HOLOCENE FISH REMAINS FROM SAANICH INLET, BRITISH COLUMBIA, CANADA: A PALEOECOLOGICAL STUDY

by

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ABSTRACT

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Fish remains in Saanich Inlet sediments are investigated for environmental and fish population signals. Recent trends (1867-1992) are explored using high-resolution box cores. Herring (*Clupea harengus pallasi*) and hake (*Merluccius productus*) comprise over 90% of remains. Spectral analyses indicate Aleutian Low Pressure explains much of the variance in fish scale deposition; it is postulated to affect juvenile herring and hake recruitment at a seven-year periodicity. Predator-prey dynamics, sea surface temperature, a diatom proxy of primary production, and fishing further explain variance in scale deposition. Ocean Drilling Program Leg 169S retrieved a low-resolution Holocene sedimentary sequence from Saanich Inlet. Fish remains appear in the record just before 12000 BP and diversity increases around 6000 BP. Correlations of fish bones with diatom abundances are significant. A paleoscientific approach to investigating fish population dynamics shows promise as a means to chronicle past environmental and fish stock variability.

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CHAPTER 1: Introduction

Significant research effort throughout the world has gone into understanding pelagic fish fluctuations. Detailed long-term records that chronicle environmental and fish stock variability are essential to understanding the complex relationship between fish and their environment. Equally important, is the ability to discriminate between anthropogenic and natural variability within such records. As reliable fisheries records do not exist prior to the mid-20th century, determination of past fish population dynamics requires assessment using proxy records.

In most areas of the ocean, settling organic matter that reaches the bottom does not remain long in the sediment and is rapidly scavenged by benthic organisms or bacteria. The environments that do favour sequential preservation of organic debris are consequently of great interest. Saanich Inlet is one such favourable environment. The purpose of this study is to assess the value of using the fish remains preserved in the varved sedimentary record of Saanich Inlet as a proxy record for past fish population dynamics. The methodology involves developing chronologies of abundances of coastal pelagic fish populations from fish scales and bones recovered in sediment cores. The primary focus of this study is on the past 130 years of sediment. New methods and results may provide insights into important fisheries and environmental issues into the next century including: 1) global climate change effects on marine biota, 2) the relationships between anthropogenic impacts and natural effects in these systems, and 3) the relatively long-term patterns inherent in the natural scales of variability of these ecosystems over many centuries. This thesis is presented, in part, in the form of scientific journal articles. Due to the format, there is some repetition of material in Chapters 2, 3 and 4.

In Chapter 2, I investigate the premise that the temporal structure and distribution of pelagic fish scales at depth act as a consistent proxy for long-term pelagic fish productivity and change. A summary and review of the literature is presented to introduce the concepts and to discuss previous studies using fish remains in sediment cores. The details and difficulties of coring, alignment and sub-sampling are discussed. The cores used for this section of the study were obtained in 1995 on board the Department of Fisheries and Oceans vessel *Vector* and were aligned and sub-sampled by Dr. M. McQuoid and C. Wright. I treat alignment and sub-sampling in some detail in Chapter 2 and have based my descriptions and discussions on written notes, personal communications, and field experience. Next, the value of replicates and the relative strength of the signals obtained from scale and bone deposition records are considered; attention is given to potential input and output preservation and bias issues in the sediment record. Data smoothing and formal time series analysis are investigated to evaluate their potential in discerning low- and high frequency trends, cycles and events in the data. Overall, this chapter looks into potential difficulties in using sedimentary records of fish remains to determine how best to approach a paleoecological analysis of fish remains from Saanich Inlet, British Columbia.

In Chapter 3, the herring and hake scale-record is considered as a relative population record to examine long-term herring and hake interactions, relationships to environmental parameters, and response to anthropogenic influence (fishing). 110 years of sediment are examined against environmental parameters investigated including Aleutian Low Pressure, sea surface temperature, and a diatom proxy of primary production. Herring biomass estimates are evaluated as a means to investigate effects of fishing. The objective is to develop a comprehensive picture of herring and hake dynamics in Saanich Inlet and the Strait of Georgia ecosystem.

In August 1996, Saanich Inlet was the site of a mini-leg of the Ocean Drilling Program (ODP). The ODP ship *JOIDES Resolution* extracted a complete Holocene sedimentary record for a multidisciplinary project looking at changes in and around Saanich Inlet since deglaciation in this area. In Chapter 4, fish remains and diatom abundance patterns are considered along the length of this sedimentary sequence. This chapter synthesizes the work of a number of people. L. Franklin and Dr. M. McQuoid sub-sampled the cores. Dr. M. McQuoid completed the diatom work. T. Forbes picked the fish remains and R.J. Wigen helped identify the fish bones. The first author of this chapter is Dr. V. Tunnicliffe. My contribution consists of identification of fish scales and some bones, data analysis, management, and cross-checking of the remains database, as well as some interpretation and writing.

In Chapter 5, I synthesize the projects, combining the findings from the 3 main chapters (2, 3, and 4) into a brief synopsis within a concurrent context.

Canada's fisheries will continue to face a variety of pressures imposed by an increasing global population and by increased waste inputs that impair the natural productivity of the oceans. Managing fisheries in the face of these pressures will require accurate and current information on the status of fish stocks and their responses to changes to the ecosystems that support them. Describing and understanding the nature and causes of changes in fish populations is a formidable challenge because of the need for sampling vast temporal and spatial scales over which these changes occur. The work presented in this thesis demonstrates the possibility for reconstructing the natural dynamics of populations of pelagic fish over time scales of decades to centuries from variability in fish scale abundances preserved in the sediments.

CHAPTER 2: Critical Assessment of the Use of Fish Remains for Paleoecological Interpretation of Fish Population Fluctuations.

ABSTRACT

Five high-resolution box cores are examined from Saanich Inlet, British Columbia, sampling 1133 cm^2 sediment area and spanning the last 130 years (1867-1992). Alignment of the replicates is based on stratigraphic features of the core, including well-dated diatom horizons from other studies; core geochronology is estimated to be correct with a maximum error of +/- five years. Cores are sub-sampled for fish remains at two-year intervals and scales and vertebrae identified and enumerated. Scales are most consistently and reliably represented through the last century in Saanich Inlet. Experiments conducted to investigate scale flux due to shedding and predation in herring show that these mechanisms are a regular source of scales to the sedimentary record. The sedimentary scale deposition data are autocorrelated and the cross replicate and cross basin signals obtained from scale flux were assessed using data smoothing and spectral analyses for low- and high-frequency trends, cycles and peaks. Herring and hake scales make up over 90% of remains. Thus, the sedimentary fish scale record shows promise as a means to identify long and short term dynamics in herring and hake populations over the last century in Saanich Inlet, British Columbia.

INTRODUCTION

The cause of rise and decline cycles of pelagic fisheries has been debated for centuries (Lasker and MacCall 1983). Due to the paucity of long datasets, especially for pre-fishery periods, the long-term dynamics of pelagic fish populations require assessment by alternative means. Paleoecological techniques are used to obtain site or region-specific data, and to characterize natural background or reference conditions in aquatic ecosystems (Birks and Birks 1980). Knowing background or reference conditions is vital for ecosystem assessment and management because without these data, it is not possible to accurately determine the extent of change, nor is it possible to set realistic goals for recovery.

Paleoecology uses a combination of biological and geological evidence to reconstruct the dynamics of natural populations and to document environmental change. Paleoecologists reconstruct these relationships using proxy information preserved in environments such as ocean sediments. Marine sediments are often subject to reworking by animals and water movement. However, under anoxic and quiescent conditions, sediments and delicate organic remains of marine organisms accumulate undisturbed and thus preserve a chronological sequence of biological and oceanographic events through time. Using paleoecological techniques in anoxic basins, fish populations and environmental fluctuations can be reconstructed using the sedimentary temporal framework and pelagic fish remain distributions (Francis and Hare 1994; Soutar 1966).

The concept that fish population fluctuations may be reflected in variations in scale abundances in the sediment was first explored in the late 1960s and early 1970s (Soutar and Isaacs 1969; 1974). Methods are still being developed and thusfar, these studies have been based on small samples with little or no replication, and on a number of assumptions regarding the relationship between the density of scales accumulating in the sediments and the abundance of the fish populations producing them.

My investigation into use of fish remains to infer past fish populations is based on work done in Saanich Inlet, British Columbia, Canada. Collection, analysis and interpretation of time series of fish remains data from sediment cores are explored in detail. There are difficulties and uncertainties inherent in paleoecological studies using fish remains and I investigate and discuss many of these. I present pertinent background information including a review of the literature, and I explore difficulties in aligning and sampling laminated sediment cores and critically assess the reliability and consistency of the signal obtained from fish remains (scales and vertebrae) across Saanich Inlet. I discuss some of what I see as potential sources of bias in this sedimentary record and explore a major source of uncertainty - remains transfer from fish to the sediments - in an experimental context. I consider how these uncertainties can alter final interpretations of the sedimented fish remains record, and suggest how to maximize the effectiveness of a paleoecological study using fish remains in Saanich Inlet.

BACKGROUND

Faunal remains and bias in the sedimentary record

The taxonomic composition of faunal assemblages is a useful indicator of past ecosystem condition but these data are constrained by the accuracy with which the remains record reproduces an original living assemblage (Jablonski and Sepkoski 1996). Drawing reasonable inferences in a paleoecological context requires an estimation of the effects of physical and biological processes on remains and sediments (Jablonski and Sepkoski 1996; Birks & Birks 1980).

All specimens do not have an equal probability of preservation and thus the sedimentary record cannot be assumed to be quantitatively complete. It can also not be assumed that the original proportions of all biologic assemblages are preserved through time; if destructive processes are not random, a systematic bias is introduced into the record. These factors may lead to misinterpretation.

Numerous processes may act to modify the original living assemblage (input) into a sedimentary assemblage (output). The timing, composition, and volume of biogenic input influence the nature of an assemblage. Further, the effect and pattern of remains settling through the water column may affect the sedimentary record. Once in the sediments, the degree of preservation of remains is variable and depends on a number of factors including: the condition of the items at incorporation into the sediments, the environmental conditions in the sediment through time, and the loss or damage incurred during sampling and handling. Differences in the size, shape and firmness of fish skeletal elements will affect their abundance in the sediments and will influence paleoecological interpretations (Falabella et al. 1994).

Until the nature and degree of input and output bias can be defined, paleoecologists are in the awkward position of working with material that they know is incomplete but are not sure to what degree. Thus paleoecologists must consider factors that could potentially alter or bias the fossil record before they make meaningful ecological interpretations.

Paleoecology and fish

Reconstructing fish population histories using fish debris in sediments has evolved through the years. Studies have been done at a number of sites including the California coast (Baumgartner et al. 1992; Holmgren-Urba and Baumgartner 1993; Soutar 1966; Soutar and Isaacs 1969; Soutar and Isaacs 1974), the upwelling zones off central Peru (DeVries and Pearcy 1982) and Venezuela (Llano et al. 1991), and off West Africa (Shackleton 1986). In contrast to this present study, most of these projects have used few replicates, small volumes of sediment, and have focussed on lower resolution changes through time (Table 2-1).

Table 2-1. Summary and comparison of this and previous studies of paleoecological application of fish remains from ocean sediments. (Sampling area was often calculated from information available only from the text of the paper - a question mark indicates uncertainty in interpretation).

PARAMETER	SOUTAR	SOUTAR AND ISAACS	SOUTAR AND ISAACS		DEVRIES AND PEARCY	SHACKLETON	BAUMGARTNER ET AL	HOLMGREN-URBA & BAUMGARTNER	THIS STUDY
Year	1966	1969	1973		1982	1986	1992	1993	1998
Location	Santa Barbara Basin California, U.S.A.	Santa Barbara Basin California, U.S.A.	Santa Barbara Basin, California U.S.A.	Soledad Basin, Mexico	11°S - 13°S off Callao, Peru	Walvis Bay, Namibia	Santa Barbara Basin, California, U.S.A.	Gulf of California, Mexico	Saanich Inlet, British Columbia Canada
Water Depth (m)	570	585	550-589	520	Average: 413m	125	See Soutar and Isaacs 1969 & 1974	650	203
Core Length (cm)	Average: 90	250	~ 40		Variable: the 2 most intensively studied = 222 & 168	150	Piston: 250 Box: refer to Soutar and Isaacs (1974)	85	1A: 140.4 1B: 91.5 1C: 137 2A: 138 2B: 135
Coring Device	?	Kullenberg piston core	Soutar box cores		Kasten cores and Reineck box cores	Vibrocorer	Box cores Piston core	Soutar box core	Soutar box cores
Sampling area	90 cm^2	45cm^2	~375 (?) cm^2		Not calculable	?	~700 (?) cm^2	200 cm^2	1133cm^2
Major Species	P. hake P. sardine N. anchovy	P. hake P. sardine N. anchovy	P. hake P. sardine N. anchovy P. saury P.mackerel		Anchoveta Peruvian hake P. sardine Lanternfishes	Pilchard Anchovy	P. sardine N.anchovy	P. sardine N.anchovy P.mackerel P. hake Myctophids	P. herring P. hake
Resolution	10 years	10 years	5 years		Laminae indistinct	~ 4 years	~10 years	10 years	2 years
Sub-sampling	1 cm intervals	1cm intervals	Laminae counts	Linear estimates of 5 year blocks (laminae indistinct)	Kasten - 5 cm intervals Reineck - 1 or 3 cm intervals	1 cm intervals	Piston cores: 1 cm intervals 4 longitudinal box core slabs at 1 cm intervals	10-year intervals based on varve counts (25 samples)	2 year intervals from varve counts

PARAMETER	SOUTAR	SOUTAR AND ISAACS	SOUTAR AND ISAACS		DEVRIES AND PEARCY	SHACKLETON	BAUMGARTNER ET AL	HOLMGREN-URBA & BAUMGARTNER	THIS STUDY
Type of remains	Scales	Scales	Scales	Scales	Vertebrae and Scales	Scales	Scales	Scales	Scales and vertebrae
# of core Replicates	4-subcore longitudinal slices	Single core	16 subcore samples	4 subcore samples	12 cores – subsampled @ 200 g/sample…but not true replicates due to changing sampling intensity.	Single core	2 piston cores 4 slices from 4 box cores	¼ box core	5 full box cores
Time period covered	(1000 years)	(1850 years)	1810-1970 (160 years)	1780-1970 (190 years)	Pre-Holocene – present (16 000 years) with disconformity	(100 years)	A.D. 270 –1970 (1700 years)	1730-1980 (250 years)	1867-1994 (127 years)

(Table 2-1 continued)

The Soutar and Isaacs legacy

In the 1960s, A. Soutar, of the Scripps Institution of Oceanography, postulated that the remains of fishes in marine sediments could act as proxies to provide a relatively long time-perspective into past fishery and oceanographic conditions (Soutar 1966). In this pioneering paper, he described the anoxic conditions in the Santa Barbara Basin, California that allowed fish debris to accumulate undisturbed by benthic organisms and aerobic bacterial decomposition.

Subsequently, Soutar and Isaacs (1969) undertook a detailed study of pelagic fish scales in a single piston core from the laminated sediments of the Santa Barbara Basin. The goals were to obtain information concerning the series of scales of one species and information on the interrelationships between several species (Soutar and Isaacs 1969). They discussed the inferred relationships between sardine and anchovy over the last 2000 years and from the scale deposition record in a single core, they observed cyclicity in the sardine peaks and a consistent decline in anchovy numbers.

Several aspects of the Soutar and Isaacs study may be addressed. First, data obtained from a single small-diameter piston core were used to represent scale deposition over the entire Santa Barbara Basin. Making an inference from a single sample reduces statistical power (Krebs 1989) and also ignores questions of the reliability and consistency of the signal. Further, Soutar and Isaacs (1969) assumed that scales were contributed to the record by dead fish. No alternative means of fish scale deposition other than death were considered and preservational issues were not considered.

In 1974, Soutar and Isaacs compared box cores taken from the Soledad Basin, Baja California, Mexico, with those taken from the Santa Barbara basin. Preservation of the fish scale record through consideration of the frequency of scales at depth and through analyses of trace levels in dissolved phosphate down-core indicated that the scale record was intact and well preserved.

Soutar and Isaacs (1974) also estimated past biomass for Pacific sardine, Pacific saury, northern anchovy and Pacific hake from scale accumulations by comparing the average scale deposition rate to available fisheries averages (1930-1959). In most cases, they found a parallel but offset decline in biomass as indicated by scale deposition and converted scale counts to biomass based on these comparisons. Although there was a fairly consistent relationship between scale deposition rates and pelagic fish population estimates, the extrapolations were limited by the short duration of the available fisheries records and thus by the small number of samples upon which these estimates were based (6 data points). Also, in some cases, this reconstruction of biomass was based on less than one scale/1000cm^2 x year.

DeVries and Pearcy - Holocene record

DeVries and Pearcy (1982) conducted a paleo-study on the upper continental slope of Peru; their goals were to reconstruct a Holocene record of anchoveta, the richest single-species fishery in the world. This study was different from Soutar and Isaacs' work as the sediments were only partly laminated and vertebrae as well as scales were used to derive the paleo-proxy record. The Peru record was incomplete; including the early and late Holocene but missing the mid-Holocene. Anchoveta and hake accounted for more than 90% of the scales preserved; these species exhibited similar abundance patterns through time. The authors related changes in anchoveta, sardine and hake to glacial and neo-glacial warming and cooling events.

DeVries and Pearcy (1982) investigated questions of preservation of fish remains in their cores using a scales to vertebrae ratio as an indicator of post-depositional degradation. They, like Soutar and Isaacs (1974), concluded that the dissolution of fish remains through time was negligible and unlikely to bias the sedimentary record. Similarly, DeVries and Pearcy assumed that the remains in their record were from dead fish. The geochronology and sub-sampling of the sediments in this study were rough and they found evidence of sediment reworking and unconformities indicating winnowing of fossil materials. Poor chronological alignment between and among cores and significant gaps in the record were also detrimental to their paleoecological reconstructions as it may have obscured true signals from fish remains, and time variant displacement of fish remains along with inexact sampling could also have invalidated interpretations.

Shackleton – A first major look at some potential problems

Shackleton (1986) took the first critical look at the methods of fish population reconstruction in her study of sedimented remains off Namibia. She acknowledged that while understanding the dramatic population fluctuations of pelagic fisheries was important, there was a need to quantify some of the factors which could bias the sediment record before credible reconstructions could be made. The relationship between fish scale accumulation in the sediments and past fish abundance is not straightforward and Shackleton (1988) questioned the tacit assumption that the density of scales accumulating in the sediment mirrors the abundance of the fish producing them. She determined that most of the scales in the sediments were actually a result of deciduous shedding rather than the death of the fish (Shackleton 1988). From her laboratory shedding experiments, she found that pilchard lost scales 2 to 3 times as fast as anchovy. Thus, she derived an index to more realistically hindcast pilchard and anchovy populations from their sedimented remains. Shackleton demonstrated that without careful consideration of scale shedding mechanisms, comparative population extrapolations among species from sedimented fossil fish scales are subject to misinterpretation.

Shackleton (1988) also highlighted the difficulty in positive scale identifications for some species of fish. She found that pilchard and anchovy scales were difficult to differentiate. She tested a number of ways to positively identify scales and determined that visual assessment with a comprehensive reference collection was most effective. Shackleton's work is extremely important as it addresses many of the assumptions made in past paleoecological reconstructions of fish populations and acknowledges some of the inherent difficulties in obtaining reasonable inferences from sedimentologic fish remains records.

Baumgartner, Soutar, and Ferreira-Bartrina

Baumgartner et al. (1992) expanded the Santa Barbara work of Soutar and Isaacs (1974). To provide an improved composite time series for sardine and anchovy in the Santa Barbara Basin, they collected another piston core to supplement the piston core and box cores from the previous studies (Soutar and Isaacs 1969; 1974). Beyond expanding population reconstructions for sardine and anchovy, they examined some sources and ranges of uncertainty in their scale record data.

They assessed the reliability of scale deposition rates as indices of abundance by comparing the time series of scale data from two piston cores from different sites within the basin. They found that fish remains in their two cores were significantly correlated, which they interpreted as evidence that a true signal of fish abundances can be obtained from sedimented scales. They also examined the strength of the signal obtainable from their data, and issues of bias and noise in the sedimentary record. They concluded that they required more intensive sampling to capture the variability in the basin as their study relied on small sample sizes and few core replicates. Baumgartner et al. (1992) attempted to further discern how sensitive the basin-wide scale deposition rate was to changes in regional abundance of fish. They compared their record to more recent biomass estimates than those used by Soutar and Isaacs (1974) and re-estimated population sizes from scale deposition. Lastly, despite uncertainty in the varve chronology and in the estimates of population biomass, they looked at trends in the scale data via spectral analysis and produced a 1700-year analysis of the periods at which sardine and anchovy fluctuate.

Time series analysis in paleoecology

Formal time series analysis has gained popularity for application in paleoceanographic and paleoecological studies (Baumgartner et al. 1992). A time series is a collection of observations made sequentially in time (Chatfield 1989). There are several possible objectives in analysing time series however, for this study, time series analysis is used to describe high-frequency structure in sedimentary fish remains. Spectral analyses are especially useful for sedimentary and fisheries data since these have properties that make classical statistics unfeasible. In classical statistics, observations are assumed to be independent (Krebs 1989). However, if the observations form part of a time series, then only for a purely random series will neighbouring values be independent (Jenkins and Watts 1968).

Analyses in the frequency domain allow observations taken on two or more variables to be compared in a non-dimensional, non-parametric environment. Thus, it is possible to use the variation in one time series to explain variation in another series. When two time series are compared, they may not resemble each other visually but their statistical or average behaviour may be similar. This allows interpretation of the mechanisms that generate a given time series (Chatfield 1989).

The major diagnostic time series functions used in this study include the autocorrelation function, spectral density functions, and cross-spectral analyses. Such methods are ideal for resolving structure in sedimentary time series data that are autocorrelated and allow the determination of dominant natural periodicities in otherwise difficult to resolve data.

STUDY SITE - SAANICH INLET, BRITISH COLUMBIA

Oceanography

Saanich Inlet is a temperate marine fjord on Vancouver Island, British Columbia (Figure 2-1). It is 24 km long, 7.2 km at its widest point, and has a maximum depth in the central basin of 234 m (Herlinveaux, 1962). At the mouth, a sill at 70 m depth restricts normal water flow through the Inlet (Herlinveaux 1962). The features of the Saanich Inlet basin are fjord-like, however the oceanographic processes inside the inlet are different from those of a typical fjord. Bathymetry and weak circulation create a secondary halocline below sill depth that isolates the deep waters, and the chemical composition of these waters is greatly modified by biological processes (Herlinveaux 1962). Dissolved oxygen at depth is quickly depleted by respiration and the deep water in Saanich Inlet is anaerobic and typically contains <1.0 ml/l of oxygen for most of the year (Tunnicliffe 1981). This absence of oxygen in the deep waters of the inlet is a major factor in the maintenance of the undisturbed sedimentary record as well as the preservation of organic remains.

