularly true when the estimated autocorrelation is high and the sample size is small (SAS Institute 1993). As a cautionary check on the results above, reconstructions were performed using an alternative method recommended by Meko (1981) for cases where autocorrelation in predictor or predictand variables are a concern. This method is an adaptation of Box-Jenkins time-series analysis applied to tree-ring data, and assumes a stochastic relationship between climate and tree-growth. To apply this method, autocorrelation was first removed from both the geoduck growth series and the SST series by fitting separate AR1 models to each series and then computing a prewhitened residual series. The residuals were then used to construct an ordinary least squares regression model. Parameters from the regression model were used to calculate a reconstructed SST series, and finally, autocorrelation was built back into the reconstruction by using the original AR coefficients calculated for the SST series. Fig 14 shows the estimates of Race Rocks SST produced by each method for the period 1879 to 1920. Confidence bands (indicated by dashed lines) were calculated using the $\hat{y}_t \pm 2*\text{RMSE}_v$ formula recommended by Weisberg (1985). The root mean square error of validation ($RMSE_v$) was derived from the cross-validation tests. The solid green lines above and below the dashed confidence intervals are the prediction intervals computed by the SAS AUTOREG procedure (SAS Institute 1993). To provide an accurate comparison of the two regression methods, missing values in the Race Rocks series for 1940 and 1941 were calculated by linear regression using monthly means from the Entrance Island SST record. Both models were then calibrated using the same 1922-1998 data for geoduck growth and SST.

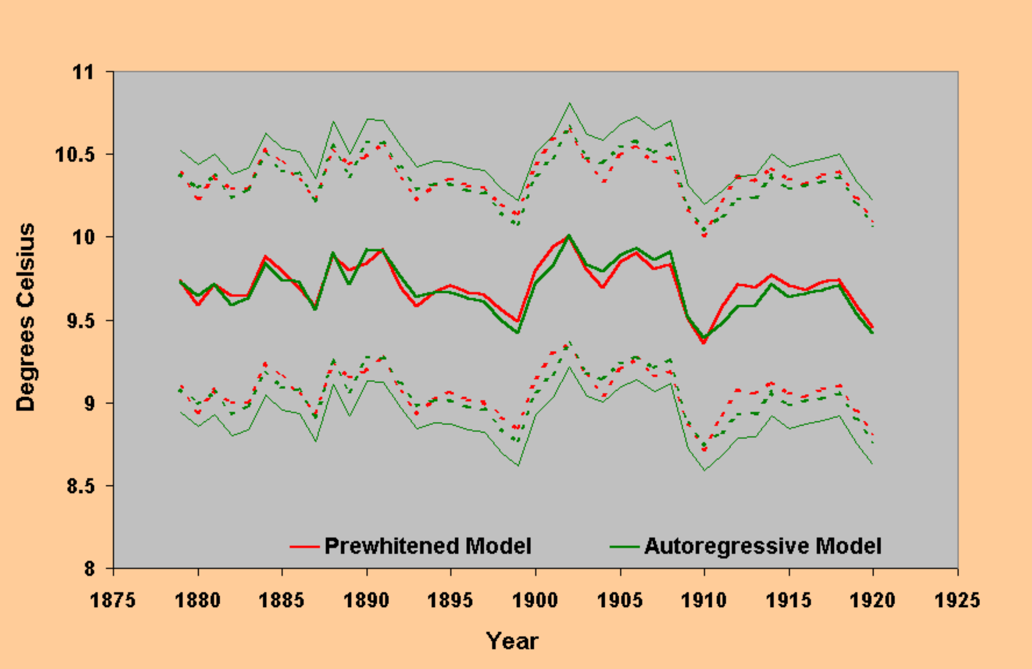

Fig 14. Comparison of reconstruction methods using the autoregressive model (in green) and the prewhitened model (in red) plotted with confidence intervals (dashed lines). Confidence bands were computed using the $\hat{y}_t \pm 2*RMSE_v$ formula recommended by Weisberg (1985). The solid outer green lines are the prediction intervals generated by the SAS AUTOREG procedure.

Results suggested that both the autoregressive and prewhitened models produced very similar estimates of Race Rocks SST's prior to the instrumental period, and that the confidence intervals produced by the SAS AUTOREG procedure were relatively conservative. Correlation tests between reconstructed Race Rocks SST's and Port Townsend air temperatures from 1896-1920 indicated that the prewhitened model produced a slightly better fit to instrument measured values (r=0.42) than the autoregressive model (r=0.38). Future climate reconstructions using geoduck growth measurements will hopefully be based on chronologies from more than one site, and may require the use of more complex regression models. For the purposes of this study, however, the autoregressive model appeared to provide a relatively simple and reliable means to estimate SST given that only one relatively short growth chronology was available.

2.4.6 Spectral and Wavelet Analysis

Spectral and wavelet analysis was used to identify dominant frequencies in the reconstructed Race Rocks series, and to determine how these frequencies were distributed through time. Significance tests for the wavelet analysis were set at the 95% level. Results indicated that nearly all the interannual variability occurred after 1930 (fig 15). The Race Rocks reconstruction exhibited decadal-scale variability (10-20 years) over most of the series, but no periods greater than 6 years approached significance.

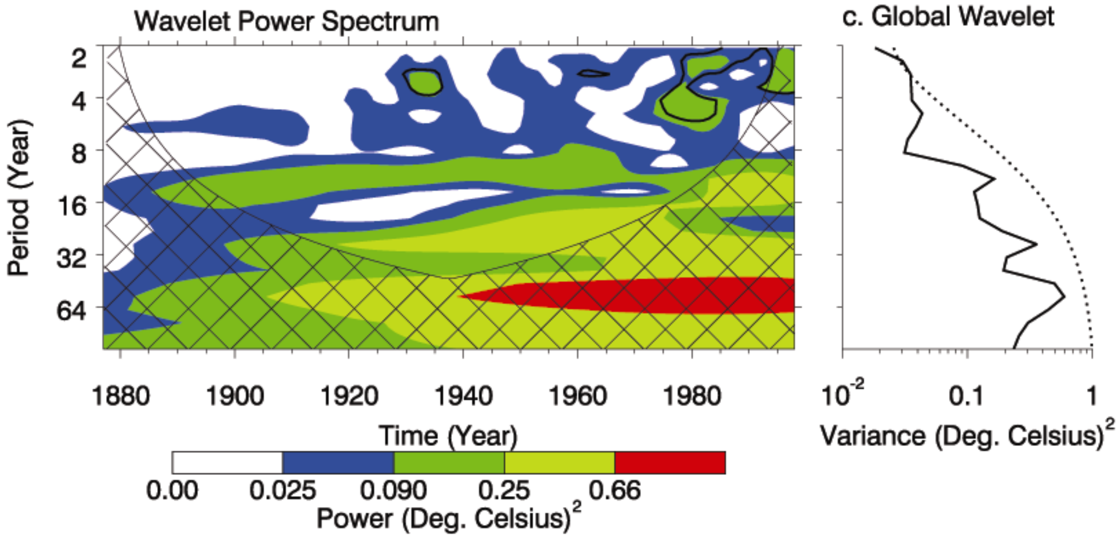

Fig. 15. Wavelet power spectrum and global wavelet spectrum for the Race Rocks SST reconstruction. Black contours indicate areas of significant power at the 95% confidence level relative to a red noise (autoregressive lag 1) background spectrum. The cross-hatched region indicates where zero-padding has reduced the variance. The global wavelet indicates marginally significant peaks at 2-3 year periods over the full chronology (Torrence and Compo 1998).

Spectral analysis, using the smoothed periodogram method (Bloomfield 2000), identified peaks in the reconstructed Race Rocks series at 42, 11.5 and 5 year periods, but none of these peaks were significant at the 95% level. Figure 16 shows the frequency spectrum along with the null continuum (in green). The null continuum is a highly smoothed version of the periodogram that was used to test specific peaks for significance. Because this method requires separate tests of each spectral frequency of interest using confidence bands around each peak, only the spectrum and the null continuum were displayed to avoid clutter. The absence of any significant peaks may have been due to the short length of the predicted SST series, and the prevalence of low frequency variance. The reconstructed SST series would probably need to be considerably longer before meaningful inferences could be made regarding dominant periodicities.