Sediment

Saanich Inlet sediments are annually laminated and these rhythmites provide a tool to derive a precise chronological background for paleoecological studies. Rhythmically laminated marine sediments are rare, but because of their potential for studying paleoenvironmental changes, they have recently attracted much attention (Kemp 1995). A stable oxygen minimum layer at the bottom of the water column, and a rhythmically varying sediment supply are the two prerequisite conditions which result in undisturbed laminated sediments that preserve a detailed sedimentary geochronology. Replicable geochronologies are an essential foundation for paleoecological reconstruction as standardized chronology permits comparison and correlation with other temporal datasets (Jablonski and Sepkoski 1996). Like most marine laminae, Saanich Inlet varves are formed by alternations in deposition between growing and non-growing seasons (McQuoid and Hobson 1997). Diatom cells from spring and summer blooms make up most of the light coloured laminae deposited through the growing season (McQuoid 1995). The dark laminae consist primarily of silts and other terrigenous material from fall and spring freshets of the Cowichan River and are indicative of the non-growing season. The thickness of the sediment

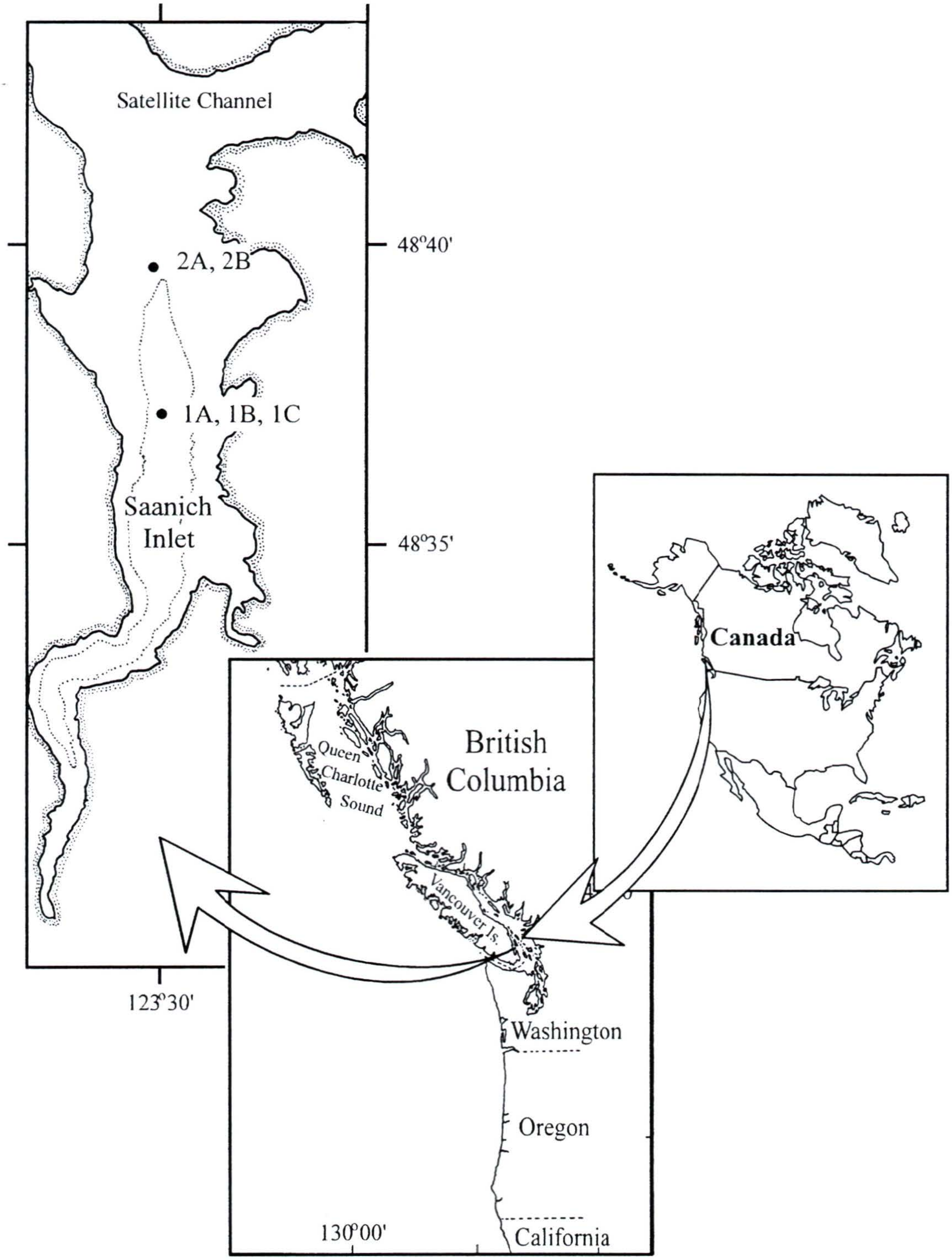

Figure 2.1. Study site: Saanich Inlet, British Columbia, Canada. Core sites are indicated; Site 1:(48°37.9', 123°30.0) and Site 2: (48°39.6', 123°30.5')

layers increases as one moves closer to the sill. This gradation occurs because most terrigenous sediment (Cowichan River runoff) and nutrients enter the inlet at the mouth and because productivity is greater closer to the nutrient sources at the mouth of the inlet. The laminated anoxic sediments of Saanich Inlet make it an attractive study area for paleoecological research.

MATERIALS AND METHODS

PART I – Core collection and fish remains data

Box core collection

The five high-resolution sediment cores used in this portion of the study were obtained June 26-29, 1995 from Saanich Inlet, British Columbia. The Soutar box-corer used to extract the sediments consists of a square, aluminum box (30x30x100 cm), a head weight, and a scissor arrangement of spade-type lever arms (Figure 2-2). The head weight is a platform to which lead weights are added or removed to control the corer penetration into the sediment. The spade lever arms lie horizontally during deployment and descent, but on recovery, the scissors shut as they are pulled into a vertical position. This closes the bottom of the core box prior to returning the corer to the surface. The scissor arrangement also maintains the corer in a vertical position during deployment and coring. The top of the corer is open to permit gas-escape.

The sediment cores were collected on the Department of Fisheries and Oceans vessel, *Vector*. Box cores 1A, 1B and 1C are from Station E just south of Patricia Bay and Mill Bay (48°37.9’, 123°30.0’). Box cores 2A and 2B are from a site near the sill (48°39.6’, 123°30.5’) (Figure 2-1). Deployment of the corer was facilitated using an A-frame from which the coring device was lowered into the sediments. Once it had penetrated the sediments, the corer was slowly returned on board the ship, secured and frozen. After the core was removed from the box, it was cut into two pieces with a handsaw, wrapped in plastic, labeled, and placed in the freezer. This was repeated for each of the five cores. Box-corers are especially advantageous for collecting fish remains in laminated sediments as they obtain large-volumes of sediment with minimum disturbance to the sedimentary structures.

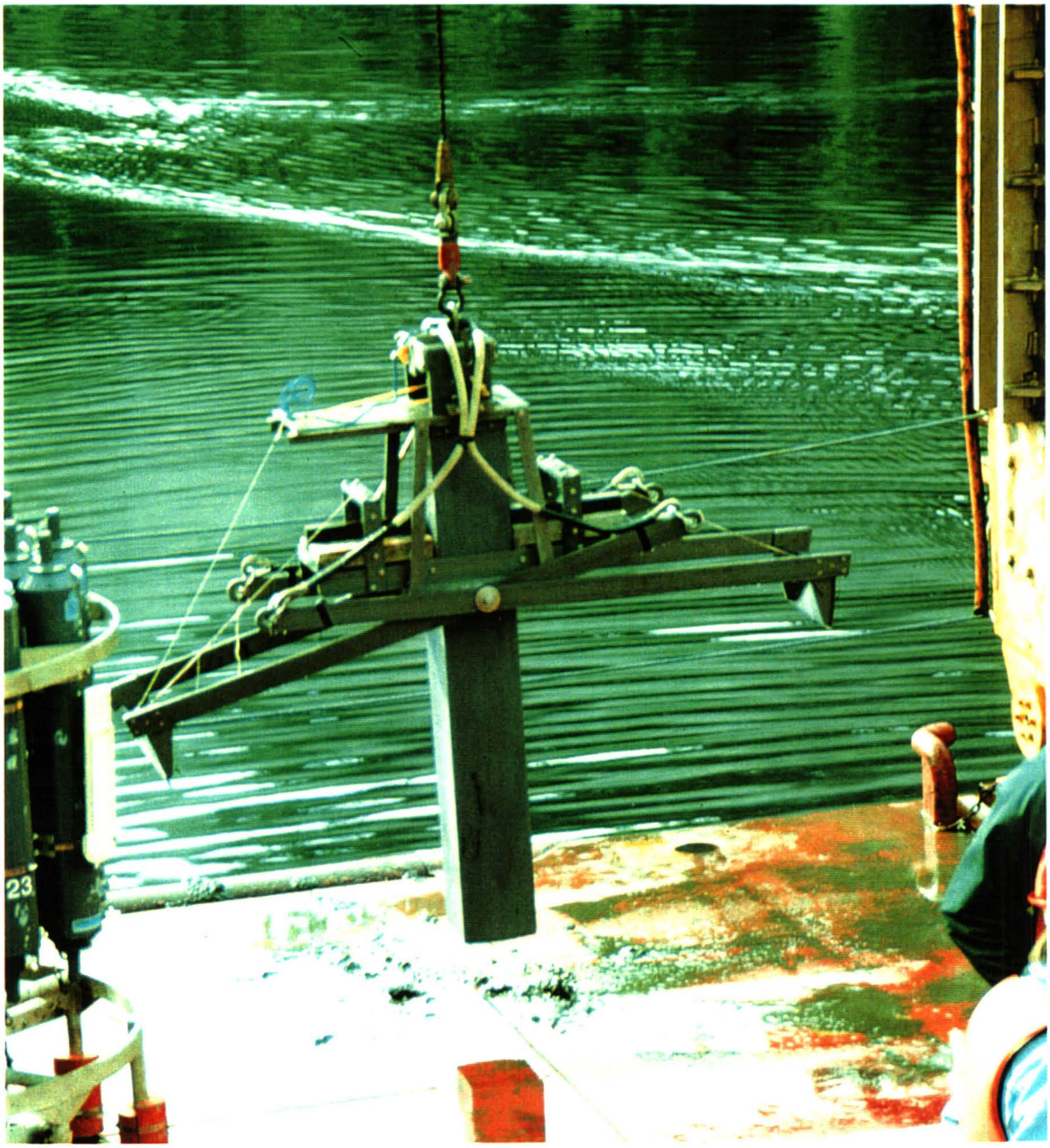

Figure 2.2. Soutar box corer used to extract Saanich Inlet sediments.

Core characteristics and sub-sampling

Varve counts, stratigraphic and visual distinctions, prominent presence or abundance of diatom species (McQuoid and Hobson 1997), and the presence of woodchips (Collins 1997) were all used to establish core geochronology (Figure 2-3). Comparisons were made with reference to freeze cores from Station E (1863-1991); dating was confirmed using ^{137}Cs (Collins 1997; McQuoid and Hobson 1997).

There is greater input of terrigenous materials near the mouth of Saanich Inlet (Blais 1996) therefore the varves are thicker in cores 2A and 2B than in any of the cores from Station E (1A, 1B and 1C). Since the freeze cores used to determine the geochronology were taken from Station E (McQuoid 1995), alignment and chronology establishment for cores 1A, 1B and 1C used these freeze cores as direct templates. Temporal alignment of cores 2A and 2B (from near the sill) was less certain as direct comparisons of varve widths and sedimentary features were not as straightforward due to the differences in sedimentation and distance across the inlet. Thus, the chronologies for cores 2A and 2B were determined primarily using diatom marker-horizons and varve counts. Care was taken to ensure that these cores were aligned as well as possible with one another however, correspondence with calendar time is not as certain as with cores 1A-1C.

The cores were sub-sampled at two-year intervals. Each core year begins with a light layer on the bottom and a dark layer on top. For sub-sampling, core years were marked with dissecting pins and the core was then allowed to thaw for a few hours before being sliced. Varves would often curve more in the center of the core but years were followed as closely as possible when sampling (M. McQuoid, personal communication). Indistinctly varved sediments, which had not compacted with the weight of successive layers, were incrementally sampled at 2-cm intervals and subsequently re-apportioned to years. Alignment and sampling was straightforward at known horizons (Table 2-2). All samples were bagged and kept frozen until sieving.

The sliced samples were thawed prior to sieving. Once soft, the sample bags were emptied and rinsed into large bowls and this mixture was passed through a 500 μm and 250 μm mesh sieve (Figure 2-4). Both fractions were retained.

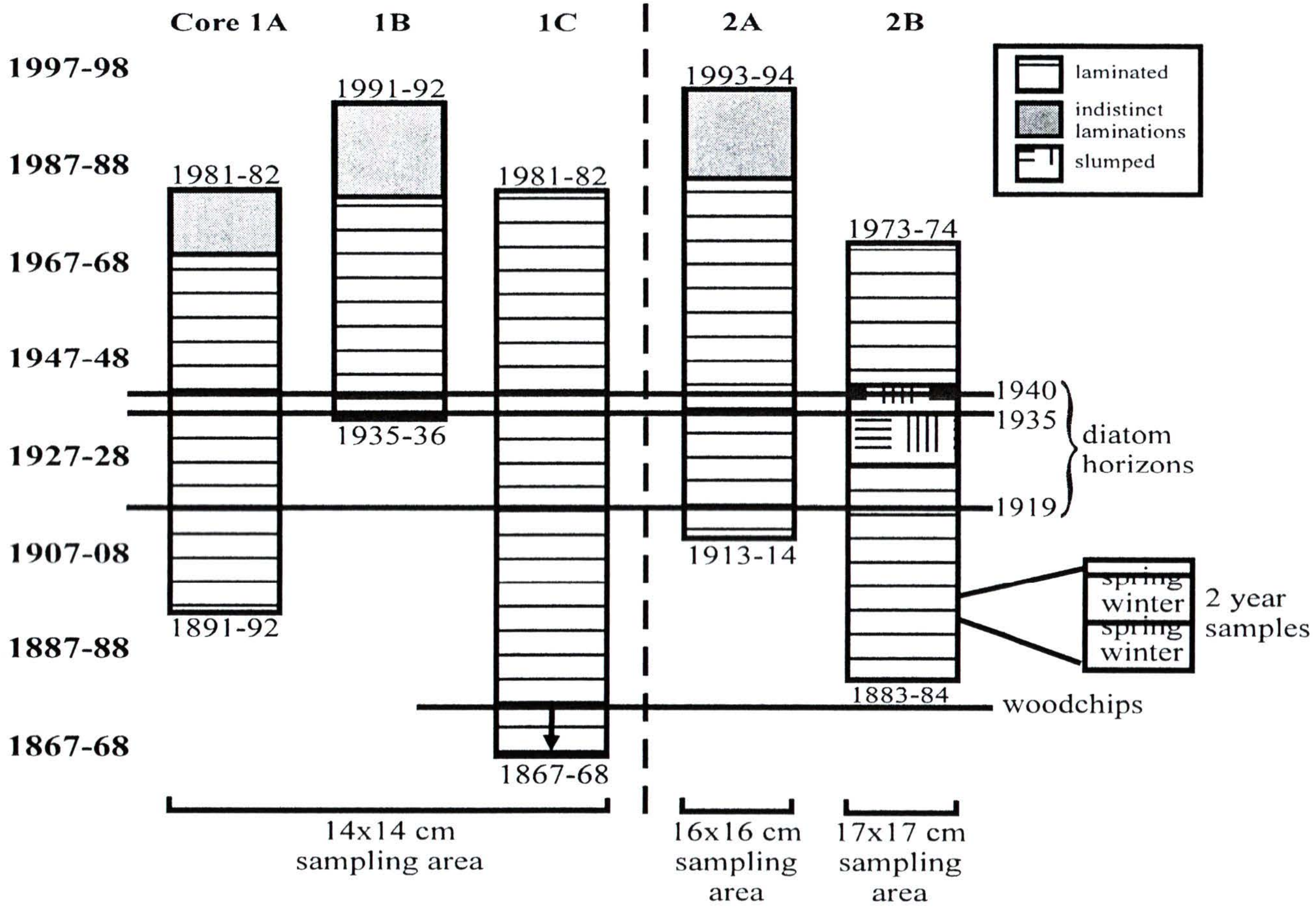

Figure 2.3. Schematic illustration of aligned cores. Indicated are the *Rhizosolenia* horizon (1940), the *Chaetoceros* horizons (1919 and 1935) (McQuoid 1995) and a woodchip horizon (1863-1879) (Collins 1997).

Table 2-2. Box core specifications and features used for alignment to freeze core 11.

CORE	CORE LENGTH (CM)	AREAL DIMENSIONS OF THE CORE (CM^2)	SPAN OF YEARS	TOTAL # YEARS	AVERAGE & STANDARD DEVIATION OF 2 YEAR SAMPLE THICKNESS (CM)	ALIGNMENT COMMENTS
1A	140.4	196	1891-1982	91	2.9 (+/- 0.5)	Top ~23.2cm indistinctly varved split into 2 equal samples
1B	91.5	196	1935-1992	57	3.4 (+/- 1.2) pre-80s = 2.9 post-80s=4.8	Top of core comprises thick recent uncompacted varves
1C	137	196	1867-1982	115	2.7 (+/- 0.6)	
2A	138	289	1913-1994	81	3.6 (+/- 0.8)	Indistinct laminations: top 12 cm above 1982 split into 6 even samples
2B	135	256	1883-1974	91	3.3 (+/- 0.7)	Indistinct laminations: top 9 cm split into 5 samples, samples between 1933 and 1955 sampled every 2 cm for 13 samples

When the samples did not pass easily through the mesh, the sample was gently stirred as more water was poured over the sieve. Samples were rinsed until the sieve fraction was "clean". Residues were rinsed into plastic storage vials labeled with the core designation, sample years, and mesh size. Samples were preserved in 70% ethanol. Due to the abundance and persistence of fecal pellets (from zooplankton) and other solids after sieving, both the 250 and 500μm sample were re-sieved down to 250 μm prior to picking for fish remains.

Identification, enumeration and summaries

Most other paleoecological studies use only fish scales for interpretations. I enumerated and identified scales and vertebrae to investigate their potentials as proxies of past fish abundance. Vertebrae and scales were picked and identified under a dissecting microscope, and were stored in glass vials in 70% ethanol. Fish scales were identified using a reference collection compiled specifically for this study. Only those scales that were either 50% or more intact or for which the focus was intact were counted as whole scales. The reference collection consists of scale specimens of 35 taxa (Appendix 1). Reference scale specimens were obtained as dried scales from the Anthropology Department at the University of Victoria, and were sampled from live material at the Bamfield Marine Station and aboard the *C.S.S. W.E. Ricker*. Scales exhibit species-specific morphologies and identification of "typical scales" to species with an adequate reference collection is straightforward. Conversely, the extreme variants and regenerated scales may be quite hard to identify, as there is high variability among scales from different body areas on the same fish (Casteel 1976). Scales used in the reference collection were chosen to cover a spectrum of scale types where possible (Figure 2-5). Scale features considered in taxonomic identification include: size, shape, wing join, cracks/radii, scale margin, thickness and depths of cracks (Figure 2-6). The scale collection is now housed in the Department of Anthropology at the University of Victoria.

The vertebrae picked from the box core samples were identified using the bone collection in the Department of Anthropology at the University of Victoria, and with the help of R.J. Wigen (Pacific Indentifications, Ltd.). Only intact vertebrae or those that consisted of at least 50% of the bone were

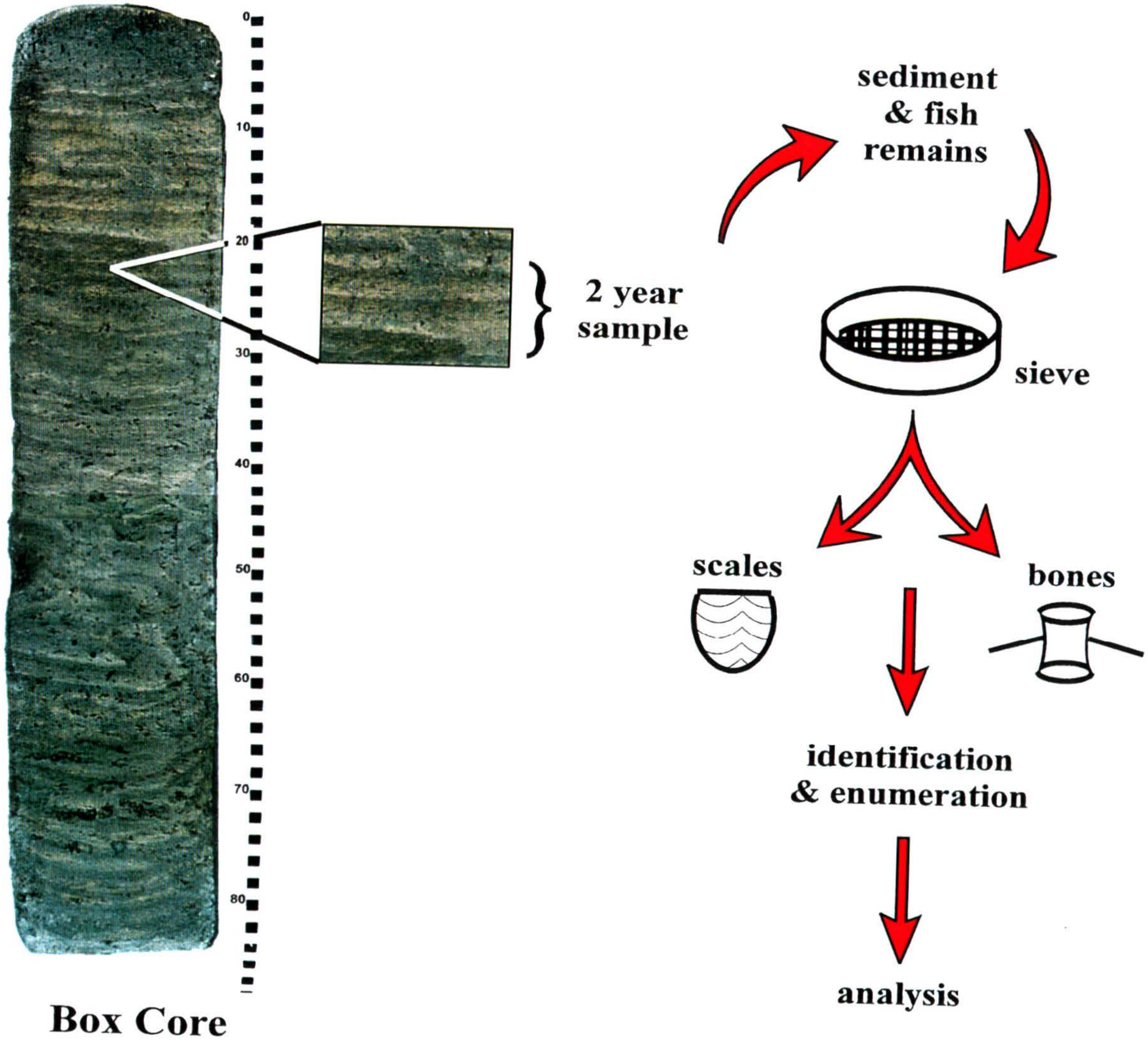

Figure 2.4. Schematic illustration of core sub-sampling protocol for fish remains.