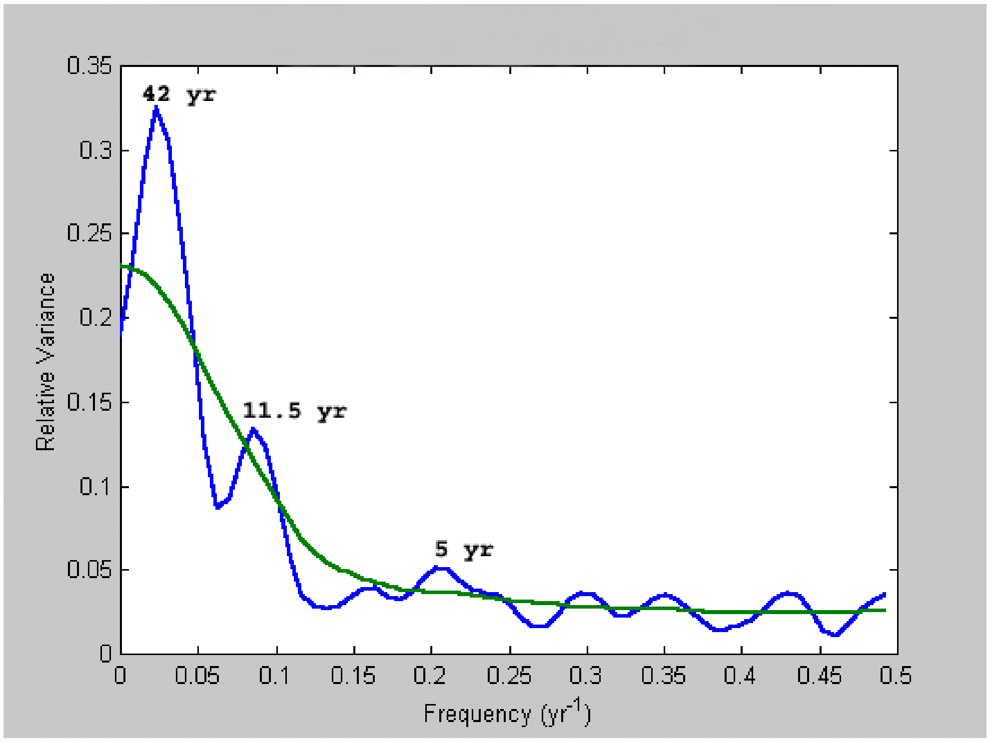

Fig 16. Smoothed periodogram of the reconstructed Race Rocks SST series (green line) and the null continuum (a highly smoothed version of the periodogram) used to test specific peaks for significance. None of the peaks identified in the Race Rocks series were significant at the 95% level.

2.4.7 Conclusions

The primary objectives of this study were to determine if geoduck clams could be used as proxies to reconstruct historical climate records, and to develop the methods needed to accomplish this task. In this regard all objectives were met. Chronology and validation statistics showed that geoduck growth rings were comparable to high quality tree-rings in their ability to record climate variability. Geoducks also provide an added dimension in that they live in direct contact with the ocean environment. Tree rings have proven to be exceptionally useful in recording terrestrial climate variability, and the results of this study indicate that geoduck shells provide an opportunity to reconstruct ocean temperatures with the same annual resolution and comparable statistical quality.

The main limitation of this study was that the statistically acceptable portion of the geoduck growth chronology was only 122 years long. This was used to extend the Race Rocks SST record by 44 years, but it falls far short of the century to millennium-scale reconstructions produced from tree rings. There is no practical reason, however, to prevent geoduck growth chronologies from being extended several hundred years further back in time. Results of this study showed that crossdating techniques commonly used in tree-ring research can also be used to accurately date floating time-series of geoduck growth measurements. Now that a reliable master chronology has been constructed for Protection Island, extending the growth record is limited only by our ability to find geoducks with enough years of overlapping growth. Accumulations of dead geoduck shells are commonly encountered by geoduck divers, and could provide an abundance of shell material to build extended chronologies. Geoduck shells may also exist in shell middens at archeological sites. This study has shown that geoducks can be useful tools in the ongoing effort to define historical climate variability. The next step will be to build on these early results to extend the geoduck growth network both in time and space.

CHAPTER 3

TEMPERATURE, GEODUCK SHELL GROWTH, AND PERIODIC OCCURRENCES OF SARDINES IN THE PACIFIC NORTHWEST

3.1 Introduction

When growth measurements from trees or geoducks are used to reconstruct climate, it is assumed that the relationships being modeled have stayed constant through time, and that the environmental conditions which prevailed during the calibration period were similar to conditions in the past (Fritts 1976). Though circumstances vary, this may not always be a safe assumption. Growth measurements often span several centuries, but the instrumental data used to calibrate climate models rarely exceed one century. Briffa et al. (1998) found that the relationship between temperature and growth of European trees had changed dramatically since about 1850. They noted that trees had become more sensitive to temperature since the onset of industrialization, and that the increase in growth witnessed since the mid 1800s may have been caused by CO_2 and nitrate fertilization. They suggested that widespread impacts from human activities raised serious questions about the reliability of European temperature records hindcast more than one or two centuries into the past.

The long-term reliability of the geoduck growth response is also open to question. Though shell accretion is clearly *related* to temperature at Protection Island, there is no solid evidence that the relationship between temperature and growth has remained constant over time. It is possible that temperature is only indirectly linked to growth, and that broader ecological changes associated with climate regime shifts are the primary factors.

To investigate the stability of the relationship between shell growth and temperature in greater detail it would be useful to compare the growth response of geoducks to historical data on the abundance or growth of other temperature sensitive marine organisms. If predictive relationships could be established between temperature and some measure of biological response in other species, it might also allow the reliability of geoduck-derived reconstructions to be tested. This would be especially persuasive if the biological response in these other species could be reasonably attributed to the direct influence of temperature. To provide useful comparisons, such records would need to match the length of the geoduck growth series. Unfortunately no long-term quantitative records of this kind have been located. Instead, the following sections focus on a qualitative reconstruction of Pacific sardine (*Sardinops sagax*) occurrences in the Pacific Northwest.

Sardines appear to be useful indicators of ocean climate for two reasons: 1, Sardine abundance trends have been linked to low frequency climate variability in the Pacific Ocean (Chavez et al. 2003), and 2, large-scale northward migrations of sardines into Pacific Northwest waters tend to occur during periods when ocean temperatures are above normal (Schweigert 1988). If sardines can serve as biological indicators of ocean temperature in the Pacific Northwest, then a history of sardine occurrences at this northern limit of the Pacific sardine range might also provide an independent source of empirical evidence to gauge the reliability of geoduck derived climate reconstructions for years prior to the calibration period.

3.2 Sardines as Climate Indicators

The Pacific sardine is one of several climate-sensitive fish species known to inhabit Pacific Northwest waters. Synchronous changes in the abundance of sardines off Japan, California and Chile during the 20th century were related to changes in ocean temperatures (Omori and Kawasaki 1995) and primary production (Chavez et al. 2003). Similar long-term oscillations in the abundance of European sardines were also attributed to climatic influences (Alheit and Hagen 1997). Periodic range expansions of sardines from spawning grounds off Southern California to the Pacific Northwest (PNW) have been associated with climate regime-shifts and the ecological impacts attending such shifts (McFarlane and Beamish 2001). Schweigert (1988) suggested that northward migrations of adult sardines during summer were dependent on water temperatures and food abundance, primarily of copepods and diatoms. Chavez et al. (2003) characterized the climate regime shifts that have impacted the Pacific Ocean during the 20^{th} century as ‘sardine periods’ and ‘anchovy periods’. The ‘sardine’ periods coincided with positive (warm) phases of the PDO and higher global air temperatures, the ‘anchovy’ periods were associated with the negative (cool) phases of the PDO and cooler global air temperatures.

If the presence or absence of sardines in the PNW can serve as an indicator of temperature regimes and ocean productivity then we would expect to see some agreement between historical sardine observations and reconstructed temperature indices. To test this theory, historical occurrences of sardines in the PNW were reconstructed from the reports of early explorers and naturalists. Condensed versions of this research were published in Field et al. (2001) and Francis et al. 2001).

3.3 Sardine Periods in the Pacific Northwest

Periodic northward range expansions of sardines probably occurred long before the first explorers arrived on the Pacific Coast. According to oral histories, Native Americans fished for sardines long before the European immigrants (Forester and Forester 1975), and scale deposits in sediments off Santa Barbara, California indicate that the southern sardine population collapsed and recovered in dramatic fashion on at least nine separate occasions over the last 1700 years (Baumgartner et al. 1992). It was not until the late 18th century, however, that written eyewitness accounts became available to date historical occurrences.

Three PNW sardine periods can be documented from historical accounts. Between 1786 and 1792 a number of observers, including trained naturalists, described Native American fisheries for sardines along the PNW coast. The first accounts were by fur traders. Alexander Walker described sardines as being “in the greatest plenty” on the West Coast of Vancouver Island in 1786, along with herring and anchovy (Walker 1982). In 1788 John Meares wrote a detailed description of the methods used by Vancouver Island natives to catch sardines and mentioned that "…the herrings as well as the sardines, frequent the coast in vast shoals…The sardine resembles that of Portugal, and is very delicious: they are taken here by the people in prodigious quantities” (Meares 1790). A 1792 entry in the logbook of John Hoskins noted "The herrins and sardines as is usual with those fish come in at stated seasons in large shoals…" (Howay 1990). The sardine reports by fur traders were corroborated by several additional accounts from Spanish explorers in the same area between 1791 and 1792 (Wagner 1982). The first scientific observations were by the Spanish naturalist Jose Mariano Mozino, who spent five months in Nootka Sound on Vancouver Island in 1792, and inventoried sardines as among the fishes to be found locally (Mozino 1991). Evidence from these reports suggest that sardines were not only *present* during the late 1780s and early 1790s, but also *abundant*.

By the beginning of the 19th century, however, sardines were no longer being noted in the journals of explorers, naturalists or traders, despite more extensive exploration and trade activity following the Lewis and Clark expedition. Scientific investigations of fisheries resources, including those conducted by the Wilkes expedition in 1841 (Wilkes 1852), the Pacific railroad surveys of 1853-57 (Suckley 1860), and the investigations of the U.S. Fish Commission in 1880-81 (Goode 1884), all failed to locate sardines in PNW waters.

Apparently, sardines did not return to the PNW until the late 1880's. The U S Fish Commission reported in 1884 that sardines ranged from Chile to Cape Mendocino, California (Goode 1884). By 1887-89, however, this range had expanded to Puget Sound and the Strait of Juan de Fuca. In 1888, sardines were found in Puget Sound during "the warmer part of the season, and are taken with herring and other species for market" (Collins 1892). Landings of fresh sardines were reported to be a modest 60,000 lbs that year (Collins 1892). The Canadian Dept. of Fisheries reported that sardines were abundant along the Canadian side of the Strait of Juan de Fuca in 1887 (Ware 1999). The same report series failed to mention sardines again until 1917, suggesting that sardines were only sporadically present in Canadian waters over the intervening twenty years (Ware 1999). We do know they were not entirely absent because two sardines were captured in the Staits of Georgia near Nanaimo in January of 1900 (Clemens and Wilby 1981). There were reports of sardines from Puget Sound as well. Jordan (1895) reported that there were "large numbers" of sardines in Puget Sound in 1895, and in 1902 they were described as "abundant" (Kershaw 1902). Sardine abundance increased dramatically in the early 1920s, and by mid-decade sardines constituted the largest commercial fishery in British Columbia. The fishery lasted for thirty years, ending abruptly in 1947, when stocks once again collapsed (McFarlane and Beamish 2001).