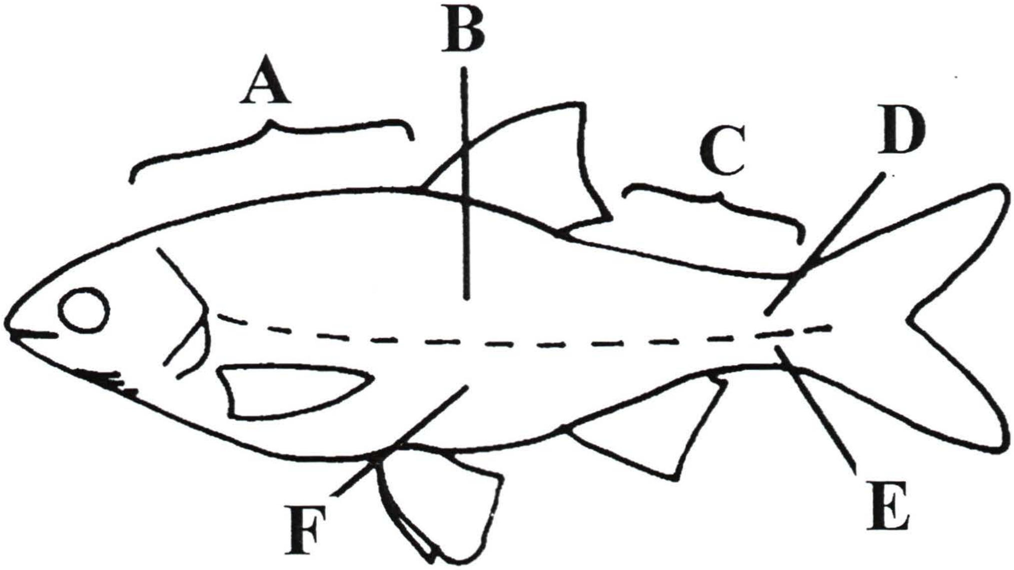

Figure 2.5. Areas sampled for scale collection (Modified from Casteel 1976)

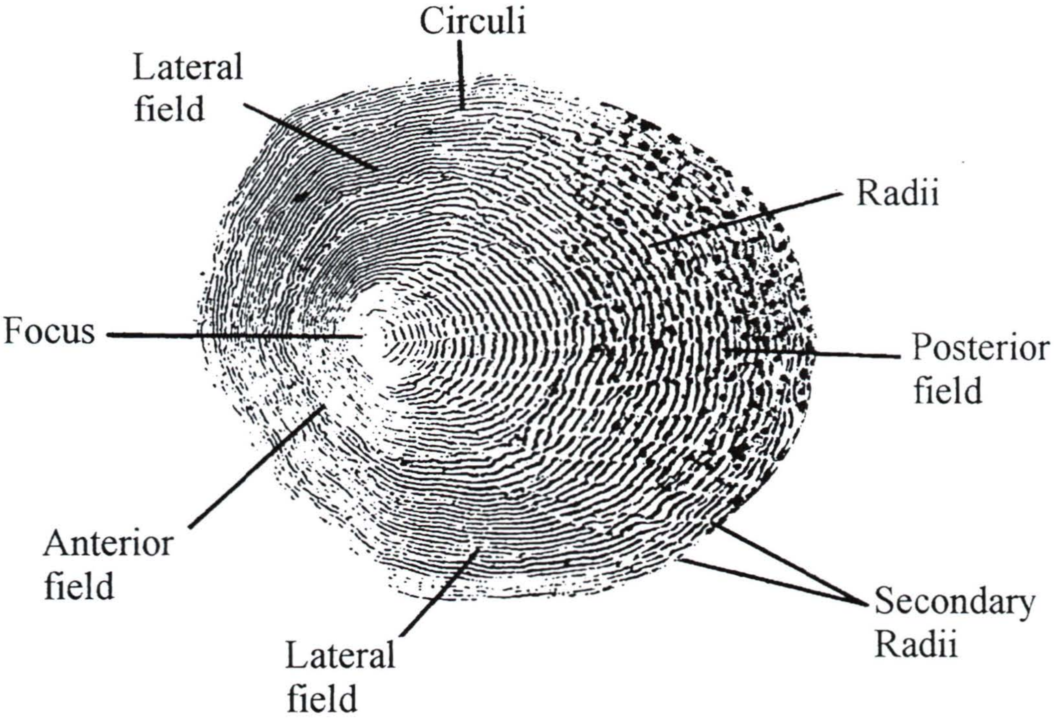

Figure 2.6. Morphological features of fish scales used in identification (Modified from Casteel 1976).

counted. The features of the vertebrae that facilitate identification include centrum pattern, texture, and shape of the vertebral processes (Cannon 1987).

All scale and bone data were organized and managed in spreadsheets using Microsoft EXCEL© (Appendix 2). The data were standardized to a common unit of "# enumerated remains/1000cm^2 x 2-years" (*sensu* Soutar and Isaacs 1974) to account for differences in core sampling areas. This standardization was required because the sampling area of the cores was not consistent due to trimming of cores 1A, 1B and 1C. Summary statistics (total, mean and standard deviation) were calculated using SPLUS©.

Outliers and replicates

Once enumerations were complete, outliers were removed from the scale datasets. Outliers were defined as those enumerations that fell above or below two standard deviations from the mean. The removed outliers (X) were replaced by calculating 40% of each of the immediate neighbour values ($n_{t+/-1}$) and 10% of the next-to-neighbour ($n_{t+/-2}$) values ($X= 0.1*n_{t-2}+ 0.4*n_{t-1} + 0.4*n_{t+1} + 0.1*n_{t+2}$). This treatment of outliers assumes that the system has memory of past occurrences and that what happens in the future depends on the past. As data in most time series are autocorrelated, this assumption was posited to be relatively low-risk (M. Tsao, pers. comm.).

Five cores were taken from Saanich Inlet for this study, each covering between 57 and 115 years. Due to the variation in core recovery lengths, total overlap across all cores was not achieved (Figure 2-3).

Preservation

The condition and numbers of the scales and vertebrae down-core were considered to assess the degree of damage or dissolution of remains through time. Preservation was also assessed using scatterplots of scales to vertebrae as well as interpretation of the bone-to-scale ratio down-core. The scatterplots were also used to assess the correspondence of scales to vertebrae through the cores.

PART II - Time Series Analysis

Low –frequency peaks

Subsequent to outlier removal and analysis of replicates, congruency of smoothed data between cores was investigated using 5-sample running means. Running means were posited to allow a clearer illustration of low-frequency robust trends, cycles and peaks in the data. Running means may also smooth out incongruencies resulting from potential uncertainties in core chronologies and alignment.

High frequency peaks

All formal time series analyses were done using SPLUS© to explore high-frequency peaks in the data (SPLUS© 1998).

Stationarity

An underlying assumption in time series analysis is stationarity. A stationary series is in statistical equilibrium and contains no trends. Most methods of dealing with non-stationary time series are based on techniques for removing or filtering out the non-stationary parts and leaving behind a series that can be treated as stationary (Bendat and Piersol 1986; Bloomfield 1976; Chatfield 1989; Jenkins and Watts 1968)

To meet the assumptions of stationarity, the data were filtered using a high-pass filter to remove low frequency trends and cycles. For the filter, a 10-sample running mean was subtracted from each dataset in EXCEL©. The resulting high-frequency residuals were subsequently used in all time series analyses. SPLUS© automatically detrends and demeans the data when performing time series functions so that after filtering and detrending, the data were assumed to be stationary.

Autocorrelation

Autocorrelation analyses of the high-frequency scale and bone datasets were tested for sample-to-sample influences through time. Autocorrelation measures the correlation between observations at different distances (k) apart (in this case, "distance" means core depth). Interpretation of a set of autocorrelation coefficients (ACF) was facilitated by generation of correlograms in which r_k (autocorrelation coefficient) is plotted against the lag k. Integral time scales (ITS) of peaks in the data were calculated using ACFs. The ITS is a measure of the time between independent peaks that explain the most variance in the data. For this study, the ITS is calculated as the sum of the autocorrelation coefficients to the zero crossing on the correlogram.

Scatterplot correlation and cross-spectra

A major concern over the value of fish scale deposition as a proxy for estimating relative changes in fish population sizes is how sensitive the "basin-wide" scale deposition signal is to changes in the regional distribution and abundance of fish. Core replicates both within and among sites were preliminarily assessed for similarities between points of overlap using visual correlation of the time series and scatterplots. Spectral density plots and coherency and phase spectra were derived from the filtered low-frequency residuals to look for similarities in spectral amplitude between cores (Denman 1975).

Scatterplots were generated for each combination of cores using SIGMAplot©. Coherency spectra were derived from the scale data to look for similarities in frequency signals at different sites. This technique is especially useful considering the inconsistent overlap between cores – analysis in the frequency domain will "tease out" the underlying structure in the data and will not require that data consideration be limited only to regions of overlap. Another function derived from cross-spectral analysis is the phase spectrum. The phase spectrum shows whether frequency components of one series lag or lead the components at the same frequency in the other series (Bloomfield 1976; Kendall et al. 1983).

PART III – Experiments in remains transfer to the sediments

In this portion of the study, an experimental analysis of scale and bone transfer to the sediments was undertaken at the Vancouver Aquarium, Vancouver, British Columbia. Previously, little attention has been given this detail and its potential to alter paleo-interpretations.

Scale loss experiments

When considering processes involved in scale transfer from fish to the sediments, it is useful to know the average number of scales found on the fish species in question. Scales form on fish when they are small (~25mm), just as they begin to metamorphose into their juvenile form (Hourston and Haegele 1980), and their numbers are thought to remain constant over the lifetime of the fish (Miller 1955).

Assuming bilateral symmetry, scales were removed and counted from the left side of 10 dead three to five year old Pacific herring (*Clupea harengus pallasi*). The specimens were selected to cover as wide a spectrum of lengths and widths as was possible with the available fish. The fish were killed using chloroform as this method resulted in the lowest number of scales dislodged during dispatch. The scales were removed and counted and standard length and weight were recorded for each fish.

Scale loss due to deciduous shedding

To quantify scale shedding, a large experimental tank was stocked with herring for experimentation. Care was taken that the tank remained undisturbed over the trial period. One hundred young-of-the-year herring were placed into the tank and given a week to acclimate. The tank was siphoned at regular intervals for shed scales. Prior to siphoning, the tank inflow and outflow were shut off to allow solid material to settle to the bottom of the tank. Care was taken to minimize disturbance of the fish during the siphoning.

Sampling effort was assessed in terms of "siphoning passes". A single siphon pass was considered complete when three 10-liter buckets were filled. Scales and other material collected during siphoning were sieved through a 125 μm sieve and were subsequently stored for counting in 70% ethanol. In addition to the weekly intensive scale siphoning, a standard siphoning/cleanup was undertaken three times a week by the aquarists and the residue retained. At the University of Victoria, the scales collected were picked and counted under a dissecting microscope.

To assess the recovery efficiency of the experimental siphoning technique, 100 scales from adult herring were dyed with crystal violet, and dropped into the tank. After an hour settling, the scales were siphoned using the same regimen as in the experimental trials.

Scale loss due to predation

Before human exploitation, most fish mortality was due to natural predation. Pelagic fish stocks in Saanich Inlet support piscivorous fish, birds, marine mammals, and other predators. If fish shed more when they are being attacked and consumed, these scales may potentially contribute a corresponding pulse of scales to the sediments. In a paleo-study, these pulses could mistakenly be interpreted as increased scale flux to the sediments due to larger populations of fish.

Lingcod (*Ophiodon elongatus*) and black rockfish (*Sebastes melanops*) were selected as major herring predators to assess the effects of piscivorous predatory feeding on the transference of herring remains to the sediments. Both of these fish are common in Saanich Inlet and were thus considered realistic experimental models for this system.

For the lingcod trials, five juvenile lingcod predators were moved to an experimental tank at the Vancouver Aquarium. The tank was the same size and shape as the herring tank and was set away from major traffic. The fish were left to acclimate for a week. For each feeding trial, five herring were fed to the lingcod once a week. Observations of behaviour and characteristics of herring scale shedding were noted. Immediately after the herring were consumed, the shed scales were siphoned, sieved, and counted. In the week between herring feeds, the lingcod predators were fed chopped euphausiids.

Collected solids were sieved and rinsed into vials for analysis and scale counting, and were preserved with 70% ethanol. During the weekly feeding trial, three siphoning passes were conducted immediately after each feeding to assess scale loss during a predator attack and consumption. Subsequent to herring feeds, and only once the scale collection for predatory scale loss assessments was complete, the debris that accumulated at the bottom of the tanks was siphoned and sieved twice a week by the aquarists at the Vancouver Aquarium. The tanks were also more thoroughly and intensively siphoned once a week immediately prior to the introduction of the herring for the feeding trials. The solids collected were amalgamated, and taken to represent weekly fecal samples. The lingcod feces were qualified and vertebrae and otoliths quantified to assess the degree to which these remains are digested as they pass through the gut of this predator.

Black Rockfish, *Sebastes melanops*, was chosen as another predator with which to investigate the amount of shedding that occurred due to predation, and to look at the passage of remains through the gut of this predator. Unlike lingcod, rockfish did not immediately consume the herring over the course of a weekly visit. Instead, the herring were consumed over a few days and thus, the rockfish tanks were siphoned only to collect feces to assess passage of herring remains through the gut of this predator. As with the lingcod, five rockfish were selected for the trials, were given a week to acclimate to the experimental tank, and were fed five herring a week. All other procedures were as for the lingcod.

RESULTS

PART I – Core collection and fish remains data

Core Characteristics and sub-sampling

The years between and around the known diatom horizons (Figure 2-3) are postulated to be very accurately aligned and dated however calendar dates on more recent indistinctly laminated sediments should be taken as estimations within +/- 5 years (M. McQuoid, personal communication).

Identification and enumeration

The remains of 16 taxa were recovered from these cores. Identifiable remains include Pacific herring (*Clupea harengus pallasi*), Pacific hake (*Merluccius productus*), Pacific sardine (*Sardinops sagax*), lingcod (*Ophiodon elongatus*), Northern anchovy (*Engraulis mordax*), Pacific mackerel (*Scomber japonicus*), Pacific cod (*Gadus macrocephalus*), eulachon (*Thaleichthys pacificus*), and Pacific sandlance (*Ammodytes hexapterus*). Remains of perch, rockfish, salmon (*Onchorhynchus* sp.), sculpins, flatfish, and gunnels were not possible to identify to species.

Most (~90%) of the scales were herring or hake and most vertebral remains were herring, hake, or sandlance (Table 2-3). From the scale data (Table 2-4), high average herring counts corresponded to low average hake counts (e.g. core 2B: 73 herring/11 hake, 1C: 42 herring/6 hake) and vice versa (2A: 26 herring/16 hake). Also, in core 1A, the lowest maximum count of herring (82) corresponded to the highest maximum count of hake (77). Standard deviations were high for all scale counts, as the data were highly variable.

The hake and herring vertebra data showed different trends (Table 2-5). The highest maximum count and mean of herring vertebrae corresponded to the highest maximum and mean of hake vertebrae (2A: 62.3/19.7 herring, 17/2.9 hake).

Table 2-3. Percentage of fish scales and vertebrae in Saanich Inlet box cores identified as herring, hake, sandlance, or other. All data are standardized (# remains/1000cm^2 x 2-years) and outliers have been removed.

CORE	SCALES			VERTEBRAE			
	%herring	%hake	%other	%herring	%hake	% sandlance	%other
1A	54.9	39.4	5.7	79.2	5.4	13.7	1.6
1B	75.9	15.9	8.2	92.2	1.8	5.4	0.6
1C	76.9	10.9	12.2	87.6	7.6	0	4.7
2A	51.0	30.0	19.4	72.4	10.5	5.4	11.7
2B	80.2	13.4	6.4	72.5	6.6	8.1	12.8

Table 2-4. Standardized herring and hake scale summaries: total # samples, total # scales, mean and standard deviations and maximum enumerations in a 2 year sample. The data have been standardized and outliers removed.

Core	Total # samples	Total # herring scales	Mean # & s.d. herring scales	Max # herring scales	Total # hake scales	Mean # & s.d. hake scales	Max # hake scales
1A	46	1327	29 (+/- 27)	82	635	14 (+/- 14)	77
1B	29	919	32 (+/-31)	138	440	15 (+/- 9)	41
1C	58	2454	42 (+/- 38)	138	321	6 (+/- 6)	20
2A	40	1030	26 (+/- 23)	97	656	16 (+/- 11)	38
2B	46	3341	73 (+/- 35)	156	489	11 (+/- 9)	35

Table 2-5. Standardized box core herring and hake vertebra summaries total # samples, total # vertebrae, mean and standard deviations and maximum enumerations. The data have been standardized however due to low numbers, no outliers were removed from the hake vertebra data.

Core	Total # samples	Total # herring vertebrae	Mean # & s.d. herring vertebrae	Max # herring vert.	Total # hake vert.	Mean # & s.d. hake vertebrae	Max # hake vertebrae
1A	46	606	13 (+/- 13)	56	87	2 (+/- 4)	15
1B	29	248	9 (+/- 11)	36	15	1 (+/- 2)	10
1C	58	395	7 (+/- 7)	56	51	1 (+/- 3)	15
2A	41	789	20 (+/- 17)	62	114	3 (+/- 4)	17
2B	46	432	9 (+/- 6)	23	55	1 (+/- 2)	8

Outlier removals and replicates

For all summaries and in all analyses, standardized data are presented and used. Figures 2-7A) and 2-7B) illustrate the importance of removing outliers. Without outlier removal, anomalously high counts are exaggerated and relatively lower amplitude changes are muted. The sources of anomalous pulses in the sediment record are postulated to be variable across a basin, therefore outlier removal is necessary. The standardized, outlier-free herring scale abundances are noisy through time (Figure 2-8A and B). Cores 1A-1C illustrate the fact that the high frequency abundance signals in these replicates are often incongruent (Figure 2-8A). For example, the 1955-56 samples encompass the entire variability across the records (Figure 2-8A: 1A=0, 1B=56.1, 1C=137.8 scales/1000cm^2 x 2-years).

The importance of outlier removals to facilitate the examination of trends outside of anomalous pulses is again evident in the hake data (Figures 2-9A and 2-9B). Consistently fewer hake scales were recovered than herring scales in all cores; as with the herring data, once outliers were removed, the hake record was highly variable but more amenable for interpretation (Figures 2-10A and 2-10B). There are further instances where a series high corresponds to a series low: in 1903-04, there were zero hake scales in core 1C and 76 hake scales in core 1A (Figure 2-10A). Once again, this illustrates the variability inherent in these data and highlights the potential for very different interpretations if only one core is used to hindcast fish populations from scale records. The total number of samples removed and replaced as outliers in all cores is 15 (Table 2-6).

There were only 40 years of congruent overlap across all cores. From the time series plots the differences between the sites are not obvious. Instead, these plots show a high degree of noise and variation across all cores at high frequencies.

Preservation – scales and vertebrae

Herring scales retrieved in the sediment cores were often fragmented and damaged and rarely was the wing-join still attached (Figure 2-11A). Scale fragments were broken along points of weakness. The majority of hake scales found in the sediment samples were intact and well preserved, showing little visual evidence of either mechanical abrasion or dissolution (Figure 2-11B).

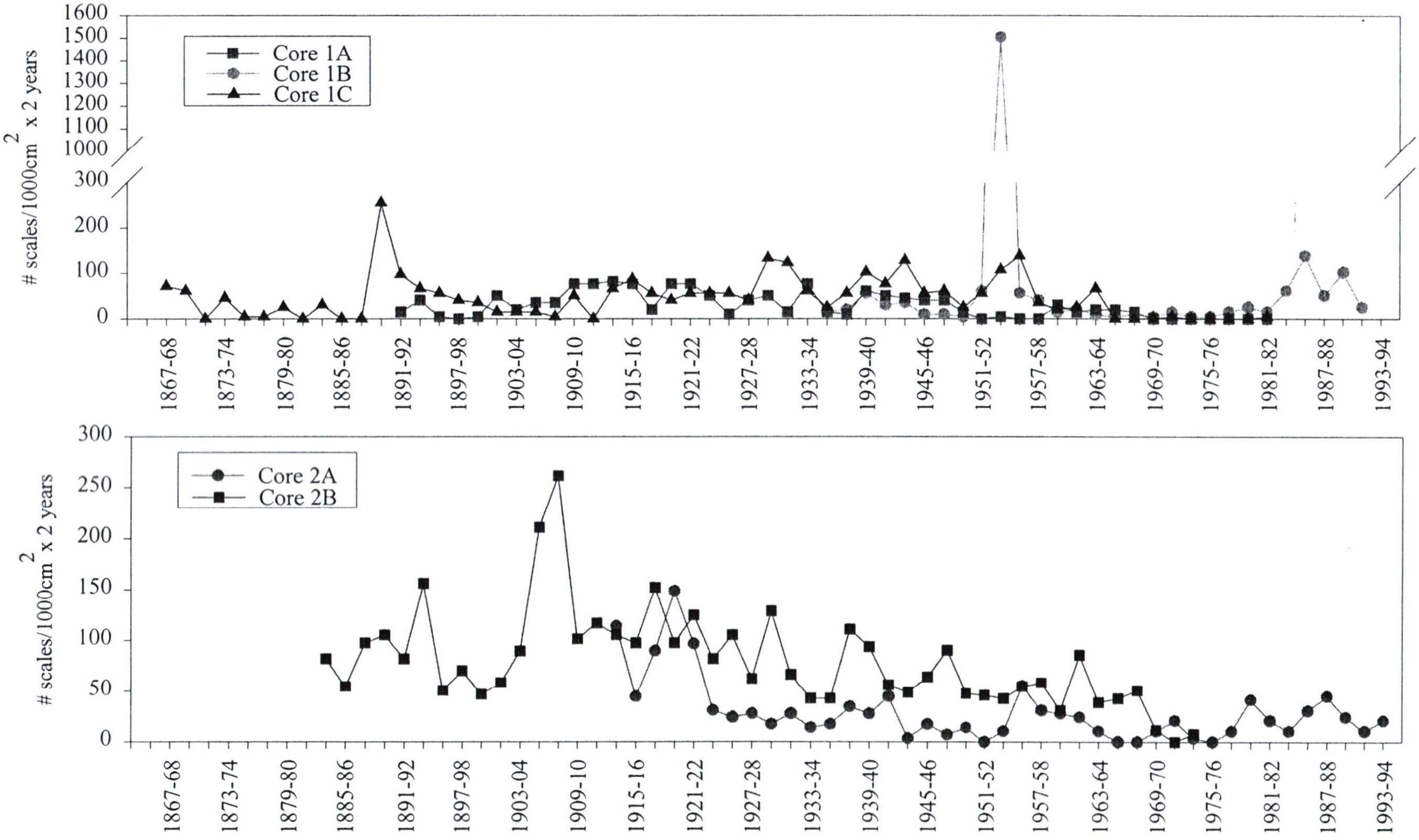

Figure 2.7. Raw herring scale data with no outliers removed (Standardized). A) Site 1(mid-Inlet); B) Site 2 (Near the sill)

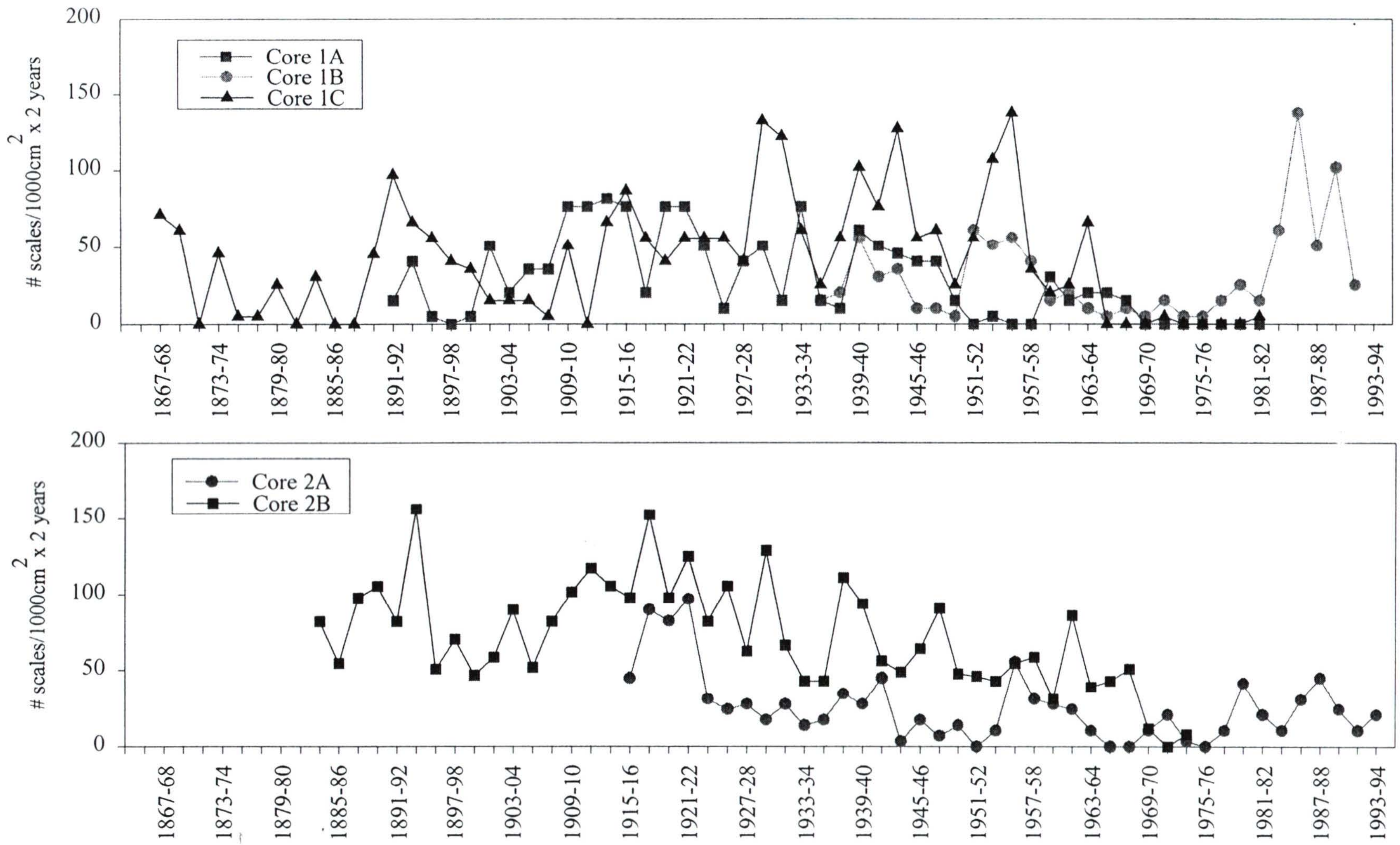

Figure 2.8. Herring scale data with outliers removed (Standardized). A) Site 1; B) Site 2.