Sardines did not return to British Columbia until 1992 (Hargreaves et al. 1994). A commercial fishery was initiated in 1995, and combined catches from commercial and research fisheries increased from 200 tons to 1500 tons by 1999 (McFarlane and Beamish 2001). In 1998 sardines were captured as far north as SE Alaska (Wing et al. 2000), and spawning was observed along the west coast of Vancouver Island (McFarlane and Beamish 2001).

3.4 Sardine Abundance and Climate Indices

Explanations for why sardines appeared in the PNW when they did are not readily apparent. McFarlane and Beamish (2001) suggested that ecological changes associated with climate-regime shifts were the main driving force, and that expansions were only indirectly linked to temperature. They hypothesized that climate-driven shifts in the abundance of phytoplankton species required by juvenile sardines were probably the most important factor. The authors did not find any significant linear relationships between local SST records and sardine abundance during the 20th century. Sea-surface temperatures along SE Vancouver Island were below normal for several of the years when sardines were present from the mid-1930s to the mid-1940s and above normal from 1977 to 1989 when sardines were absent (McFarlane and Beamish 2001). There did appear to be a relationship between climate-regime shifts and sardine abundance however. The commercial fishery in Canada expanded rapidly in 1925, just as the PDO shifted into a positive phase, and collapsed in 1947 when a negative phase began. Though sardines failed to return in 1977 when a new positive phase emerged, they did return shortly after another apparent climate shift in 1989 (McFarlane and Beamish 2001).

Comparisons of historical sardine periods with reconstructions of the PDO (Biondi et al. 2001, D'Arrigo et al. 2001, Gedalof and Smith 2001) and with El Niño activity (Mann et al. 1998), suggest that sardine occurrences were associated with both positive PDO values and strong El Niño activity. For reference, reconstructions of the El Niño Southern Oscillation (ENSO) (Mann et al. 1998) and the PDO index (Gedalof and Smith 2001), and are plotted in fig. 17.

The first sardine period coincided with consistent and prominent peaks in the estimated PDO indices during the 1790s. Peaks were evident in all three reconstructions, but especially in the latter two, which were based in part on tree-ring series from the PNW. Historical accounts reveal that the sardine expansion also coincided with extreme El Niño conditions. The South Asian Monsoons failed in 1789, and the drought that ensued lasted until 1792, a year when 600,000 people starved to death in Madras, India (Fagan 1999). Evidence from South America, suggested that a very strong El Niño event impacted that continent in 1791 (Quinn and Neal 1987). Extreme conditions were evident in Hawaii as well. Captain George Vancouver wrote in 1793 that the Island of Nihau in Hawaii had been almost entirely abandoned due to "...the excessive drought that had prevailed during the last summer..." (Vancouver 1984).

According to the PDO reconstructions cited above, temperatures remained mostly above normal during the late 1880s when sardines returned. PDO values stayed above their long-term means until about the mid-1890s. Temperatures dropped between 1895 and 1899, but then abruptly reversed as another El Niño event occurred, and a decade of higher PDO values followed. The transition occurred in 1900, during the same year that sardines were captured in mid-winter in Canadian waters, and shortly before they were reported as abundant in Puget

Sound. Based on historical accounts from South America, Quinn and Neal (1987) rated the 1899-1900 El Niño as strong, but in India the effects were devastating, Failure of the monsoon in 1896-1897 and then again in 1899-1900 resulted in over 4 million deaths from starvation (Fagan 1999). At Protection Island, geoducks recorded one of the narrowest growth rings of the 156-year chronology in 1899. This was followed by a decade of unusually wide rings starting in 1900 (fig. 18).

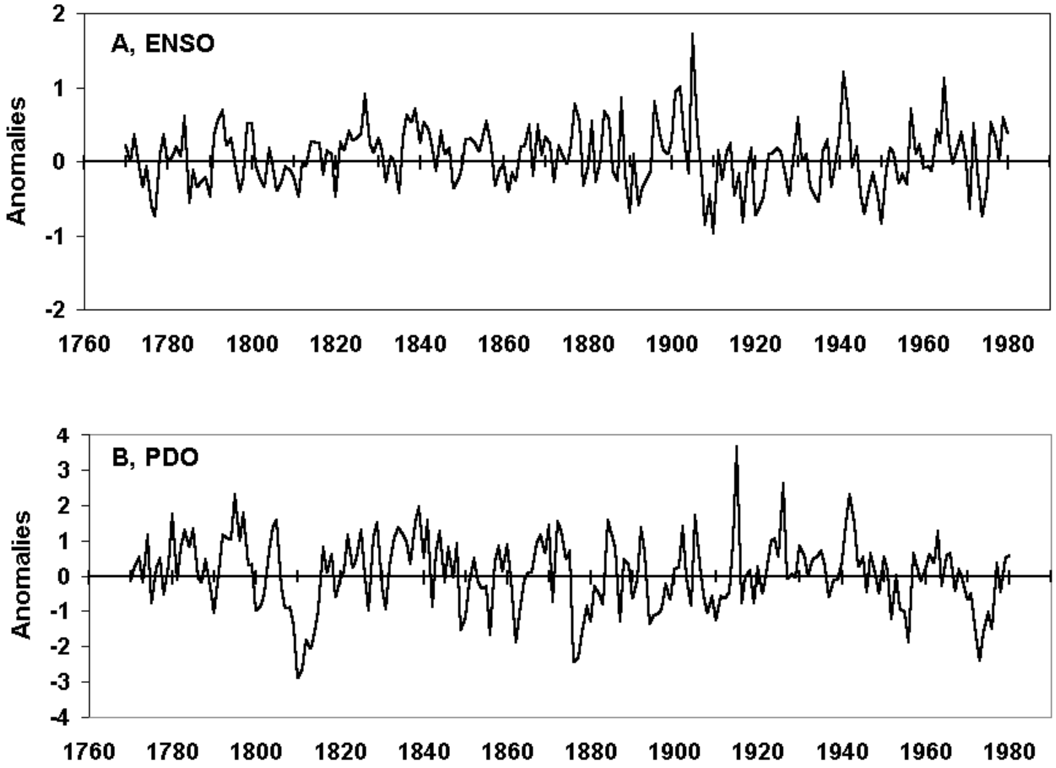

Fig 17. Time-series plots of (A) the El Niño Southern Oscillation (ENSO), and (B) the PDO index. The PDO series (Gedalof and Smith 2001) was based on tree-ring data from the Pacific Northwest and Alaska. The ENSO reconstruction by Mann et al. 1998 was derived from a global multi-proxy network, but was heavily weighted towards tree-ring data.

3.5 Sardine Abundance and Geoduck Growth

Sardine abundance in British Columbia and geoduck growth at Protection Island show similar trends. Comparisons over the historical record suggest that geoducks were better predictors of sardine abundance than either the PDO or local sea-surface temperature series. The earliest sardine catch data for British Columbia dates from 1917 (Schweigert 1988), and is plotted in figure 19 along with the full geoduck growth chronology. Sardine landings from the commercial fishery between 1917 and 1947 are indicated in green. Catches beginning in 1992 are calculated from combined landings of research and commercial fisheries (McFarlane and Beamish 2001). Recent catch data understate the recovery of sardines in British Columbia, since they were derived from a restricted experimental fishery (McFarlane and Beamish 2001). The top panel shows a wavelet spectrum of the growth chronology, and indicates the distribution of dominant frequencies in the series from 1844 to 1999 (Torrence and Compo 1998).

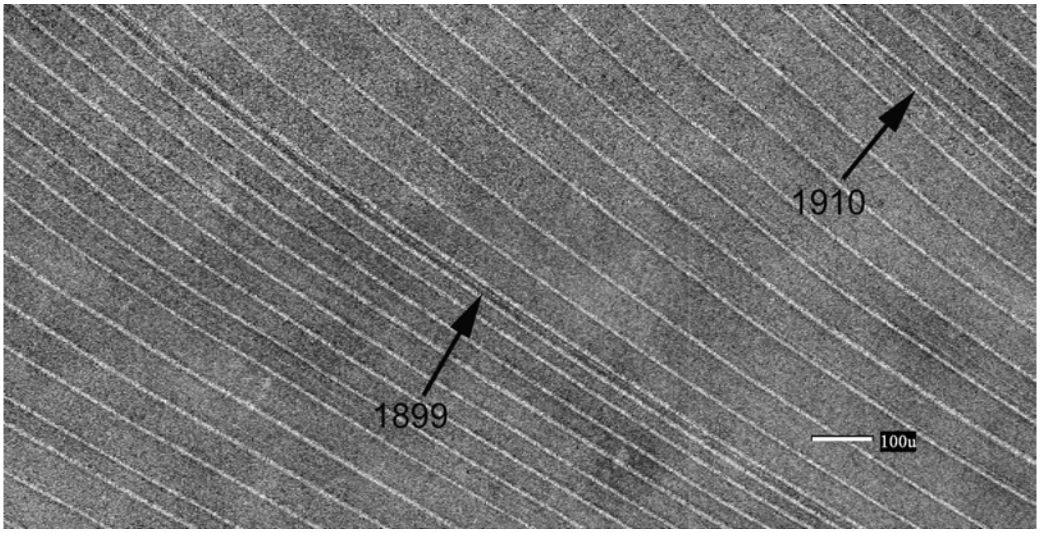

Fig. 18. Scanning electron microscope image of the oldest geoduck from Protection Island showing an abrupt change in growth between 1899 and 1910. The narrow growth ring in 1899 coincided with the great famine of 1899-1900 in India that left an estimate 4 million people dead from starvation.