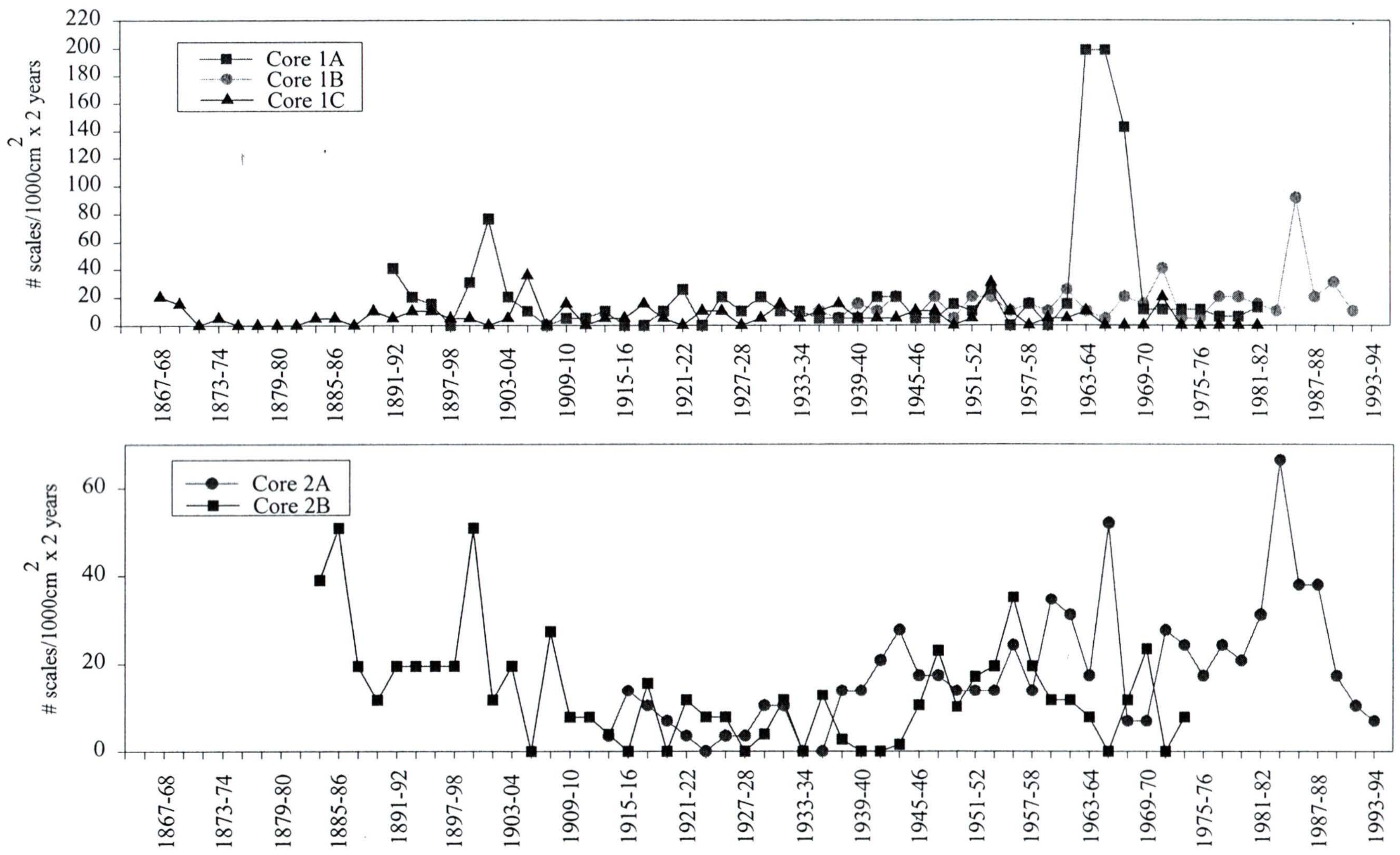

Figure 2.9. Raw hake scale data (Standardized). A) Site 1 (mid-Inlet); B) Site 2 (near sill)

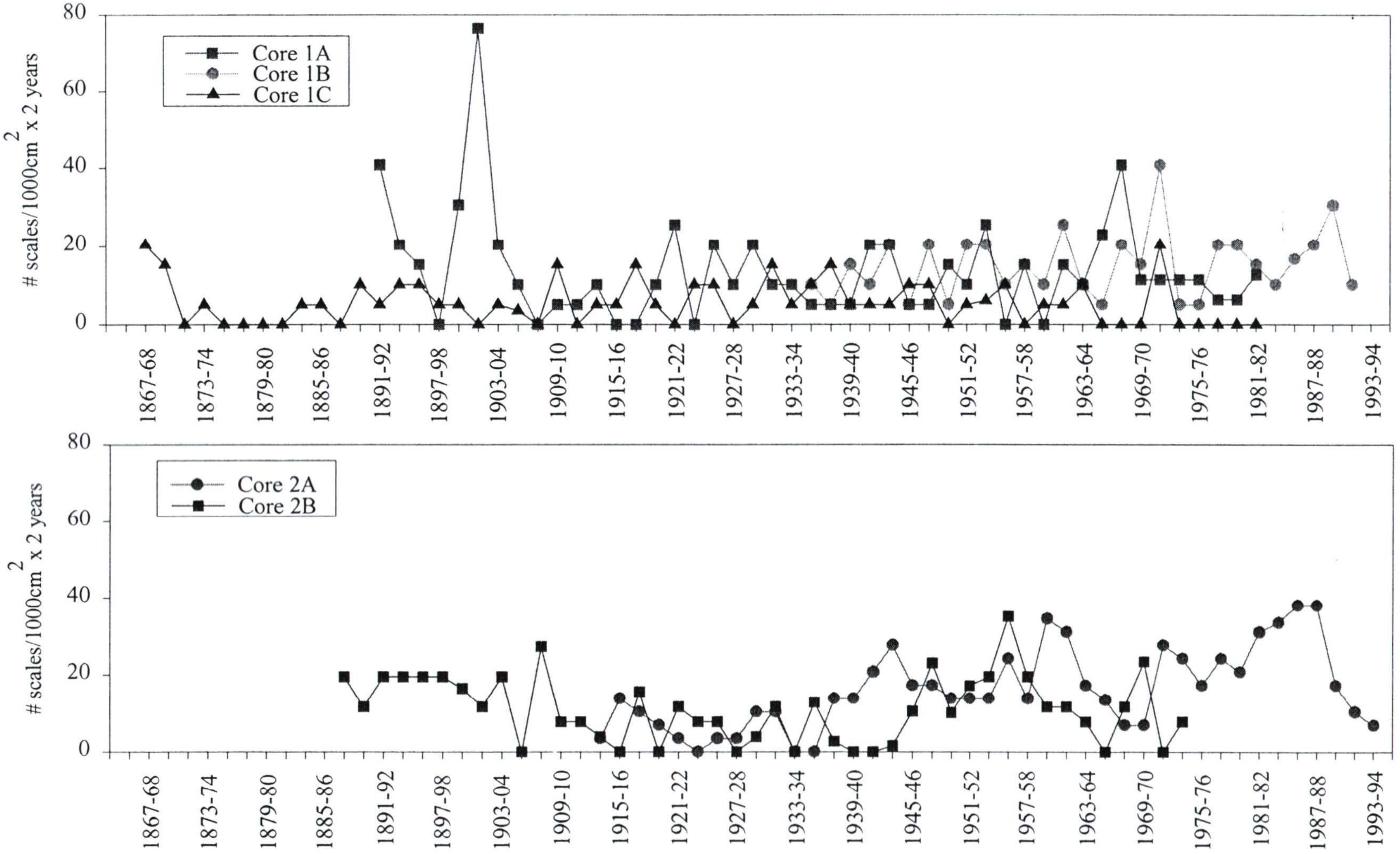

Figure 2.10. Hake scale data with outliers removed (Standardized): A) Site 1, B) Site 2.

Table 2.6. Samples removed and replaced from each core for outlier treatments as a percentage of the total number of samples in the core

Core	**Herring samples**	**Hake samples**
1A	0	4%
1B	3%	3%
1C	2%	3%
2A	5%	5%
2B	4%	4%

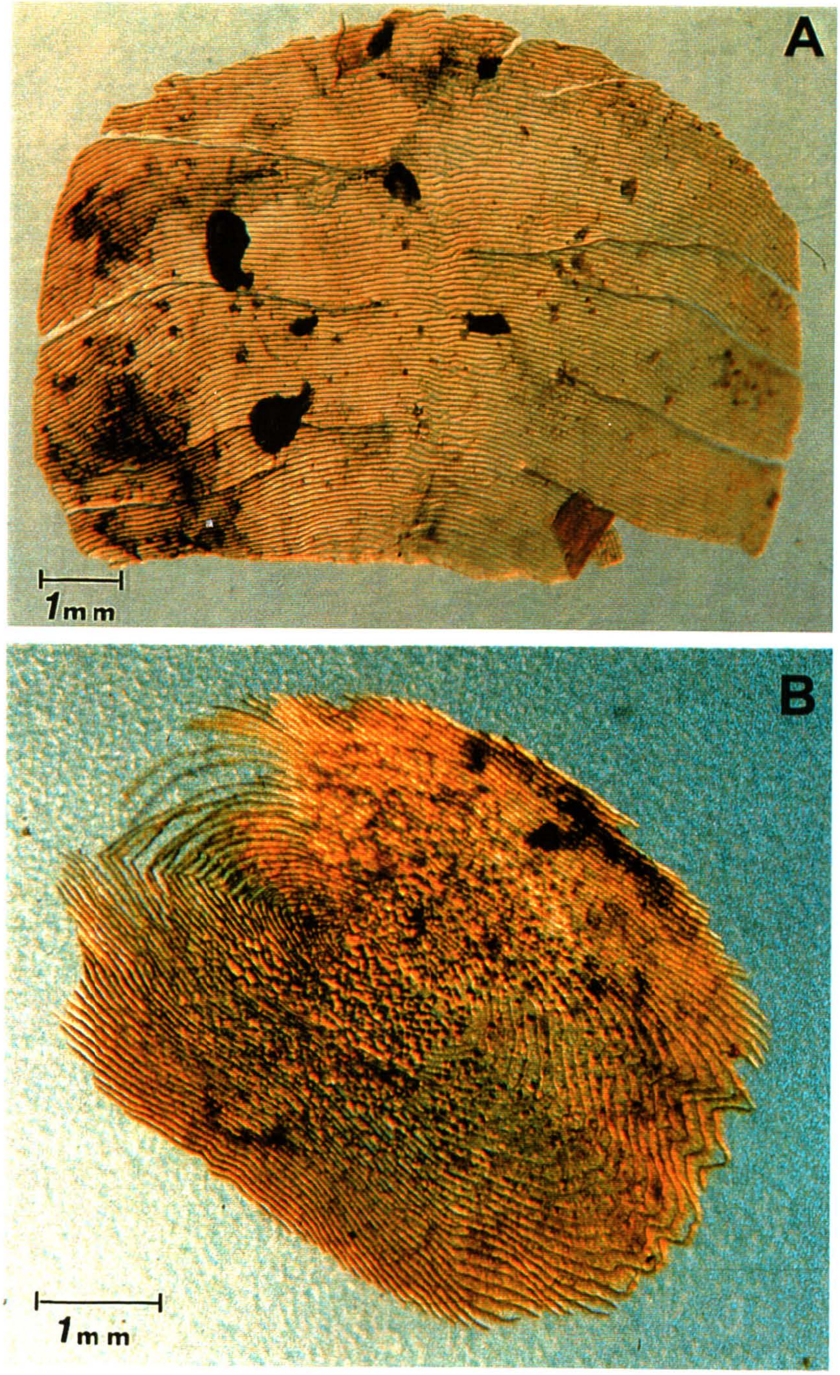

Figure 2.11. Typical Pacific herring (A) and hake (B) scales from Saanich Inlet sediments.

Fewer vertebrae were recovered than scales. Recovered vertebrae were all from very small fish and showed varying distribution throughout the cores. Although there appears to be no consistent decline in herring scale numbers with time (Figure 2-8), in many cores, herring vertebrae appear in greater abundance after 1920 (Figure 2-12). The consistent low numbers before 1920 and the lack of correspondence between the vertebra and scale data suggest that this low number could result from dissolution or poor preservation of herring vertebrae in Saanich Inlet sediments. The hake scales also show no obvious indication of dissolution (Figure 2-10); because the number of hake vertebrae recovered is not numerous, preservation is difficult to interpret (Figure 2-13).

Scatterplots of herring scales against vertebrae showed that there was no tendency for herring scale numbers to increase with herring vertebra numbers in the sediment samples (these plots are not presented). As scale numbers increased, vertebra numbers would remain unchanged or show varying responses to increases in scale numbers. Overall, scales and vertebrae do not show the same trends and vertebrae were much less numerous.

Vertebra to scale ratios calculated from the herring data show large aperiodic peaks (Figure 2-14). With the exception of core 2B, no strong or consistent trend in the ratio with depth was observed in the cores. The presence of numerous vertebrae and scales in all but one sample from this anomalous core generated a complete down-core signature however, the high average abundance of scales paired with the relatively low average abundance of vertebrae in core 2B makes this profile of vertebra/scale ratios difficult to interpret (Tables 2-4 and 2-5). Hake vertebra to scale ratios were not calculated because of the few hake vertebrae recovered in the five cores. It is postulated that vertebrae are introduced only sporadically into the sediments whereas there is a more consistent source for scales.

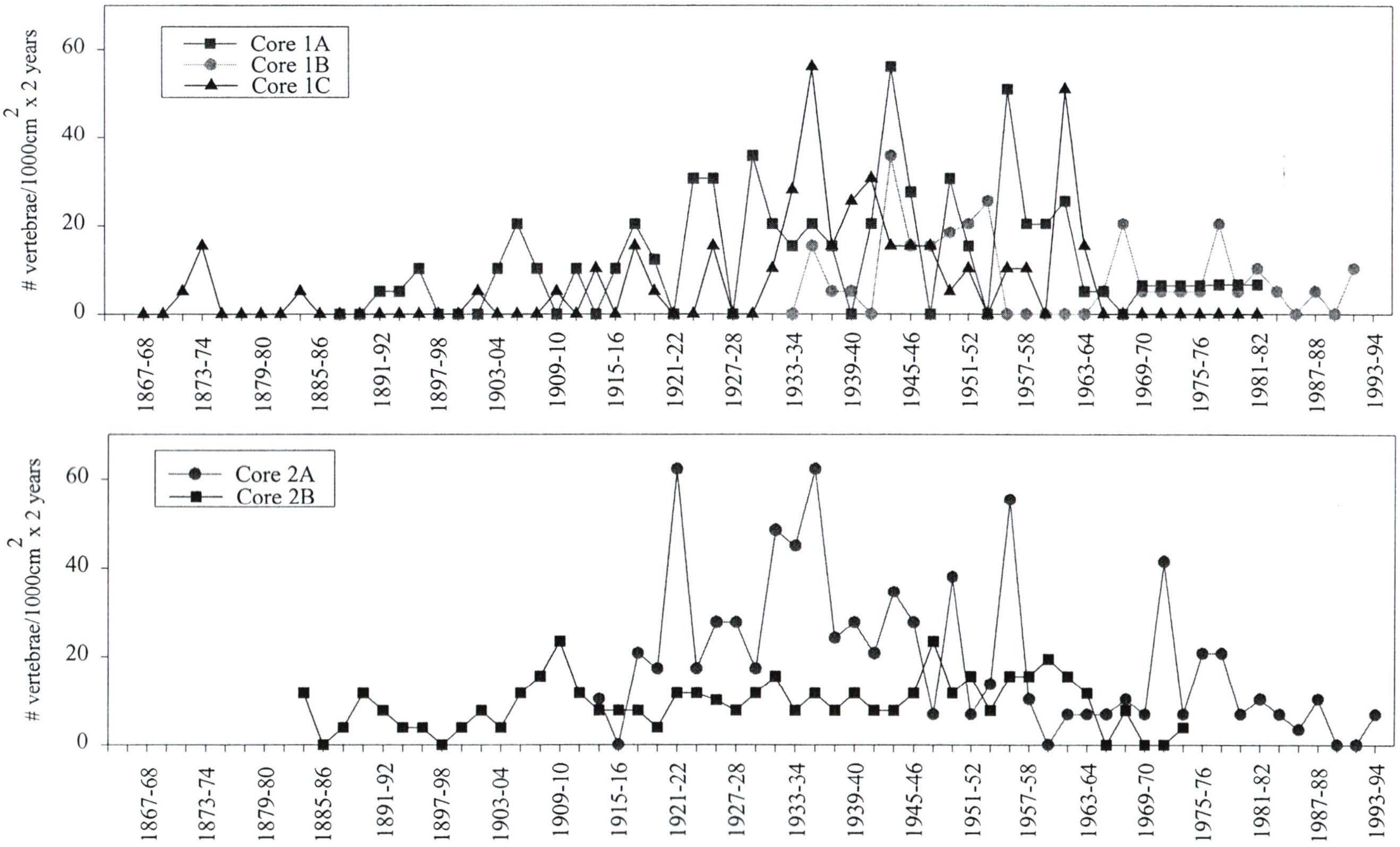

Figure 2.12. Herring bone data (Standardized, outliers removed). A) Site 1; B) Site 2.

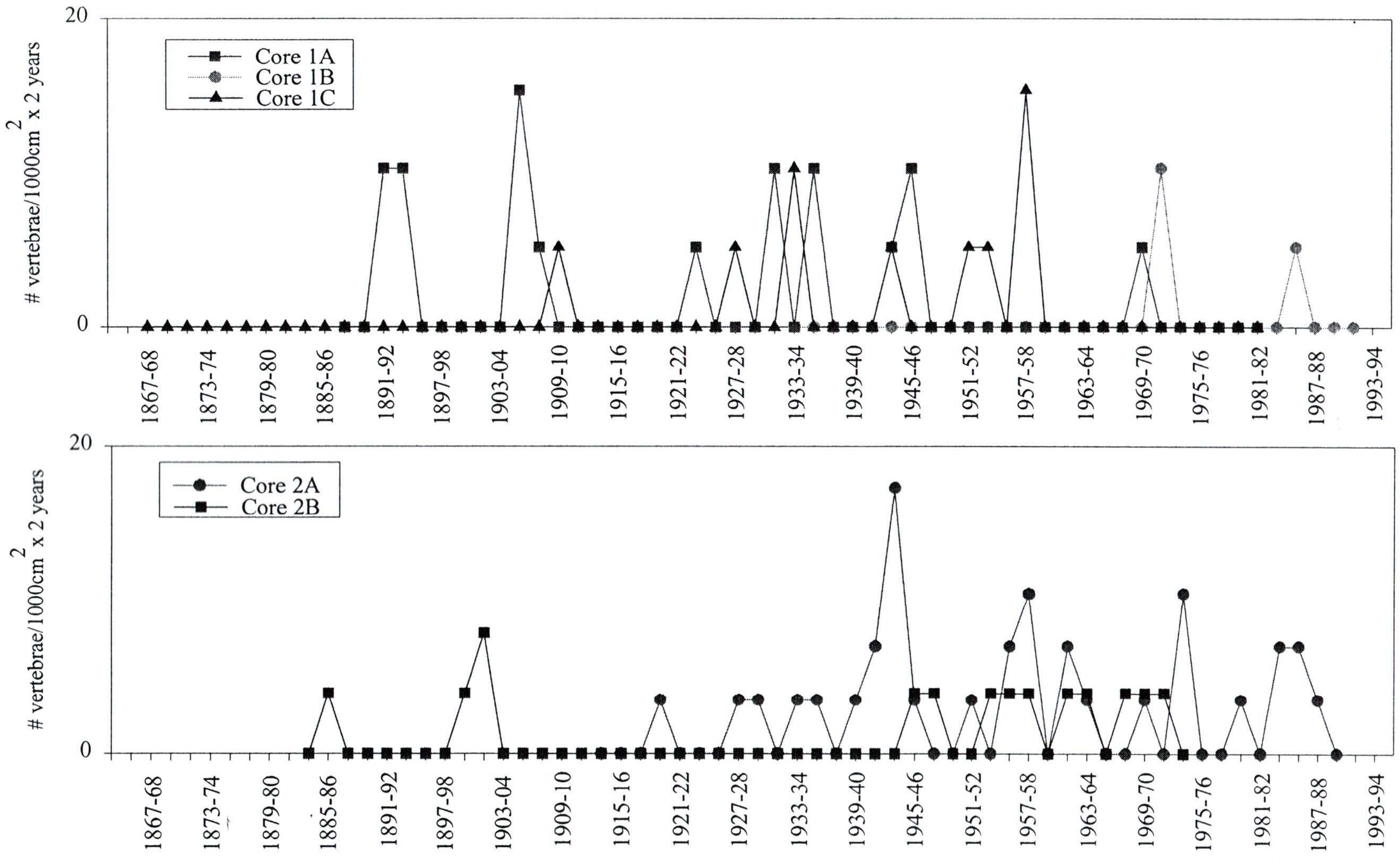

Figure 2.13. Hake bone data (Standardized, no outliers removed). A) Site 1; B) Site 2.