Dramatic increases in sardine abundance in 1925 (Schweigert 1988) and in 1995 (Ware 1999) coincided with unusually high rates of geoduck growth. The 1925 increase also coincided with a very strong El Niño event (Quinn and Neal 1987, Fagen 1999) and the beginning of a positive PDO phase (Mantua et al. 1997). Both sardine catches and geoduck growth declined between 1931 and 1938, but sardine catches rebounded in 1940 due primarily to an exceptionally strong year-class that was produced in 1939 (Ware 1999). Though this appears to have been the last strong recruitment event of the northern sardine stock, it apparently sustained the fishery until the 1947 collapse (Ware 1999). Geoduck growth increased only moderately when the PDO shifted into a positive phase in 1976, and sardines remained absent from the PNW. The return of sardines in 1992, however, occurred just as geoducks began growing at extraordinarily high rates. Shell accretion increased dramatically between 1992 and 1999, with ring widths commonly 2-3 standard deviations above the long-term mean. Sardine abundance also increased sharply through the 1990s. By 1997, stocks had recovered to the point where they were once again described as dominant species in Canadian waters, and the biomass along the outer coast of Vancouver Island was estimated at 88,843 metric tons (McFarlane and Beamish 2001).

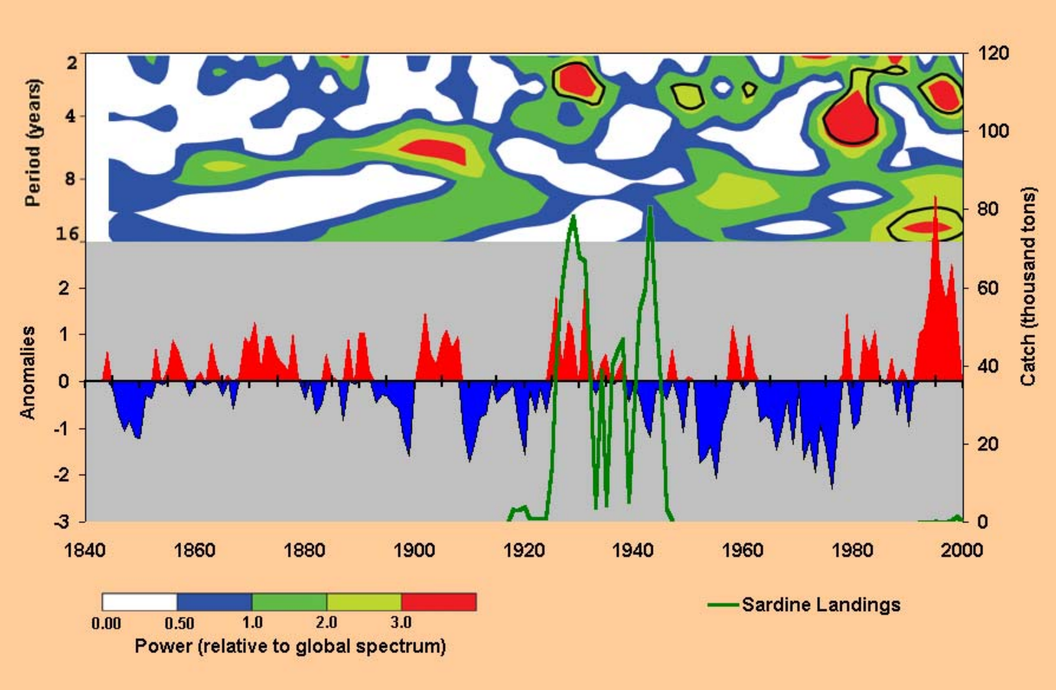

Fig. 19. A composite graph showing two representations of the Protection Island growth chronology. The time-series portion (in red and blue along the main axis) is plotted against a wavelet power spectrum of the same series (top panel) and sardine landings in British Columbia (green line). The wavelet spectrum (normalized by the global spectrum) indicates relative power at frequencies ranging from 2 to 16 years. Periods of increased power in the wavelet spectrum are indicated in red. Black contours indicate significant variance at the 95% level. Sardine landing are in thousands of tons. Catches from 1992-99 understate the relative abundance since only a limited fishery has been allowed. (Wavelet software was provided by Torrence and Compo, 1998, and available at: http://paos.colorado.edu/research/wavelets/).