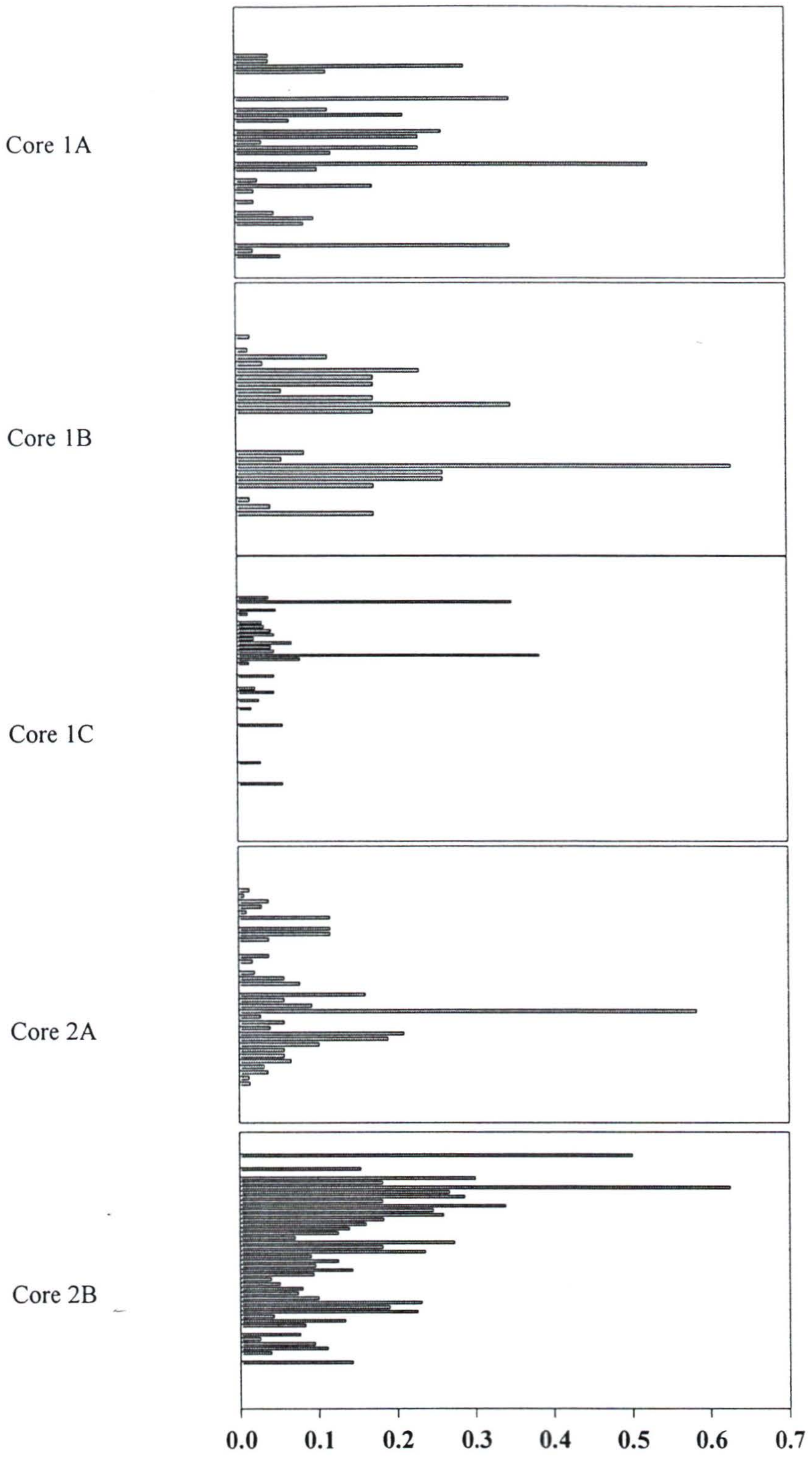

Figure 2.14. Herring vertebra:scale ratios with increasing depth in the cores.

PART II – Time series

Low frequency peaks

In an attempt to smooth the noisy scale data to enhance robust low-frequency trends and matching, a 5-sample running mean is presented (Figures 2-15 and 2-16). The 5-sample running means show robust variation and the herring and hake data appear to be better aligned. This smoothing helps to define some consistent low-frequency congruencies across cores. The herring scale data in core 2B has consistently higher scale counts throughout the record (Figure 2-15).

High frequency peaks

Autocorrelation

Herring data were autocorrelated between two and four lags (Appendix 3A). The integral time scales calculated for the herring scale data fell between four and seven. The hake correlograms were inconsistent and hard to interpret, falling between zero and 18 lags (Appendix 3B), however, integral time scales varied between two and six. In spite of the differences in significant autocorrelation lags, the integral time scales indicated that the underlying frequencies of peaks in the two time series were similar.

Spectral analysis

Herring scale data in most cores had a substantial amount of variance concentrated in the five to seven, 20 and 40-year periods (Appendix 4A). Most variance in the hake scale data was concentrated in the five to seven, 13, and 20-year periods (Appendix 4B). Both datasets had a large proportion of variance concentrated at 60-80 years but as the core datasets are all within 10-20 years of this period in length, interpretation is difficult.

Correlation and cross-spectra

Scatterplots of the overlapping herring data illustrate the direct sample-to-sample relationship between series (Figure 2-17). In most cores, there is a positive relationship between the majority of scale series across overlapping samples; where there are high numbers in one core, there tend to be highs in another core. Hake scale scatterplots (Figure 2-18) show a similar consistent tendency for increases in scale numbers in one core to be reflected in another core.

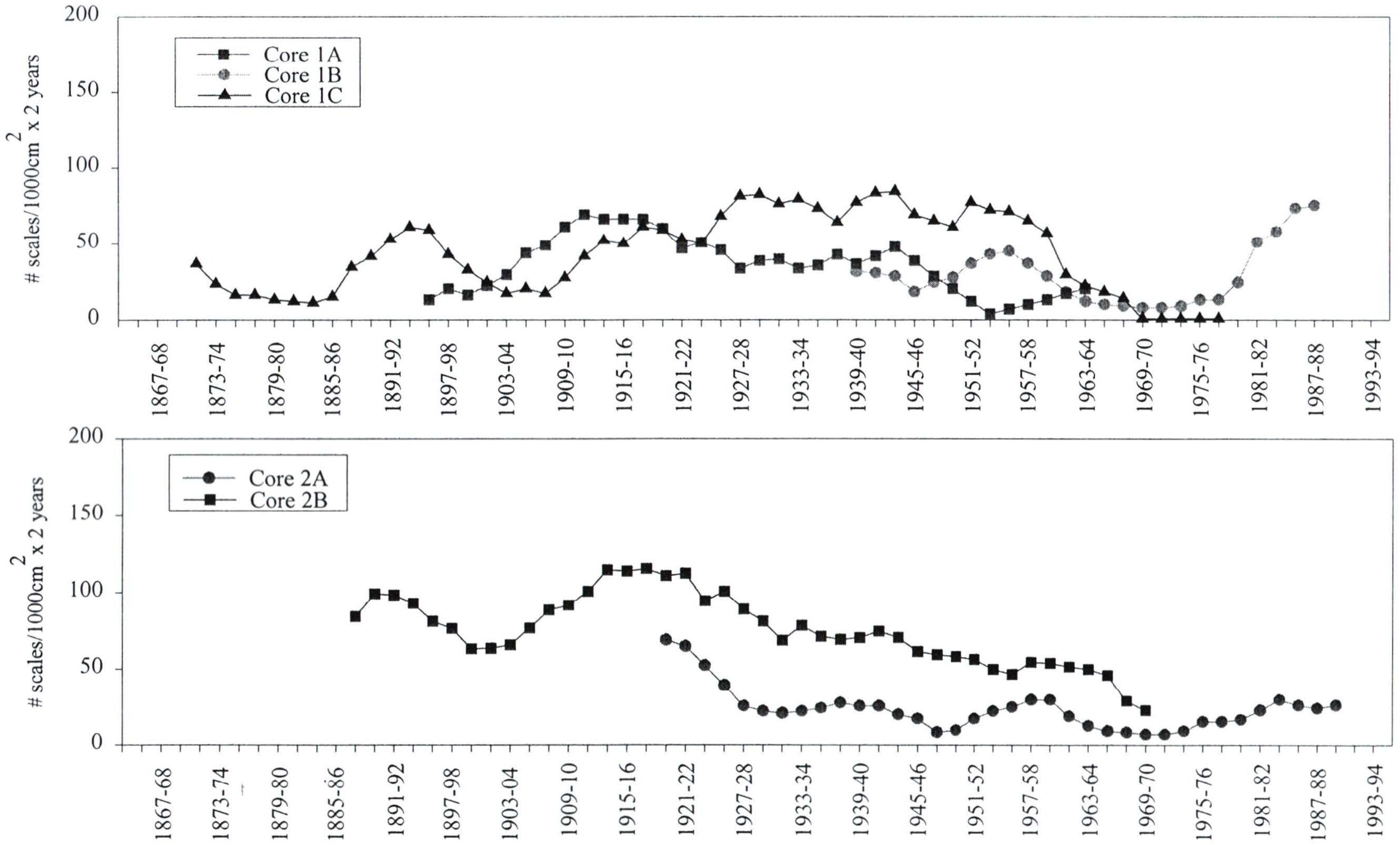

Figure 2.15. Smoothed herring scale data (5-sample running mean) across all cores showing low-frequency events. A) Site 1; B) Site 2.

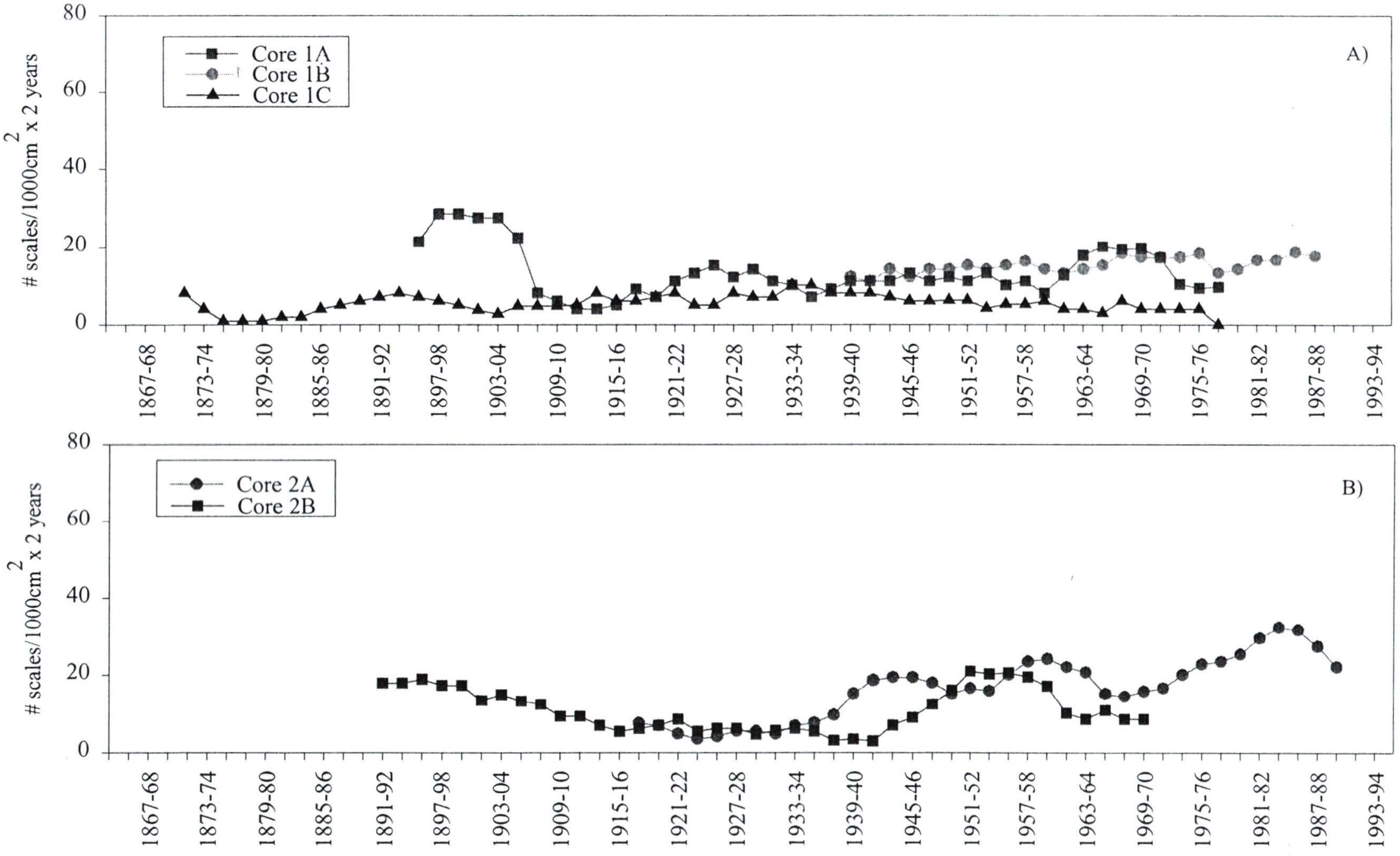

Figure 2.16. Smoothed (5-sample running mean) hake scale data showing low-frequency events. A) Site 1; B) Site 2

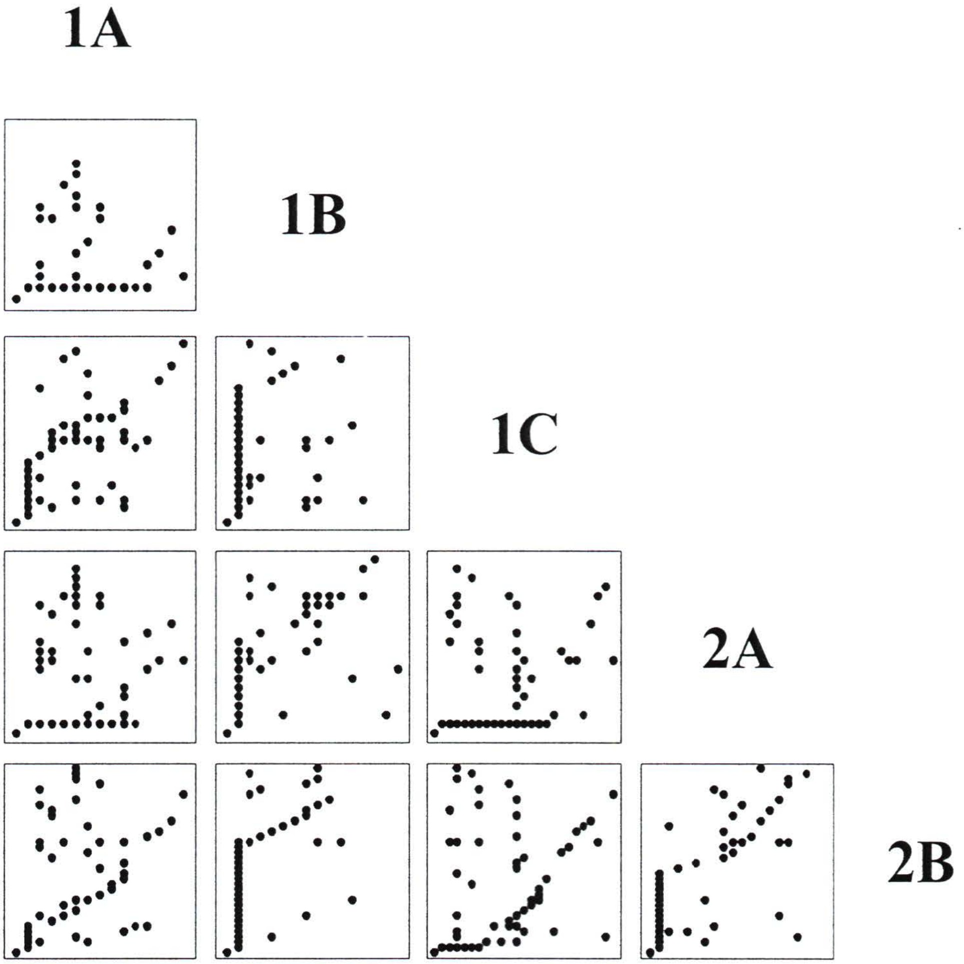

Figure 2.17. Scatterplots: herring scale data across overlap in all cores.

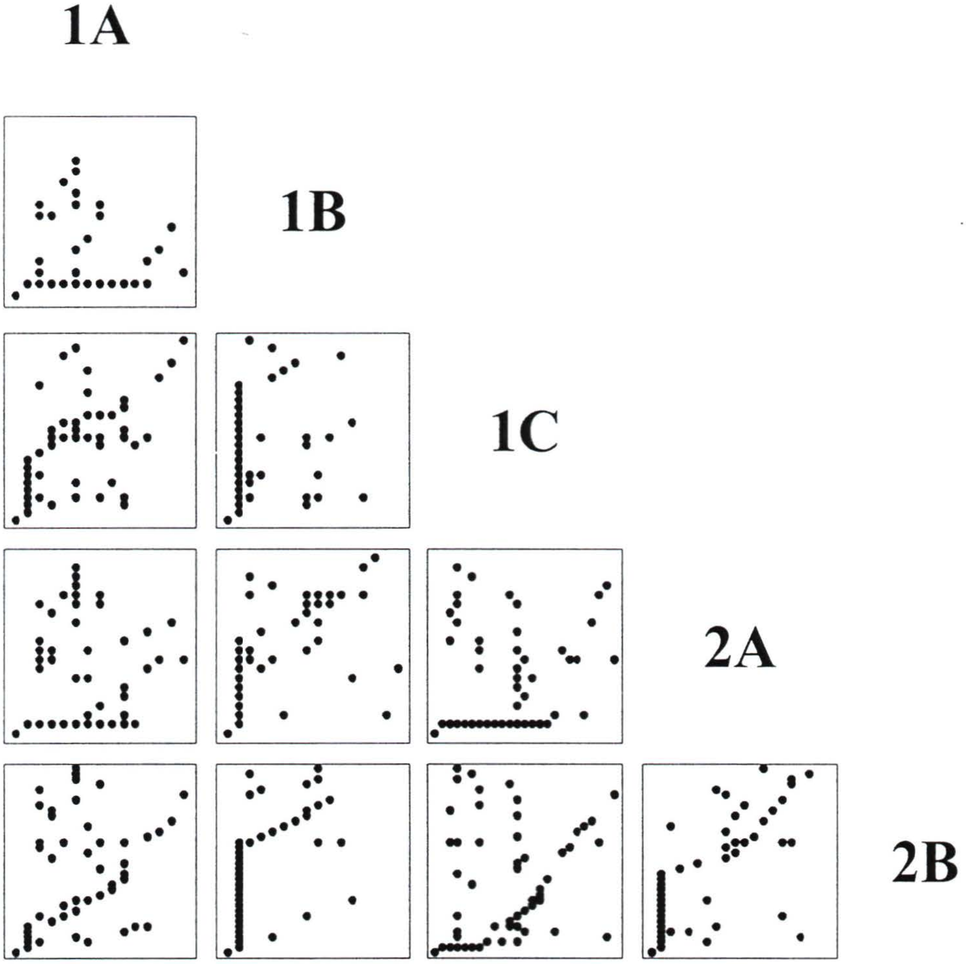

Figure 2.18. Scatterplots: hake scale deposition across all cores.

A sample cross-spectrum generated for the herring scale data is presented (Figure 2-19). Overall, the phase lags are not consistent across cores, however, there are consistent coherent peaks at periods of approximately 20, 10 and five years (Table 2-7) (Appendix 4A).

An example of a hake cross-spectrum is included (Figure 2-20). The hake cross-spectra indicate major peaks at 20 and five to seven years. The lag structure of the hake data is inconsistent (Table 2-8) (Appendix 4B).

PART III- Experiments in remains transfer to the sediments

Number of scales on a fish

The average number of scales on herring between 11-23 cm is approximately 1277 scales (Appendix 5). Assuming complete transfer to the sediment, this number of scales is the maximum that could be introduced into the sediments upon the death of one herring. Relationships between scale number and length and weight were not quantified for Pacific hake due to the difficulty in obtaining undisturbed specimens.

Scale loss due to deciduous shedding

The 100 dyed scales were retrieved by siphoning with approximately 80% recovery (Trial 1, 83% retrieved; Trial 2, 76% retrieved). The average number of scales lost per herring per week due to deciduous shedding was consistent at approximately 2.4 scales (+/- 0.7 scales) (Figure 2-21).

Scale loss due to predation

Herring scale loss due to predation also showed little variability across trials (Figure 2-21). Assuming that all fish of the same species have similar propensities for shedding, the average scale-loss for herring consumed by lingcod is 234.7 (+/- 24.3) scales/fish x week. Juvenile lingcod feeding on juvenile herring required extensive manipulation of their prey before consumption. This prey manipulation seemed to dislodge most of the scales that were lost and later collected. Individual herring lose approximately 100 times more scales when attacked by a predator than when schooling (Figure 2-21).

Figure 2.19. Sample cross-spectral output for herring scale data from cores 1A and 2A. A) Periodogram with 95% confidence intervals for core 1A; B) Periodogram with 95% confidence intervals for core 2A; C) Coherence spectrum cores 1A and 2A. Significant peaks are indicated by 95% confidence bars; D) Phase spectrum cores 1A and 2A.

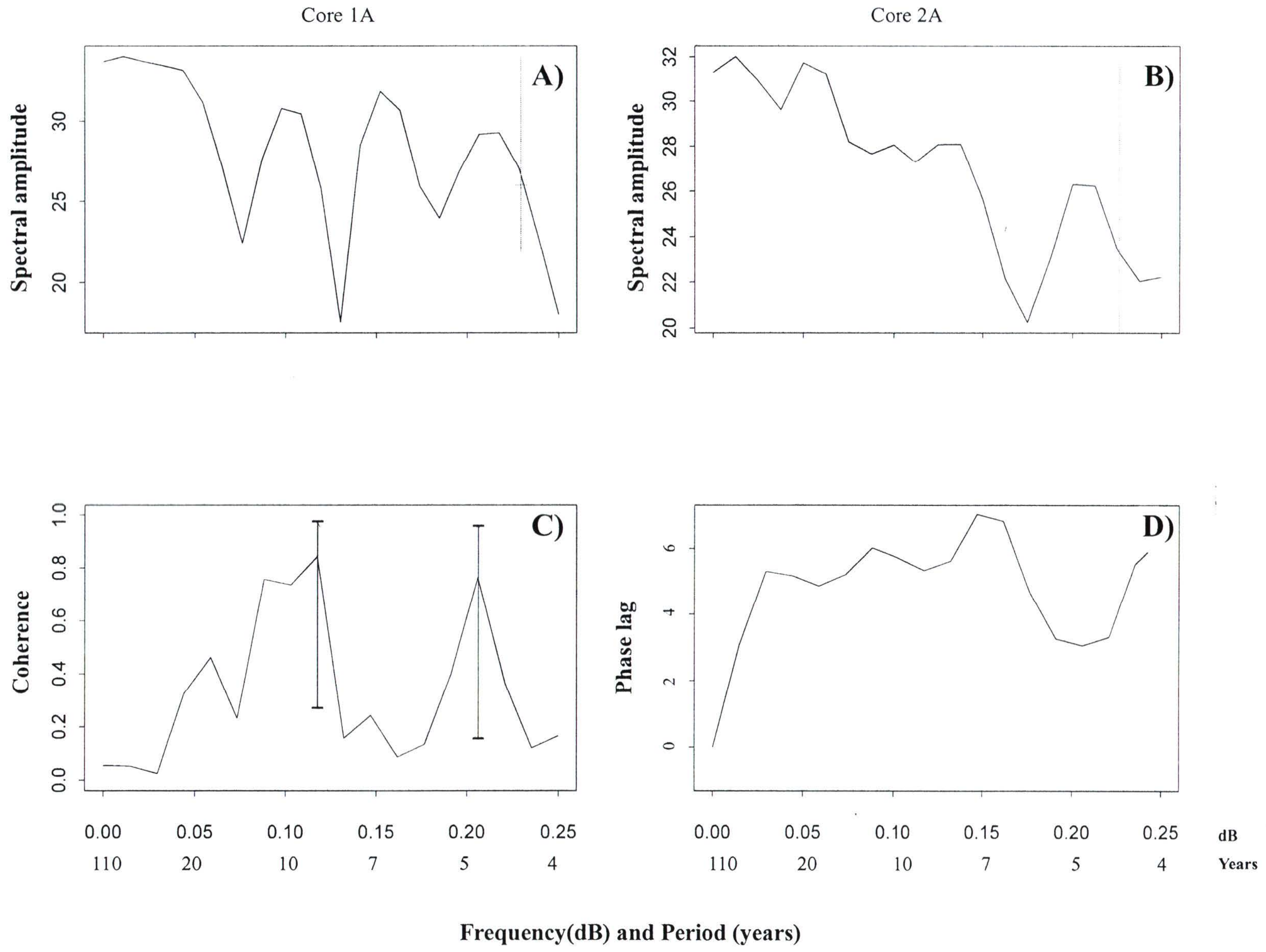
Core 1A
Core 2A
A)
B)
C)
D)
Spectral amplitude
Spectral amplitude
Coherence
Phase lag
20
25
30
20
22
24
26
28
30
32
0.0
0.2
0.4
0.6
0.8
1.0
0
2
4
6
0.00
0.05
0.10
0.15
0.20
0.25
110
20
10
7
5
4
dB
Years
Frequency(dB) and Period (years)

Table 2-7. Coherent periods and phase lags for herring scale data among all cores. Coherence is presented below the diagonal and phase above the diagonal. (All indicated periods and phase lags are subject to error due to the estimated +/- 5-year alignment error.)

1A	-2.5 -1.5	-1.0	+6.0 +5.5 +3.0	0 +2.5
20 7	**1B**	0 +0.5		+1.0
13	20 9	**1C**		
11 8 5			**2A**	
20 7	20			**2B**

Figure 2-20. Sample cross-spectral output for hake scale data from cores 1A and 2A. A) Periodogram with 95% confidence intervals for core 1A; B) Periodogram 95% confidence intervals for core 2A; C) Coherence spectrum cores 1A and 2A. Significant peaks are indicated by 95% confidence bars; D) Phase spectrum cores 1A and 2A.

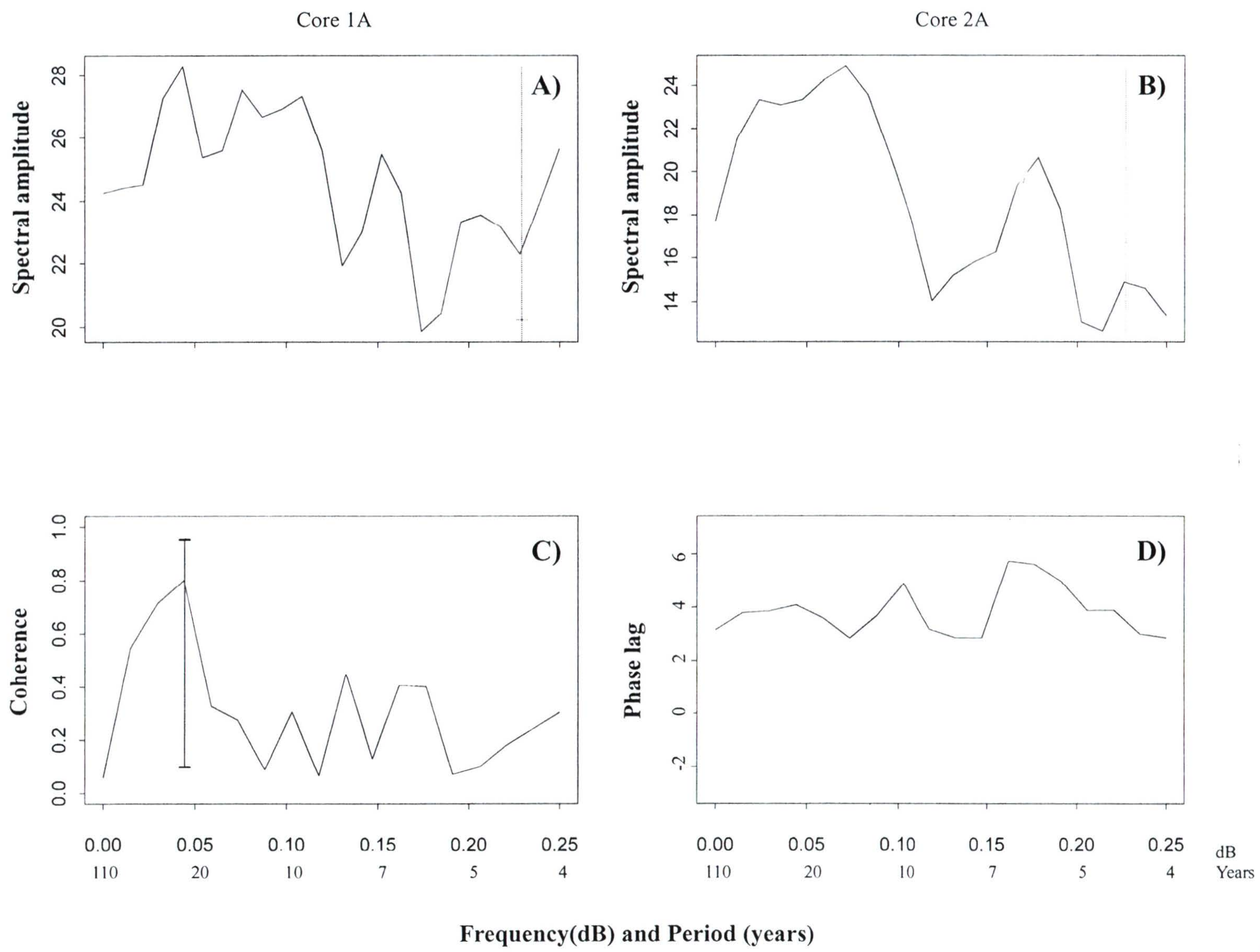
Core 1A
Core 2A
A)
B)
C)
D)
Spectral amplitude
20
22
24
26
28
Spectral amplitude
14
16
18
20
22
24
Coherence
0.0
0.2
0.4
0.6
0.8
1.0
Phase lag
-2
0
2
4
6
0.00
0.05
0.10
0.15
0.20
0.25
dB
110
20
10
7
5
4
Years
Frequency(dB) and Period (years)

Table 2-8. Coherent periods and corresponding phase lags for hake scale data among all cores. Coherence is presented below the diagonal and phase above the diagonal. (All indicated periods and phase lags are subject to error due to the estimated +/- 5-year alignment error.)

1A	+1.0 +6.0	-2.5 -3.0 +1.0	+4.0	
20 5	**1B**	-4.0 -5.0 -5.0	-2.0 -1.0	
20 14 5	10 7 5	**1C**		-1.5 -3.0
20	20 7		**2A**	
		7 5		**2B**

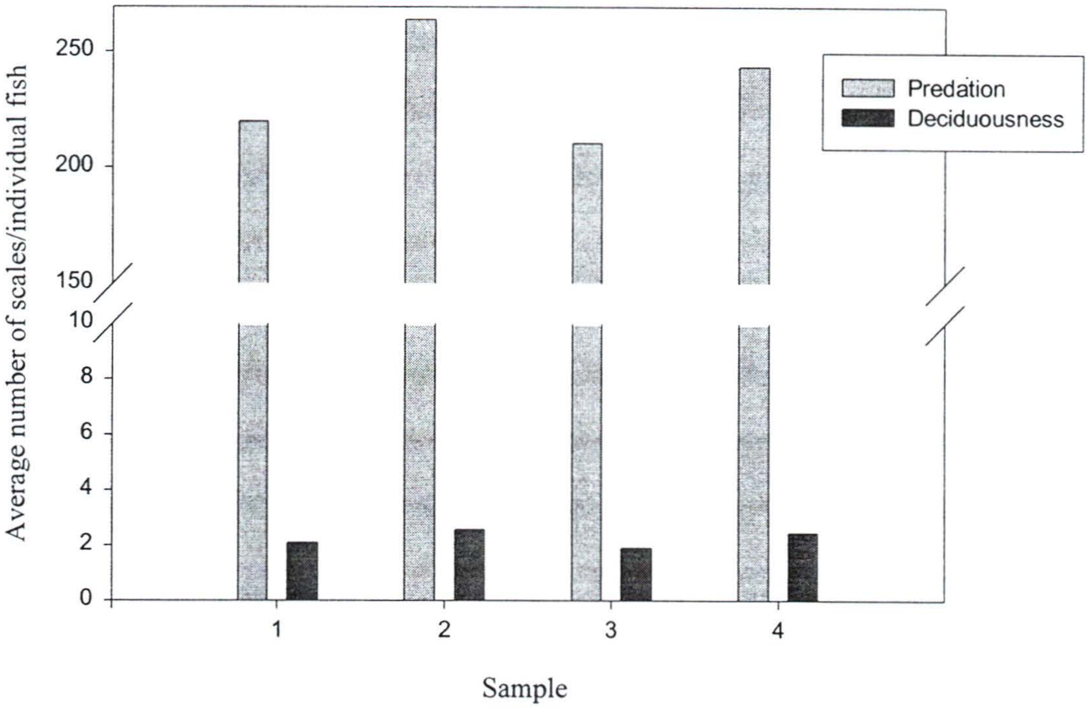

Figure 2.21. Weekly counts for the number of herring scales lost due to shedding (Deciduousness) and predation by lingcod (Predation).

Scale preservation through the gut of a predator

Examination of lingcod feces suggests that herring scales and other remains are not preserved after passage through the gut of this predator. In all lingcod fecal samples examined, no intact or identifiable remains were recovered. Conversely, over three rockfish trials, 87 vertebrae and 15 otoliths were recovered (15 fish were consumed in total). In neither predator did scales pass through the gut intact.

DISCUSSION

PART I – Core collection and fish remains data.

Core collection, alignment and characteristics.

Preservation of sedimentary strata and lamination is good using box corers (Weaver and Schultheiss 1990). Box cores or similarly large-volume cores are required to obtain sufficient material for analysis in paleoecological studies using fish debris. The coring device used in this study has a 289-cm^2 sampling area. In comparison to similar studies of sedimented fish remains, this study in Saanich Inlet examines greater volumes of sediment over the time frame in question, hence sample sizes and replicate numbers are greater (Table 2-1). In all, five box cores covering the past 127 years and 1133 cm^2 of total sediment surface area were obtained. Other studies have hindcast populations of fish from very few scales retrieved from small volumes of sediment without replication (Baumgartner et al. 1992; DeVries and Pearcy 1982; Soutar and Isaacs 1974). Improved sampling effort and large volume box cores increase statistical power and confidence (Krebs 1989).

Despite optimal preservational and sedimentary conditions (i.e. varves) in Saanich Inlet, alignment of the five box cores used in this study was difficult. Due to incidences of slumping and differences in varve structures across the inlet, visual core alignment was not straightforward. Slumping can occur for a number of reasons and may even provide a useful horizon when caused by seismic or other basin-wide activity (Blais 1996). However, where a slump is unique to a core, as in core 2B (Figure 2-3), sampling must work around the slump as best as possible and time-dependent interpretations must be made with caution. Stratigraphic and chronologic correlation difficulties are common in paleoecological study. A poor chronological context weakens high-resolution analysis as it contributes uncertainty to the timing of inferred peaks and makes consistency in sampling difficult. Although alignment of replicates was difficult, the error associated with the geochronology in these cores is estimated as plus or minus five years. The greatest uncertainty occurs in the surface sediments, where compaction is minimal and laminations indistinct. Also, there is some uncertainty between cores at site 1 and site 2; through alignment of diatom horizons and varve counts, however, alignment uncertainty between sites is still estimated to be approximately five years. This error is quite low considering the high-resolution nature of the study.

Identification and enumeration

Shackleton (1986) addressed the difficulties in identifying non-characteristic scales of some clupeoid species in her work off Namibia. From detailed analyses of anchovy and sardine scales, she determined that there are roughly six or seven different types of scales on clupeoid fish and advised that reference collections document these different morphologies to maximize accurate scale identification (Shackleton 1988). Only by recognizing the variety of scales across a fish, she argued, could identification error be effectively reduced. The scale collection compiled for this study encompasses these major scale types (Figure 2-5). Despite this effort, it was still difficult to distinguish between certain species based on scales (i.e. sardine and herring). Only after careful inspection of the scale morphologies from a number of specimens and with increasing experience, were identifications made with confidence. Bone indentifications were also only possible due to the extensive collection available (Department of Anthropology, University of Victoria) and the expertise of R.J. Wigen (Pacific Identifications Ltd.). The difficulty in positive identifications to species is a large hurdle for paleo-studies using fish remains. Fish scale collections are uncommon (I know of two in the Pacific Northwest: the collection I compiled for this study and a smaller collection at Scripps) and therefore must be compiled as required. Extensive bone collections are also not common. Accurate identification of remains is essential as paleoecological inferences and interpretations are often based on the known ecological characteristics of the identified organism.

Overall, the remains of Pacific herring and Pacific hake make up over 90% of the fish remains record in Saanich Inlet sediments (Table 2-3). This result is not surprising as these are among the most abundant fish in this region (Ware and McFarlane 1986). Most paleoecological studies using fish remains have investigated the dynamics of pelagic fish, such as clupeoids and hake, that achieve high numbers and biomass (Baumgartner et al. 1992; DeVries and Pearcy 1982; Holmgren-Urba and Baumgartner 1993; Soutar and Isaacs 1974; Shackleton 1986). Nevertheless, the reason such studies are limited to these pelagic species has not been addressed. In this study, it is apparent that the sedimentary fish scale record does not act as a presence-absence record. Rather, species represented in the scale record are those fish that are most numerous and, more importantly, from which scales are readily lost. In Saanich Inlet, scales and bones from only 16 taxa of fish were recovered despite the higher species diversity the Inlet supports (the total number of species in Saanich Inlet is estimated to be ~140 by Dr. Alex Peden, former curator of the fish collection at the Royal British Columbia Museum). Other than herring and hake, the numbers of sedimented scales from other fish are extremely low and in some cases are singular occurrences. Thus, paleoecological studies using fish remains records are not feasible for all species.

Outliers and replicates

Outlier removal is unique to this study. In other cases, extremely large peaks in remains abundances are often attributed to sudden increases in fish populations over that sampling interval (Baumgartner et al. 1992; Holmgren-Urba and Baumgartner 1993; Soutar and Isaacs 1974). However, because of the many potential sources of fish remains to the sedimentary record, I believe outlier removal to be necessary to uncover robust abundance signals in the data. Anomalous pulses of scales to the sediment may have a number of sources unrelated to increases in fish abundance. The death of a single fish and its deposition directly into a sampling interval, the death of many fish due to fish kills, and dumping of fisheries waste can all result in concentrated pulses of remains. Although documentation of these "pulse-peaks" is interesting, it is impossible to determine what caused a pulse. Outlier removal with replacement thus allows examination of "true" population abundance signals in the sediments.

There are numerous sources of uncertainty in the sedimentary record of fish remains at both the input and output stages. Input will be discussed in the context of the shedding experiments (Part III). From an output perspective, an important question is how many samples and replicates are required to represent deposition across the basin? Although there is considerable uncertainty, smoothed, herring and hake scale time series in replicate cores show synchronicity in low-frequency variation (Figures 2-15 and

2-16) suggesting that the scale record does respond to changes in fish abundances across the Inlet. From the unsmoothed time series plots (Figure 2-8 and 2-10), high-frequency variability is noisy but congruent signal are clarified using spectral analyses (Figures 2-19 and 2-20).

There does not appear to be a clear means to distinguish between data obtained from Site 1 and that from Site 2. Core 2B is unusual in that herring scale counts are consistently higher throughout the core than in other cores and this is interpreted to demonstrate the potential for variability in scale deposition. I suspect there is not a large enough spatial or environmental gradient to support handling these sites as distinct experimental treatments. Only after a more extensive sampling effort has been attempted can the extent of replication required for a representative record of remains be estimated. In order to look at driving factors for variation in scale deposition (and thus relative fish abundance), a composite series averaging across the five replicates is postulated to provide the best representation of general trends in scale deposition as sampled in this study (Chapter 3).

Preservation

Investigation of preservation is necessary before meaningful ecological analysis of the scale data can be attempted (Birks and Birks 1980). Scales in recent Saanich Inlet sediments are more abundant than bones and are more consistently represented. Post-burial degradation of herring and hake scales is relatively low over the past 130-year period, as there is little indication of declining numbers with time in the cores (Figures 2-8 and 2-10). Conversely, vertebrae are scarce in most cores pre-1920 (Figures 2-12, 2-13). Herring vertebra numbers appear to decline with depth although this tendency (as illustrated in the vertebra to scale ratios) requires further investigation (Figure 2-14). Very few hake vertebrae were recovered and quantitative analysis of these remains is not feasible. The possible loss of bone requires further investigation. Because of the greater abundance and more straightforward preservation and identification, fish scales are a more attractive quantitative proxy of fish abundance in recent Saanich Inlet sediments.

Preservation of fish remains on the ocean floor depends on the degree of mechanical abrasion, the chemical composition of the remains and surrounding sediments, and the rate of bacterial degradation. Mechanical abrasion is virtually non-existent in Saanich Inlet as the depth of the basin and the presence of the sill at the mouth of the Inlet restricts water flow from Satellite Channel. Fragmentation in clupeoid scales recovered from Saanich sediments appears to coincide with points of weakness such as along the cracks and radii of the scales. Similar clupeoid scale fragments were also found by Shackleton (1986) and by Holmgren-Urba (personal communication, 1997). Fragmentation compounds identification difficulties and thus decreases the amount of useable data for study in sediment cores.

Fish scales are composed of an intermixture of microcrystalline apatite and a collagen-icthylepidin matrix (Wallin 1957). Since bacteriological action is decreased in an anaerobic environment, scales are unlikely to degrade rapidly in Saanich Inlet (Berger 1976). Ohwada et al. (1983) described scales exhibiting perforations due to the action of microorganisms and suggested that scale fragmentation may be a result of these perforations. No scales from Saanich cores exhibit these perforations although clupeoid scale fragments are found throughout the samples (Figure 2-11A). This fragmentation may occur in the sediment, due to sample treatment, or a combination of both factors; however, biasing effects on sample counts is postulated to be negligible. Hake scales, though frayed along the edges, are relatively well preserved throughout the core (Figure 2-11B). Van Oosten (1957) and Ohwada et al. (1983) note that the chemical composition of the hard tissue and organic constituents of fish scales varies from species to species, as does the thickness and physical structure of the scales. Hake scales are thicker than herring and most other clupeoid scales, and presumably their thickness combined with the absence of deep cracks or radii contribute to their enhanced preservation through time.

PART II – Time Series

Autocorrelation

The scale data from Saanich Inlet are autocorrelated and, therefore, scale samples are not independent of one another from sample to sample. Autocorrelation in sedimentary time series is not surprising as it indicates that the "population" of each interval influences that of the next interval. This phenomenon can result from a number of possible factors. The presence of an organism may lead to conditions that facilitate the presence of that organism in subsequent years. Fish population abundances affect one another from year to year (recruitment and year class strength) and this phenomenon is recorded in the relative amount of scale shedding in each successive year. Death and deposition of bones to the sediments are more isolated peaks than shedding and will not as readily record year-to-year effects. The bone data for both species are not autocorrelated; bone inputs are postulated to be from chance or pulse peaks (exception: Core 1C).

Although features of the natural system can explain autocorrelation, it may also result due to the properties of the material in question. Fish scales are macro-remains and may be subject to winnowing or may be readily displaced or sorted with disturbances. Sampling error may also be implicated. When a box core is extracted from the sediments, the varve structure (though still intact) tends to bow through the middle of the core. Sampling across bowed laminations may contribute to autocorrelation as slicing across the interval may result in the inclusion of a portion of a previous or subsequent true interval. Overall, because of the tendency for these data to be autocorrelated, time series analysis is appropriate.

Data smoothing – Low frequency peaks

Smoothing the data with a 5-sample running mean enhances congruent low-frequency peaks. The congruency in low-frequency signals suggests a response in the sedimentary record to consistent changes in scale deposition across the basin. (Factors driving these low-frequency trends, cycles and peaks will be explored in Chapter 3).

Spectral analysis – High frequency peaks.

The integral time scales and spectral periodograms generated for the core data indicate that the herring and hake scale data all have substantial variance concentrated at similar periodicities (Figures 2-19, 2-20). The similarities in frequencies observed for both species further suggests that the sedimentary fish scale record does reflect high-frequency changes in fish abundance (The underlying driving forces behind these high-frequency peaks will also be discussed in Chapter 3).

Cross-spectra

Investigation of trends in the frequency domain allows comparison of the frequency structure of the core data. Thusfar, comparison of scale data from replicate cores within and among sites from Saanich Inlet indicates general consistency in scale deposition signals. Cross-spectral analyses support the contention that changes in scale abundances in cores show consistent periodicity across the basin. The lack of consistency across phase spectra is not surprising due to the variability in core-to-core overlap (Figure 2-

5). Since the phase lag varies between zero and positive or negative six, the estimated geochronological error of plus or minus five is confirmed.

PART III – Experiments in remains transfer to the sediments

In order to effectively use faunal remains to interpret the past, one must know what processes result in the creation of an assemblage, and how accurately an assemblage represents the original living population (Birks and Birks 1980; Chatters et al. 1995).

Number of scales on a fish

Different species of fish have different total numbers of scales (Hart 1980). Pacific hake have more scales than do Pacific herring (personal observation) thus a hake carcass will contribute more scales to the sedimentary record than will a herring carcass under similar conditions. The average maximum value for scale contribution to the sediments due to death of a herring is estimated to be 1277 scales. A sediment sample with anomalously high numbers of scales and with numerous bones suggests deposition of a carcass has occurred. As discussed, outlier treatment helps remove the effect of localized death of a fish and thus minimizes the potential for overestimation of past fish numbers.

Scale loss due to deciduous shedding

Shedding in herring was consistent from week to week (Figure 2-21). Scale shedding from a population of fish is thus postulated to contribute a consistent rain of scales to the sediments. Shackleton (1986, 1988) determined that deciduousness is the predominant source of scales to the sediment. This study confirms that herring tend to be deciduous and lose scales when simply swimming. From this study, an average herring loses approximately 2.4 scales a week while schooling. Simplistically, if a herring in the Pacific Northwest has a 13-year life expectancy, then the total contribution of scales to the sediment through the lifetime of the fish would be approximately 1500 scales. This is a greater overall contribution than if the fish died (~1300 scales). However, the crucial difference in these scale contributions is how they would manifest themselves in the sediments. Ideally, a comparison of relative shedding between hake and herring would allow for population comparisons based on scale counts to account for bias in the sediment from different shedding rates. This could lead to comparative indices to determine relative shifts in dominance between fish species. Unfortunately, due to the difficulty in raising and keeping hake in captivity, this relative index could not be derived.

Scale loss due to predation

Under experimental conditions, herring lost more scales when being pursued and consumed by lingcod predators than they did while schooling. Pacific herring use schooling behaviour as an anti-predator tactic (Hourston and Haegele 1980). The herring school may be difficult to see from below due to the combined effect of the ventral narrowing of the scale keel and the silver colour of their scales. Scale deciduousness may also confound predators during pursuits. During attack, a flurry of scales causes visual confusion. The prey may escape leaving the predator with a mouthful of scales, or it may aid the escape of the rest of the school.

The potential for variability in scale transfer to the sediments from predators is yet another factor to consider when interpreting the sedimentary scale record. Herring are prey to a number of predators, each of which will likely induce different shedding rates (i.e. lingcod versus rockfish). For some species, scales remaining on fish after predation appear to be digested in the gut of the predator (personal observation) and therefore do not make it to the sediments. Conversely, other studies have shown that scales and bones may indeed pass intact through the gut of some predators. DeVries and Pearcy (1982) noted that hake seem to excrete both scales and vertebrae and that neither shows degradation after passing through the gut. Cottrell (1995) noted that scales, vertebrae and otoliths pass readily through the gut of harbour seals in Saanich Inlet. In this study, only some bones were found to pass through the gut of rockfish. This illustrates the enormous difficulty and uncertainty in interpreting fish remains numbers as indices of fish abundance.

Although experimental shedding trials indicate that daily shedding and shedding in response to predation result in a very different rain of scales to the sediments, both are relatively consistent across trials. Thus, a regular scale rain from shedding and predation may indeed provide an index of relative fish abundances through time, assuming predatory pressures are approximately proportional from year-to-year.

SUMMARY

This exploration of the collection, management and treatment of sedimentary data confirms that Saanich Inlet fish remains are useful in a paleoecological context. Although the alignment of replicates is difficult, in this case the gains from replication are expected to outweigh the potential losses from geochronological error. However, even with replicates and intensive high-resolution sampling, it is difficult to know whether the entire variability within the basin has been sampled. A composite series of averaged values will thus give the best indication of robust relative changes through time. Outlier removals help to ensure that anomalous signals from chance pulses of remains do not skew records. Scales are more numerous and are delivered to the sediments with more regularity than are bones. Further, scale deposition across the basin shows consistent tendencies with an increase in one core likely to correspond to an increase in another core. This contention is supported by the similarities in the frequency domain. Overall, this study suggests the scale record does consistently reflect changes in fish abundances.