The timing and magnitude of concurrent shifts in sardine abundance and geoduck growth suggests that the responses were not coincidental, but were due to closely related environmental factors. A number of other marine species were also strongly affected by an apparent climate shift in 1989 (Beamish et al. 1999, McFarlane and Beamish 2001). The relationship between sardines and shell growth prior to 1917 is less certain given the lack of quantitative fisheries data, but existing data do suggest that both the frequency of the climate signal as well as the magnitude may have been important. The wavelet plot in fig. 19 shows that each of the reported occurrences of sardines coincided with increased spectral energy in the geoduck growth series at interannual periods. Higher power, indicated in red, was evident at periods of 2 years in the late 1880s, at 7-8 years from 1900 to 1910, and at 3-4 years when sardine abundance was highest, during the 1920s and 1930s and during the 1990s. It also shows that prior to 1887 there was relatively little energy in the growth series at either interannual or interdecadal periods.

There appears to have been an absence of high frequency variance, and few sardines in the PNW, between the 1850s and 1880s, when ring widths indicated that temperatures at Protection Island were above normal. Empirical evidence supports this interpretation. Coastal temperatures ranging from San Diego to Monterey appear to have been considerably warmer at the time. Hubbs (1948) documented northward displacements of numerous marine fish species between 1853 and 1860. Subtropical species such as pipefish and giant seahorse moved north to San Diego, while species common to Southern California were found in the waters off Monterey. The northward shifts apparently persisted until 1880. Based on both biological and physical evidence, Hubbs (1948) argued that the displacements were the result of a prolonged warm period. Since there is strong coherence between SST records along the Northeast Pacific coast (McGowan et al. 1998) the geoducks at Protection Island were likely recording the same climatic signal. Though ocean temperatures may have been above normal from 1853 through the 1870s, the growth series indicates that SSTs along at Protection Island were far below those recorded during periods of high sardine abundance. High frequency variability was also notably absent from the growth series between 1853 and 1870. Both high frequency variability and high temperatures may be necessary for sardines to range as far north as British Columbia.

There is some evidence that sardines may have been sporadically present in the PNW during the 1850s. Holmgren (2001) reconstructed the abundance of several pelagic marine species from fish scale deposits in anoxic sediments. The sample site was located in Effingham

Inlet on Vancouver Island, and results indicated that at least a few sardines migrated north during the 1850s, and then again between 1875 and the 1900. Absolute abundance appears to have been low however. The same study also found evidence of lingering sardine presence up until the 1960s. Holmgren (2001) reported that sardine scales were generally rare in the sediments, and that absolute abundance estimates may have been unreliable for this species. Scale-deposition rates were calculated from pooled five-year blocks, so exact dates for the sardine occurrences could not be assigned.

If the relationship between shell growth and sardine abundance has remained constant over time, then we can expect that future extension of the geoduck growth chronology to the 1790s will reveal both significantly wider growth rings and more high frequency variance in the growth series during the first sardine period as well. This would provide a good test of the geoduck-sardine relationship and might help answer the question of whether geoducks can provide useful estimates of climatic change over extended periods.

SUMMARY

Results of this thesis have shown that geoduck shells sampled from appropriate locations are comparable to high quality tree-rings in their ability to record past variability in temperature. Although the exact mechanisms linking shell accretion to temperature are unknown, the relationship appears to have remained stable since 1900, and possibly since the 1850s. Geoducks are long-lived, stationary monitors of their environment. They appear to be the marine equivalent of tree rings and show great promise for reconstructing historical variability in ocean temperature.

There appears to be a consistent relationship between geoduck growth and sardine abundance in the Pacific Northwest. Years of high geoduck shell growth, coupled with increased frequency of El Nino's were associated with the appearance of sardines along Vancouver Island. A good test of this hypothesis would be to extend the growth chronology to the late 1700s when sardines were first documented in the Pacific Northwest.

Currently available data are not sufficient to define the exact mechanisms or factors responsible for geoduck shell growth, but circumstantial evidence suggests that temperature is the most important factor. A reasonable working hypothesis is that increased temperatures lead to higher metabolic activity and faster shell growth. This hypothesis needs to be tested through controlled growth experiments.

In addition to further experiments to define the physiological links between temperature and shell growth, future work should focus on extending the growth chronology at Protection Island by collecting dead shells that are reportedly abundant in the sediments. The older shells can then by crossdated and incorporated into the existing master chronology. This could potentially extend the growth record by several hundred years. New sample sites should be developed to extend the spatial coverage of the geoduck growth record. An expanded network of sites would improve the skill of regression models to reconstruct broader indexes such as the PDO. It would also add a new component to a growing multiproxy network of climate data. Such networks are proving to be increasingly important in the quest to understand patterns of climate variability and to distinguish natural from human-induced climate change (Mann et al. 1998). It would also provide an historical context for fisheries managers to investigate relationships between ocean climate and biological productivity.

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