Reconstructing entire communities from sedimented scales is not feasible, as the scale record does not act as a presence/absence record. Only deciduous and abundant fish are represented. Further, relative species abundance work must be done with caution because of the tendency for the remains of different species to preserve differentially, and because of the potential role in increasing or decreasing scale flux to the sediments through predation.

What can be done with fish scales obtained in this way is look at low- and high-frequency trends, cycles and peaks in deciduous pelagic fish abundances. Low-frequency visual trends are most clearly enhanced by smoothing noisy data, whereas high frequency peaks are effectively explored using spectral analyses.

Understanding past fish population dynamics is fundamental to understanding current natural fluctuations in fish communities. For the ichthyologist, paleoecological reconstructions of fish populations could give insight into the life history and natural long-term dynamics of fish species and populations. For the fisheries biologist, information on past fluctuations in fish populations may assist in the establishment of effective protocols for sustainable management of fisheries. There is enormous potential for the determination of factors driving trends in fish populations using these methods.

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CHAPTER 3: Paleoecology of Herring and Hake Populations in Saanich Inlet, British Columbia: Predator-Prey Interactions, Response to Environmental Parameters, and Effects of Fishing.

ABSTRACT:

Accumulation rates of fish scales in ocean sediments chronicle the dynamics of pelagic fish populations through time. A 110-year sedimentary record of herring and hake scale abundances from Saanich Inlet, British Columbia is examined. Using data smoothing and spectral analysis, low and high frequency trends, cycles and peaks are explored. The scale chronologies are compared with one another to infer predator prey dynamics, and are similarly compared with environmental and fisheries data to investigate the potential for these parameters to act as driving forces behind fluctuations. Aleutian Low Pressure explains much of the high-frequency variance in the scale data and is postulated to affect juvenile herring and hake survival and recruitment at a four- to seven-year periodicity. The El Nino Southern Oscillation phenomenon is also implicated. Predator-prey dynamics, sea surface temperature and a diatom proxy of primary production also explain some of the low and high frequency variation in the scale deposition data. These parameters all vary at ALPI/ENSO periods. The crash in Strait of Georgia ecosystem herring stocks in the late 1960s is clearly recorded in the sedimentary record of Saanich Inlet. During this period, fish scale deposition responses that were previously explained by environmental parameters break down; overfishing of the Strait of Georgia herring stocks is speculated to be a primary cause. Lastly, the 1976 climate shift is clearly manifest in the sedimentary record. Overall, herring and hake scale records provide insight into the role of ALPI/ENSO in driving fluctuations in these stocks, and confirm that these stocks (especially herring) are volatile in the face of anthropogenic pressure.

INTRODUCTION

Very little is known about interannual or interdecadal effects of the environment on population dynamics of fish (Beamish 1995), and the overall effects of fishing on the dynamics of fish populations are largely unresolved (Shepherd 1984). At present, effective management of pelagic fishery resources in the Northeastern Pacific Ocean is hindered by this poor understanding of the factors driving population changes. Reliable records do not exist prior to the mid-20th century so that an alternate approach is required.

Accumulation rates of fish scales in ocean sediments are postulated to chronicle the dynamics of pelagic fish populations over time (Chapter 2). Thus, sedimentary data coupled with environmental and fisheries data may further reflect effects of changes to fish habitats, species interactions, and fishing pressure through time (Baumgartner et al. 1992; DeVries and Pearcy 1982; Holmgren-Urba and Baumgartner 1993; Lasker and MacCall 1983; Shackleton 1987; Soutar 1966). These studies further the debate concerning the relative importance of different factors – biological, physical and anthropogenic - in effecting major changes in fish populations. A better understanding of present dynamics and more accurate predictions of future variations in fish populations depend on knowledge of past variations and our ability to find correlations to driving factors.

Chronologies of herring and hake scale abundance are developed for the past 110-years from sediment cores extracted from Saanich Inlet, British Columbia. In this study, fish scale abundance changes through time provide a proxy of relative fish abundance (Chapter 2) (Baumgartner et al. 1992; DeVries and Pearcy 1982; Holmgren-Urba and Baumgartner 1993; Shackleton 1986; Soutar 1966). The fish scale records are examined for trend, structure, and cyclicity using data smoothing and analyses in the frequency domain. Significant low or high frequency peaks in the scale deposition record of herring and hake populations are investigated, and possible species interactions discussed. Fish scale chronologies are compared with climate and oceanographic records to elucidate relationships to environmental factors. Finally, the scale records and their relations to fisheries records are considered. Overall, the objective is to develop a comprehensive picture of physical and pelagic fish dynamics of the coastal Northeastern Pacific Ocean and to introduce a new tool for adapting the time scales of fishery management to the time scales of significant variations in fish and environment around eastern Vancouver Island.

BACKGROUND

Fish paleoecology

Identification of driving factors behind pelagic fish fluctuations is useful for fisheries management and studies of fish biology and ecology. Detailed long term records that chronicle both environmental and fish stock variability within the same sedimentary matrix may further understanding of the complex relationship between fish and their environment. Equally important is the potential to use this sedimentary record to discriminate between anthropogenic and natural variability within such records.

Over the past two decades, paleoecology has evolved into a discipline that considers biological and geological evidence from proxy information preserved in media such as ocean sediments to reconstruct past environmental conditions and to document environmental change. A pilot study off California by Soutar and Isaacs (1969) postulated that fish remains archived in the sediments could introduce a relatively long time perspective into the character of fisheries and oceanographic conditions. This pioneering paper described the anoxic conditions in the Santa Barbara Basin that allowed fish debris to accumulate undisturbed by benthic organisms or aerobic bacterial decomposition. Soutar and Isaacs (1969) determined that the temporal structure and distribution of pelagic fish scales at depth was related to pelagic fish resources, and served as potential indicators of long-term productivity and change. Results from this and other studies have made significant inroads into developing these methods and providing insight into the unpredictable dynamics seen in pelagic fish populations. The reader is referred to Chapter 2 for a detailed summary and discussion of other paleoecological studies using sedimented fish remains.

STUDY SITE - Saanich Inlet

Saanich Inlet is a glacially scoured fjord on southeastern Vancouver Island, British Columbia, Canada (Figure 3-1). It varies in width from 0.4 km to 7.6 km over its 26-km length and the average depth of the inlet is 120 m with a maximum of 236 m. There is little freshwater input into Saanich Inlet and a 70-m bedrock sill at the north end of the inlet restricts water circulation. As a result, the lower part of the water column is anoxic for much of the year.

Saanich Inlet is ideal for paleo-research because the anoxic bottom water and sediments exclude epifauna and infauna resulting in minimal disruption of the inlet sediments from burrowing (Heusser 1983). These conditions have enhanced the preservation of sedimentary strata and of delicate organic remains such as fish scales. The Holocene sediments in Saanich Inlet consist primarily of rhythmically laminated silt and clay (Blais 1996; Gross et al. 1963). These laminae are made up of couplets of dark, terrigenous material deposited during fall and early spring freshets, and of lighter, diatom-rich material amassed during spring and summer blooms (Hobson and McQuoid 1997). Individual couplets are annual deposits and are thus termed "varves" that form time sequences useful for establishing a very precise

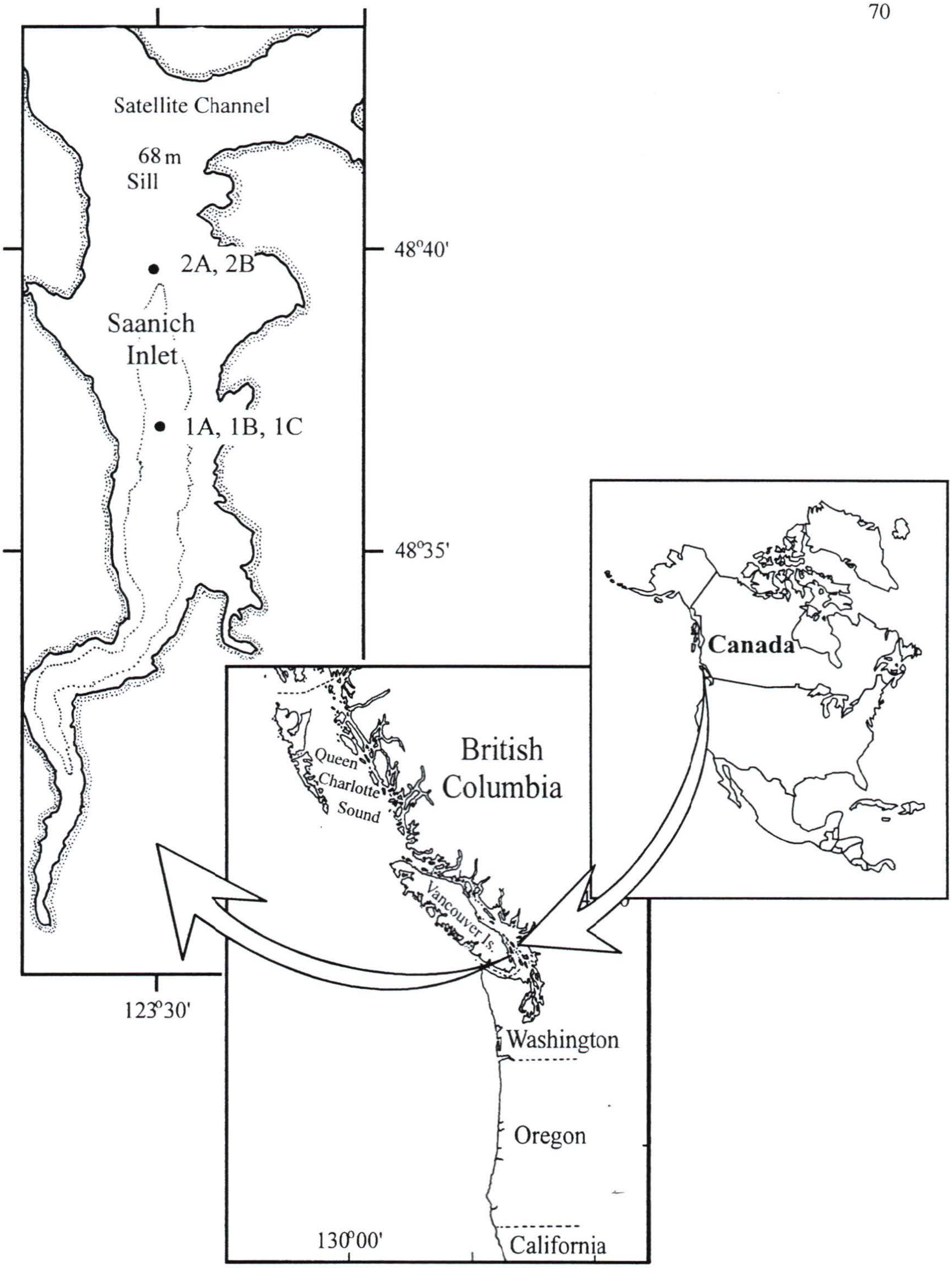


Figure 3.1. Study site: Saanich Inlet, British Columbia, Canada. Core sites are indicated; Site 1:(48°37.9', 123°30.0) and Site 2: (48°39.6', 123°30.5')

geochronology (Heusser 1983). The varved and anoxic nature of Saanich Inlet sediments thus provides an ideal medium for recovery of fossil fish materials in a dated context (Chapter 2).

Saanich Inlet is adjacent to the Strait of Georgia and is part of an important marine ecosystem in the North Pacific. Humans have relied on the Inlet's marine life for millenia. In 1912, the Government of British Columbia and the Federal Department of Fisheries declared the Inlet a recreational fishing reserve. In the 1930s, this declaration was amended to permit commercial harvests of shellfish. Recreational harvests presently focus on salmon, groundfish, crab, prawns, and clams (Howie 1995). Saanich Inlet also supports populations of Pacific hake, Pacific herring, lingcod, rockfish (Murie et al. 1994), and Pacific cod among other fish species. According to Ware (1991), two important pelagic species in the Northeastern Pacific ecosystem are herring and hake and these remains make up over 90% of all fish remains recovered from Saanich Inlet sediments (Chapter 2).

I – THE FISH

Herring - (*Clupea harengus pallasi*)

Clupeoids are the largest suborder of non-domesticated vertebrates harvested by humans (Whitehead 1985). They include the sardines, anchovies, and herring. Like other clupeoid fishes, herring are schooling fish that achieve population biomasses in the millions of tons (Schweigert 1995). The Pacific herring stocks in the Strait of Georgia and Saanich Inlet are important economically and ecologically as they are prey for salmon and other predators and sustain a commercial fishery (Beamish et al. 1994). The herring fishery in the Strait of Georgia is concentrated between Comox and Sidney (Ketchen et al. 1983). There are two herring stocks recognized in the Strait of Georgia (Ketchen et al. 1983). One is a small resident population, and the other is a larger migratory population that moves into the area in the fall to spawn in winter (Beamish et al. 1994). Herring become adults and begin spawning in their third or fourth year. They typically congregate for weeks to months prior to spawning (Haegele and Schweigert 1985) and then lay adhesive eggs on fixed vegetation (eelgrass, rockweed algae) in and below the intertidal zone. Spawning is in March and incubation lasts approximately 2 weeks. The planktonic larval stage lasts about 10 weeks and is at the mercy of currents and tides. The fish are recognizable adults by June – July when they begin to school. In autumn, the schools move seaward to overwinter off the continental shelf (Ketchen et al. 1983).

Like other clupeoids, herring exhibit a "boom and bust" life cycle, building up enormous populations that can suddenly and unexpectedly crash. Fluctuations in clupeoids have been studied extensively because of their great economic value (Lasker 1985). Although there is little question today that there are natural fluctuations of high magnitude in these populations due to factors other than fishing, the specific driving forces remain largely unknown (Lasker 1985; Zebdi and Collie 1992).

Hake - (*Merluccius productus*)

Pacific hake (*Merluccius productus*) is an abundant and commercially important pelagic fish inhabiting the coastal waters off western North America (Bailey et al. 1982; Beamish and McFarlane 1985). There are populations of hake in the Strait of Georgia, Puget Sound, and in coastal inlets of British Columbia (Shaw et al. 1989), but most hake off British Columbia belong to a large migratory offshore population (Beamish and McFarlane 1985; Hollowed 1992). During spring and summer, these migrants are in greatest abundance and there are large-scale commercial fisheries for this species in both U.S. and Canadian waters (Dorn 1995; Ware and McFarlane 1995).

Pacific hake in Saanich Inlet and the Strait of Georgia constitute a distinct population that is much smaller than the offshore, migratory hake off the west coast of Vancouver Island (McFarlane and Beamish 1985). They are now recognized as the most abundant resident fish in the Strait (McFarlane and Beamish 1985). This population spawns between March and May in the deep water of the south central Strait near the Gulf Islands (McFarlane and Beamish 1985). After spawning, they gather in shallow water in the inlets and along the East Coast of Vancouver Island. During the day, they feed on the dense plankton layer and at night the schools disperse and the hake migrate toward the surface. By late fall most hake have migrated north to Johnstone Strait and in early winter they migrate back into Georgia Strait in preparation for spawning (McFarlane and Beamish 1985).

Juveniles (age 1-3) are distributed throughout the Strait of Georgia and tend to avoid large aggregations of adults. During their third year of life they join the larger spawning aggregations and begin to migrate with these schools in winter. Hake from the Strait of Georgia generally live from 4-11 years

(McFarlane and Beamish 1983) and may be important predators of Pacific herring (McFarlane and Beamish 1985). Hake populations are well known for their enormous variability (Dorn 1995) and the dynamics of hake populations in the Strait of Georgia are still largely unknown (McFarlane and Beamish 1985, M. Saunders, personal communication).

II - ENVIRONMENT AND FISH

Concerns of global climate change have rejuvenated interest in the role of the environment in driving fish stock variability. If the effects of the environment on fish can be understood management can be facilitated and it may be possible to address how global climate change may affect the world's fisheries. Unfortunately, understanding the effect of environmental change on populations is complex. Not only does it require recognition of specific environmental changes, but also an understanding of all the stages in the life cycle of the species affected. Environmental effects are known to differ depending on the fish species in question, however as is the case with herring and hake, very little is known about specific factors driving decadal to centennial scale variability of any of the pelagic fish populations of the Northeastern Pacific (Cushing 1971).

Aleutian Low Pressure

The Aleutian Low Pressure System has strong links to oceanography and is the dominant meteorological feature in the winter and spring North Pacific atmosphere (Namias 1969). Aleutian Lows begin to form at the time of the fall transition in October and persist until approximately April of the following year. Strong Aleutian Lows intensify the strength of the eastward flowing subarctic current, the westward drift, and the Alaska current that flows poleward (Thompson 1981). As circulation around the Alaska Gyre intensifies, mixing and nutrient regimes are affected. During a strong Aleutian Low Pressure year, these altered circulation patterns cause stronger than normal poleward advection of warm coastal water along the west coast of North America. In British Columbia, these warming trends are reflected in sea surface temperature patterns. The Low begins to break down in the spring and is replaced in the summer by an area of extensive high pressure. Aleutian Low Pressure and the El Nino Southern Oscillation event are teleconnected (Gargett 1997; Thompson 1981; Ware 1995).

Changes in oceanic and fisheries production have been linked to the strength of the Aleutian Low Pressure System (Beamish and Bouillon 1993; Brodeur and Ware 1992; McFarlane and Beamish 1992). Most of this work has focussed on Aleutian Low Pressure and its relation to salmon stocks (Beamish 1993; Beamish and Bouillon 1993). Further, offshore systems rather than intermediate coastal systems such as the Strait of Georgia have been most extensively studied. Aleutian Low Pressure is postulated to have different effects on the Strait of Georgia ecosystem (Gargett 1997) and thus, a study to investigate the influence of Aleutian Low pressure on major pelagic species (that are prey to or predators of Pacific salmon) is warranted.

Sea surface temperature - SST

Aquatic animals are extremely sensitive to their environment and even small changes in regional climate can significantly influence aquatic communities (Bone et al. 1995). Cyclic changes in temperature and other oceanographic parameters can be expected to affect marine fishes. Temperature affects fish metabolism and behaviour. For example, changes in the internal temperature of a fish directly affects growth, development, and reproduction (Bone et al. 1995). From an ecological perspective, nutrient and food availability, as well as oxygen and carbon dioxide solubility are also caused by temperature changes (Laevastu and Hayes 1981). Studies in the Northeastern Pacific show that temperature, or processes for which temperature is a proxy, play an important role in determining year class strength in pelagic fish (Hollowed and Wooster 1995).

Primary Production- Diatoms

Diatoms generally dominate phytoplankton biomass in productive coastal systems and so may act as indices of primary production (Robinson 1994). Biomass transfer between plankton and fish is thought to occur via the "traditional pathway": diatoms to meso/macro-zooplankton to fish (Cushing 1982; Kiorboe 1993; Mann 1993). Robinson (1994) contends that a *Rhizosolenia ->Euphausia* -> herring/hake/dogfish food chain is the primary pathway of the Northeastern Pacific Ocean system. Due to the stochasticity of the marine environment, studies of primary production and its connection to fish production are often complicated. Indeed, the relationship between primary production and fish is often described as complex and non-linear (Cury and Roy 1989; Mann 1993; Robinson 1994). Despite the complicated relationship between diatoms and fish, since they are both well preserved in the same sedimentary matrix, they hold enormous potential for long-term studies of fish and primary production.

III – FISHING PRESSURE

The world's marine fisheries constitute a multi-billion dollar industry supplying about 10% of the animal protein consumed by humans (Lalli and Parsons 1995). Canada's marine and freshwater resources support an important part of the nation's food supply and sustain the economies of many coastal communities. Commercial fishing is the fourth largest primary industry in British Columbia (Government of Canada 1991), and Pacific herring have supported a commercial fishery since at least 1877. Through this century, herring have been harvested for reduction to meal and oil, roe, spawn on kelp, bait, and food (Hourston and Haegele 1980). The annual value of the fishery to the British Columbia economy is over $100 million (Hourston and Haegele 1980). Means to predict long-term declines in stock abundance are required as these declines will have serious economic and social implications to coastal communities (Schweigert and Stocker 1988). Herring are also an important marine food web component and therefore any major decline in their numbers due to overfishing could disrupt ecosystem balance. Overfishing has been implicated in the crash of the herring fishery in the Strait of Georgia in the late 1960s (Ketchen et al. 1983). The herring reduction fishery ended in 1967. The modern food, bait, and roe fishery only captures 20% of the spawning stock biomass (D. Ware, personal communication).

Currently, management of Pacific herring in British Columbia is based on two analytical models used to assess the escapement from the current years fishery and to forecast the abundance of spawning populations for the coming year (Haist and Schweigert 1990). Herring recruitment is highly variable, therefore, any biological and/or statistical models that can provide a better understanding of Pacific herring dynamics would be of significant value for improving management recommendations for these stocks (Schweigert and Noakes 1990).

METHODS

Box Core Collection

The high-resolution 110-year sedimentary record used in this portion of the study was obtained in 1995 from Saanich Inlet using a Soutar box-coring device. The main advantage of box-corers is that they obtain large-volumes of surface sediment with minimum disturbance. The five Soutar box core sediment samples were collected on board the Department of Fisheries and Oceans vessel, *Vector*. Box cores 1A, 1B and 1C were extracted from Station E just south of Patricia Bay and Mill Bay (48°37.9', 123°30.0'). Box cores 2A and 2B were removed from a site near the sill (48°39.6', 123°30.5') (Figure 3-1)

Sampling

Visual distinctions, prominent presence or abundance of diatom species, and the presence of woodchips, were all used for core alignment. Each year in the box cores began with a light layer on the bottom and a dark layer on top. Core years were marked with dissecting pins and the core was then allowed to thaw for a few hours before being sliced into two-year samples. Varves would often curve more in the center of the core (a coring and freezing artifact) but years were followed as closely as possible when sampling. The samples were bagged and kept frozen until sieving. Further details for dating and alignment are outlined in Chapter 2.

The sliced samples were thawed completely prior to sieving. Once soft, the samples were rinsed into large bowls and this mixture was passed through a 500 μm and 250 μm sieve. Both fractions were collected. Due to the abundance of fecal pellets, the samples were resieved prior to picking for fish remains. During the resieving, the two fractions were combined into a 250 μm sieve to facilitate enumerations.

Identification and enumeration

Fish scales were identified using a fish scale reference collection compiled from dried samples at the Anthropology Department at the University of Victoria, and fresh samples collected from the Bamfield Marine Station, and aboard the *CSS W.E. Ricker*. The scales were mounted dry between two slides and this proved to be an ideal easy-access reference set for analysis (the reader is referred to Chapter 2 for details of reference collection compilation and scale identification). Only those scales that were either 50% or more intact or for which the focus (central portion of the scale) was intact were counted.

Fish remains dataset

Examination of fish remains preservation in the sediments of Saanich Inlet suggests that scales are more numerous and consistently represented through recent time than are bones (Chapter 2). Thus, the fish scale record was used to describe variations in fish populations throughout the last century. Since there was no consistent indication that cores taken from site 1 or 2 should be considered as distinct treatments (Chapter 2), a composite series comprised of average numbers of scales across overlapping samples was derived. Only those dates with two or more overlapping samples were included to form a 110-year dataset. Prior to averaging and compilation of the composite dataset, all data were standardized (# scales/1000cm^2/2 years *sensu* Soutar and Isaacs 1974 and Baumgartner et al. 1993) and outliers were removed (Chapter 2).

Environmental datasets

The Aleutian Low Pressure Index (ALPI) dataset was obtained from Michael Folkes at the Pacific Biological Station. The ALPI is calculated annually from the Aleutian Low Pressure area in the North Pacific where pressure is $\leq$ 1005 mb. The calculation takes the average of this low pressure area for December through March inclusively and subtracts a series average. The ALPI for a specific year is thus an anomaly and can be a positive or a negative value. The ALPI dataset spans 1900-1997 (except 1944 as data were not available). Sea surface temperature data for Entrance Island were provided by the Institute of Ocean Sciences (courtesy of H. Freeland and M. McQuoid). SST data were obtained as monthly averages spanning 1937-1994. A diatom abundance dataset extracted from Saanich Inlet sediments was used as a proxy of primary production for Saanich Inlet. Monthly species abundances in numbers of cells (or spores) per gram dry weight were obtained from Melissa McQuoid of the University of Victoria for the period from 1901-1990 (McQuoid 1995). All environmental data sets obtained as yearly or monthly averages were further averaged to 2 calendar year mean values to coincide with the core-sampling regime.

Fisheries datasets

Paleoecology can make a unique contribution to fisheries management by providing information to assist in determining the historical limits of a population and the annual overlap between the distributions of populations and their predators (including fishers) (Pereiro 1995). If sedimentary evidence of increases or decreases in fish abundance reflect those recorded by fisheries surveys, fisheries biomass estimates may also provide a means to lend credence to paleo-data.

Historical records of herring in the Strait of Georgia were obtained from J. Schweigert at the Pacific Biological Station in Nanaimo, British Columbia. The methods for stock reconstructions are available in Schweigert and Stocker (1988). The data were obtained as annual biomass estimates that have been averaged over 2-years to coincide with the sedimentary data.

Preliminary investigation of relationships

Simple scatterplots of fish scale data to environmental and fisheries datasets were examined for potential relationships. Scatterplots and trendlines were generated using SIGMAplot©.

Time series

The first step in time series analysis is to plot the data to obtain simple descriptive measures of the main properties of the series. For some series, the variation is dominated by "obvious" features, and a simple model that attempts to describe these major trends and variations is adequate to describe the variation in the time series (Bendat and Piersol 1986; Chatfield 1989; Jenkins and Watts 1968). For other series, more sophisticated techniques are required in analysis.

The time series of scale data and environmental data were examined for low-frequency trend and structure by several methods: visual correlation of time series, and by smoothing the data using a 5-sample running mean of period five (Chapter 2).

Spectral analyses explore high-frequency variability in scale deposition. An underlying assumption in time series analysis is stationarity. A stationary series is one that contains no trends and is in statistical equilibrium (Bloomfield 1976; Chatfield 1989; Denman 1975). Methods of dealing with non-stationary time series include techniques for removing or filtering the non-stationary parts to leave behind a series that can be treated as stationary (Jenkins and Watts 1968). Major low-frequency trends were removed from the time series datasets using a high pass filter to meet the assumptions of stationarity. The high pass filter was applied to the data by subtracting a 5-sample running mean of 10 from the dataset and obtaining a series of the residuals (Chapter 2). This method for filtering the data was necessary due to the limitations of the software used for time series analyses (SPLUS 1998).

Spectral analysis

Spectral density functions are used to describe how the variation in a time series is accounted for by cyclic components at different frequencies (Jenkins and Watts 1968). The periodogram graphically illustrates this relationship and is a simultaneous least squares fit of a finite number of sine and cosine functions of different frequencies, to a time series of given length (Denman 1975). Periodogram estimates are defined for equally spaced frequencies ranging from $1/2N\Delta t$ up to $1/2\Delta t$. $1/2\Delta t$ is the highest frequency that can be resolved with the time interval Δt (Chatfield 1989). The lowest frequency that can be fit to the data completes one cycle in the whole length of the time series. Periodograms were generated for all datasets and were primarily used to explore the details of later cross correlations. The peaks in the periodogram were used as relative indices of variance amplitude. Spectral density functions are especially useful for this study as they permit comparisons of time series with different units of measurement.

Cross-spectral analysis – coherence and phase spectra

In time series, an analog to correlation in the frequency domain is the cross-spectrum (Chatfield 1989). Cross-spectral analysis examines the relationship between two series over a range of frequencies (ω); it compares the spectral densities. Coherency spectra were generated to compare high-frequency components of fish scale records with major oceanographic time series and to fisheries records in the frequency domain. The coherency spectrum provides a non-dimensional measure of the correlation between two time series as a function of frequency. The closer the coherency at frequency ω is to one, the more closely related are the two processes at that frequency. The significance of a peak in the phase spectrum was determined based on 95% confidence intervals. Those peaks that were significantly greater than zero at all times were "significant" for the purposes of this study. The phase spectrum shows whether frequency components of one series lag or lead the components at the same frequency in the other series. It qualifies the coherency spectrum.

RESULTS

I - THE FISH

Low-frequency peaks – Smoothed scale deposition data

Herring: The time series plot of herring scale deposition and the time series with a 5-sample running mean of period 5 shows long-term trends spanning the period 1883-1993 (Figure 3-2A). The data have an obvious peak in the late 1880s and early 1890s followed by a decline in the late 1890s. A rapid return to maximal numbers is evident in the early 1900s with a series peak in the 1920s. After the 1920s, a gradual but extreme decline in scale deposition occurs over 40 years until a series minimum in the late-1960s and early 1970s. This decline is most dramatic post-1960 and is at a series low through the early 1970s. In approximately 1976, herring scale deposition increases again to peak in the late 1980s.

Hake: The hake scale series with smoothing begins with a high through the late 1880s and 1890s and declines rapidly in the early 1900s to a series low from approximately 1905-1910 (Figure 3-2B). After 1910, hake scale deposition increases steadily to the mid-1950s when there is a slight decline through the 1960s and 1970s. In 1975-76, hake scale deposition increases rapidly to peak at a series high in the mid-80s. Herring scale accumulations are much greater and show higher amplitude variability than hake throughout the record (Figure 3-2).

Herring & hake scatterplots

Herring and hake scale deposition does not show an obvious relationship (Figure 3-3).

High-frequency peaks- Spectral analyses

The smoothed periodogram of the herring data indicates that most of the variance in the data is explained by 60, 20, nine- and four-year peaks (Figure 3-4A). Similarly, most of the variance in the hake data is explained by peaks with 88, 25 and eight-year periods (Figure 3-4B).

Cross-spectral analysis - Herring and Hake

Cross-spectral analyses indicate that herring and hake scale deposition exhibit a significant in-phase peak with a seven-year period. A significant four-year peak is lead by herring at a lag of five-years (Figure 3-4C and 3-4D).

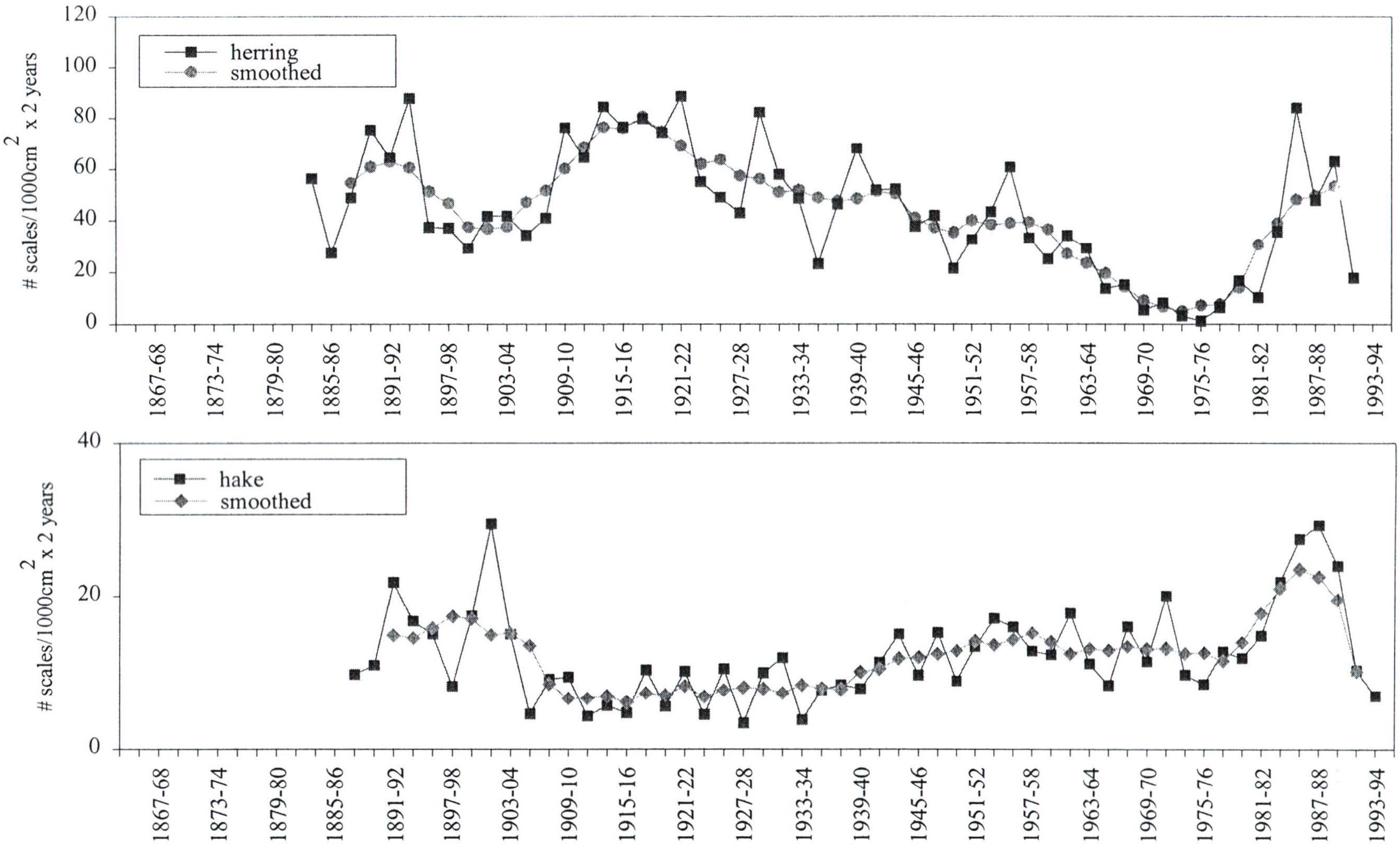


Figure 3.2. A) Herring scale composite series and smoothing with a 5-sample running mean.
B) Hake scale composite series with and smoothing with a 5-sample running mean.

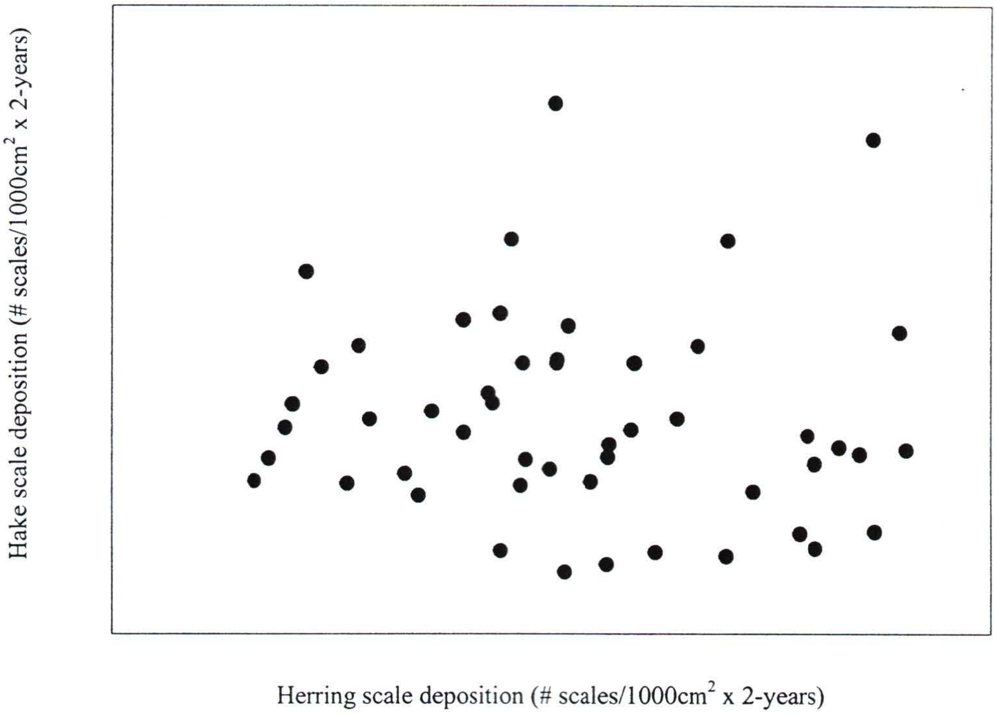
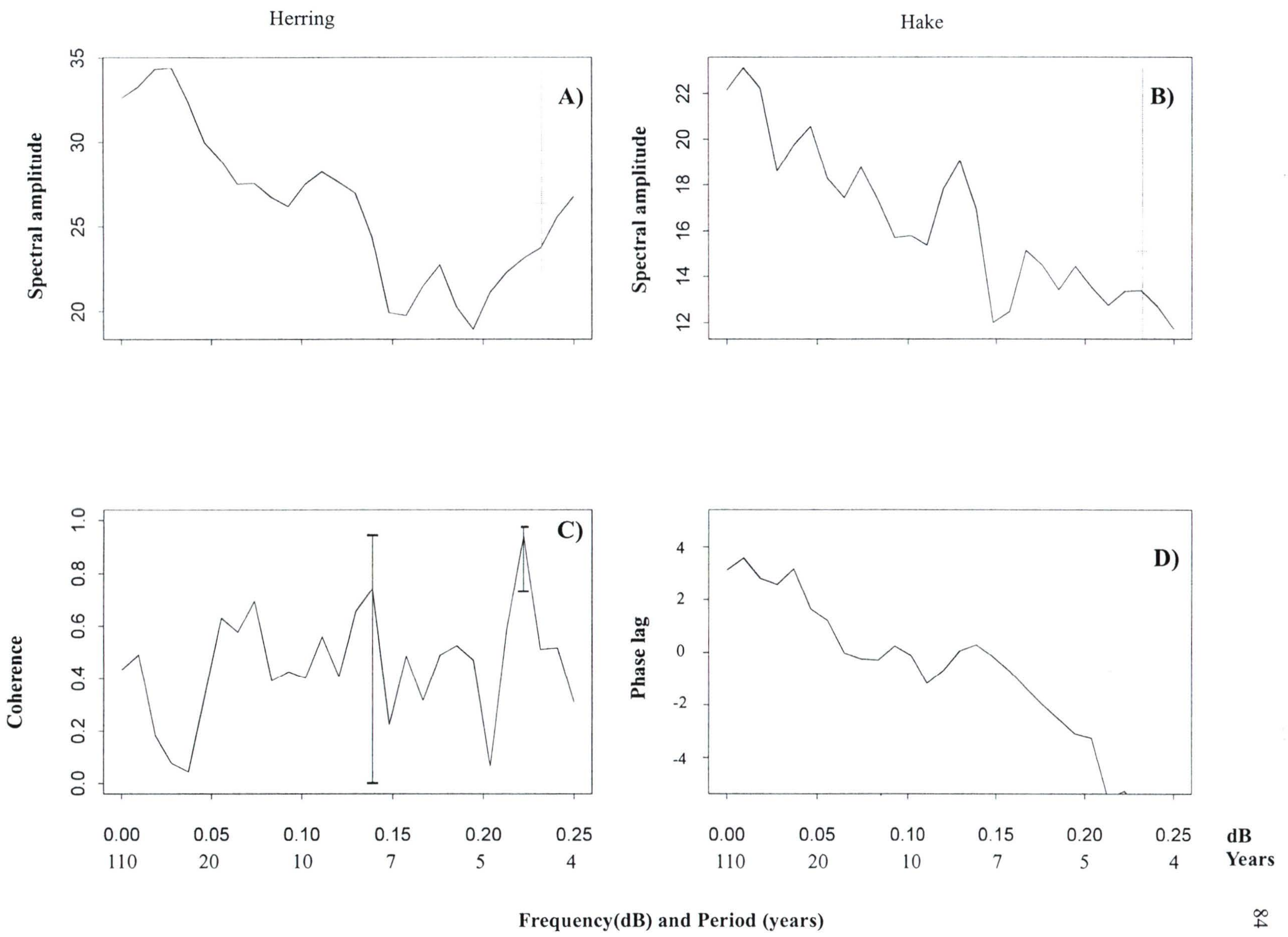


Figure 3.3. Scatterplot showing the relationship between herring and hake scale deposition

Figure 3-4. **A)** Herring periodogram with 95% confidence intervals; **B)** Hake periododgram with 95% confidence intervals; **C)** Coherency cross-spectral output of herring and hake spectral density functions. Significant peaks are indicated by 95% confidence bars; **D)** Phase spectrum for herring and hake spectral density.


Herring
Hake
Spectral amplitude
35
30
25
20
A)
Spectral amplitude
22
20
18
16
14
12
B)
Coherence
1.0
0.8
0.6
0.4
0.2
0.0
C)
Phase lag
4
2
0
-2
-4
D)
0.00 0.05 0.10 0.15 0.20 0.25
110 20 10 7 5 4
0.00 0.05 0.10 0.15 0.20 0.25
110 20 10 7 5 4
dB
Years
Frequency(dB) and Period (years)

II ENVIRONMENTAL PARAMETERS

Low-frequency peaks – Smoothed environmental data

ALPI: The Aleutian Low Pressure Index shows an initial positive value at the turn of the century followed by negative values through to the mid-1900s (series low = 1903-04). The return to average values is slow and consistent to the early 1920s where the index is positive and hovering above zero until the 1940s. The early to mid-1940s marks a strong positive peak followed by a change to strong negative values through the 1950s. The index hovers at zero and fluctuates from positive to negative values through the 60s. After a low in the early 1970s, the ALPI increases and after roughly 1976, the index is highly positive. The ALPI begins to decline to approximately zero in recent years (Figure 3-5A).

SST: The average SST between 1937-1994 is 11.2 °C (+/- 0.4°C). SST is low through the 1940s and early 1950s, briefly warm in the mid-1950s, and hovers around average values to the late 1960s. There is a prolonged cooling through the 1970s until 1976 when SST begins to steadily increase until a maximum in the early 1990s (Figure 3-5B).

Diatoms: Diatom counts are initially high in the early century (peak ~1905-06), and low and steady through the teens, 20s, and 30s. The early 1940s show a short-lived decline followed by a peak through the late 1940s and early 1950s. There are two maximum peaks in the mid-1960s (1965-66) and early 1970s (1969-70) punctuated by a series low (1967-68). In 1976, diatom numbers increase for their most prolonged peak until they begin to decline once again in the mid- to late 1980s (Figure 3-5C).

High-frequency peaks - Spectral analysis

The periodograms of the environmental datasets are presented along with the cross-spectra. The peaks explaining much of the variance are summarized in Table 3-1.

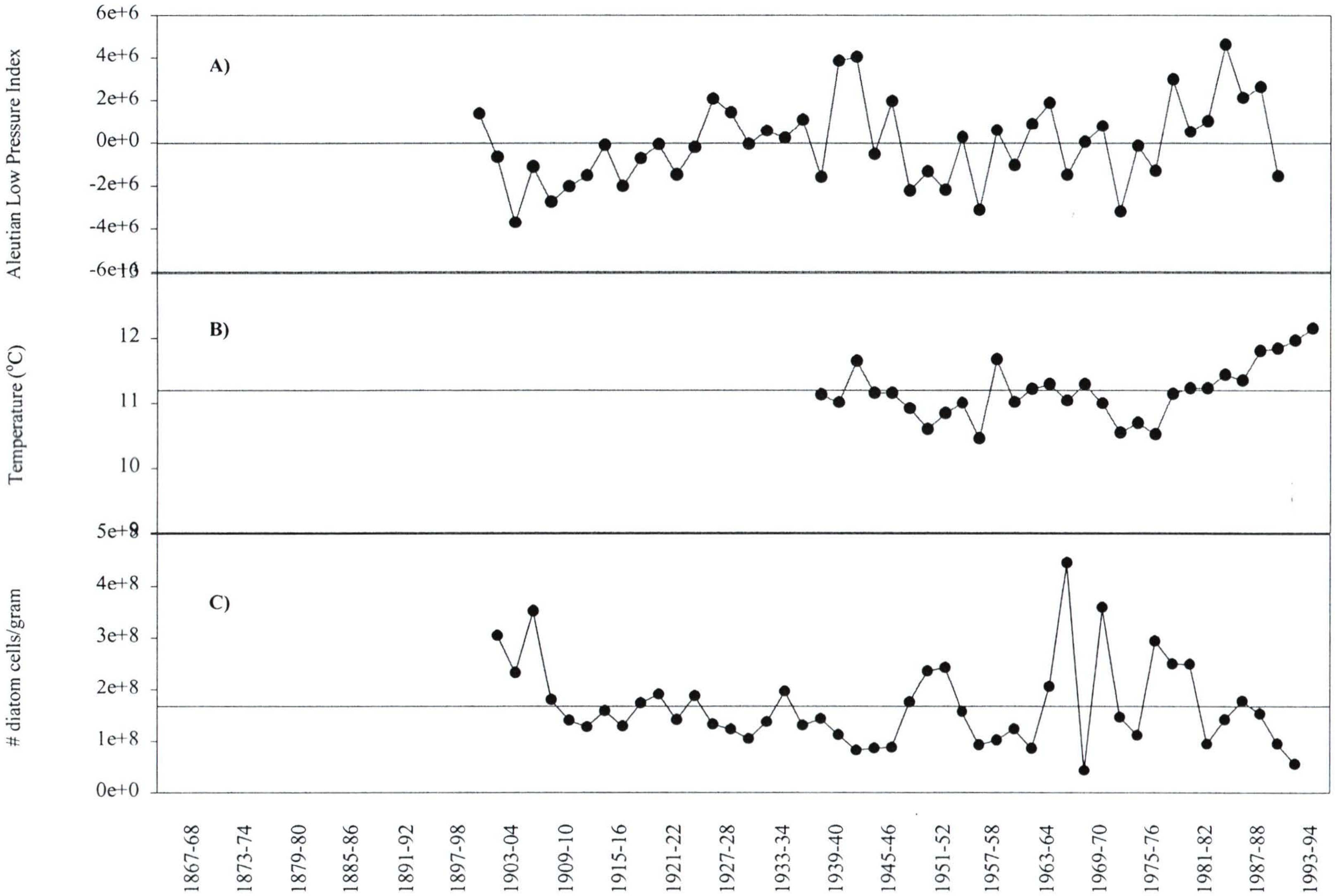


Figure 3.5. Environmental parameters (mean values are indicated). A) ALPI; B) SST; C) Diatom counts.

Table 3-1 Summary of spectral density results for ALPI, SST and diatom environmental datasets.

Environmental parameter	Dominant Periods (yrs) in the dataset
ALPI	40
	20
	7
	5
SST	20
	11
	5
Diatoms	16
	6
	5

II(i) - RELATIONSHIPS BETWEEN SCALE DEPOSITION AND ENVIRONMENT PARAMETERS

Scatterplots – Scale deposition and environmental parameters

Scatterplot diagrams reflect the following relationships:

ALPI: When the ALPI is negative, there tends to be more herring scales deposited (Figure 3-6A). Conversely, when ALPI is positive there are more hake scales (Figure 3-6B).

SST: Herring and hake scale deposition are positively related to SST: an increase in temperature coincides with an increase in scale numbers (Figure 3-6C and D).

Diatoms: Herring and hake scale deposition are negatively correlated to diatom counts (Figure 3-6E and F).

Cross-spectral analysis – Scale deposition and environment

Herring coherence and phase

ALPI: Cross-spectral analysis of herring scale deposition against the ALPI data show significant coherence at 13, seven and five-year periods. The phase spectrum puts the 13-year peaks in phase while the seven and five-year peaks are lagged by four and negative four years, respectively (Figure 3-7i).

SST: Herring and SST are not significantly coherent (Figure 3-7ii).

Diatoms: Herring scale deposition and diatoms counts have a coherent frequency peak at a six-year period with scale deposition led by diatom production by four-years (Figure 3-7iii).

Hake scale deposition and environment

ALPI: Hake scale deposition and ALPI are coherent at nine and six-years. The nine year peaks are led by hake by one year, and the six to seven year peaks are out of phase by four years: ALPI four years earlier affects hake scale deposition four years later (Figure 3-8i).

SST: Hake and SST are not significantly coherent (Figure 3-8ii).

Diatoms: Hake scale deposition and diatom counts are coherent with a five-year period. The phase structure indicates that diatom production leads hake scale deposition by four years (Figure 3-8iii).

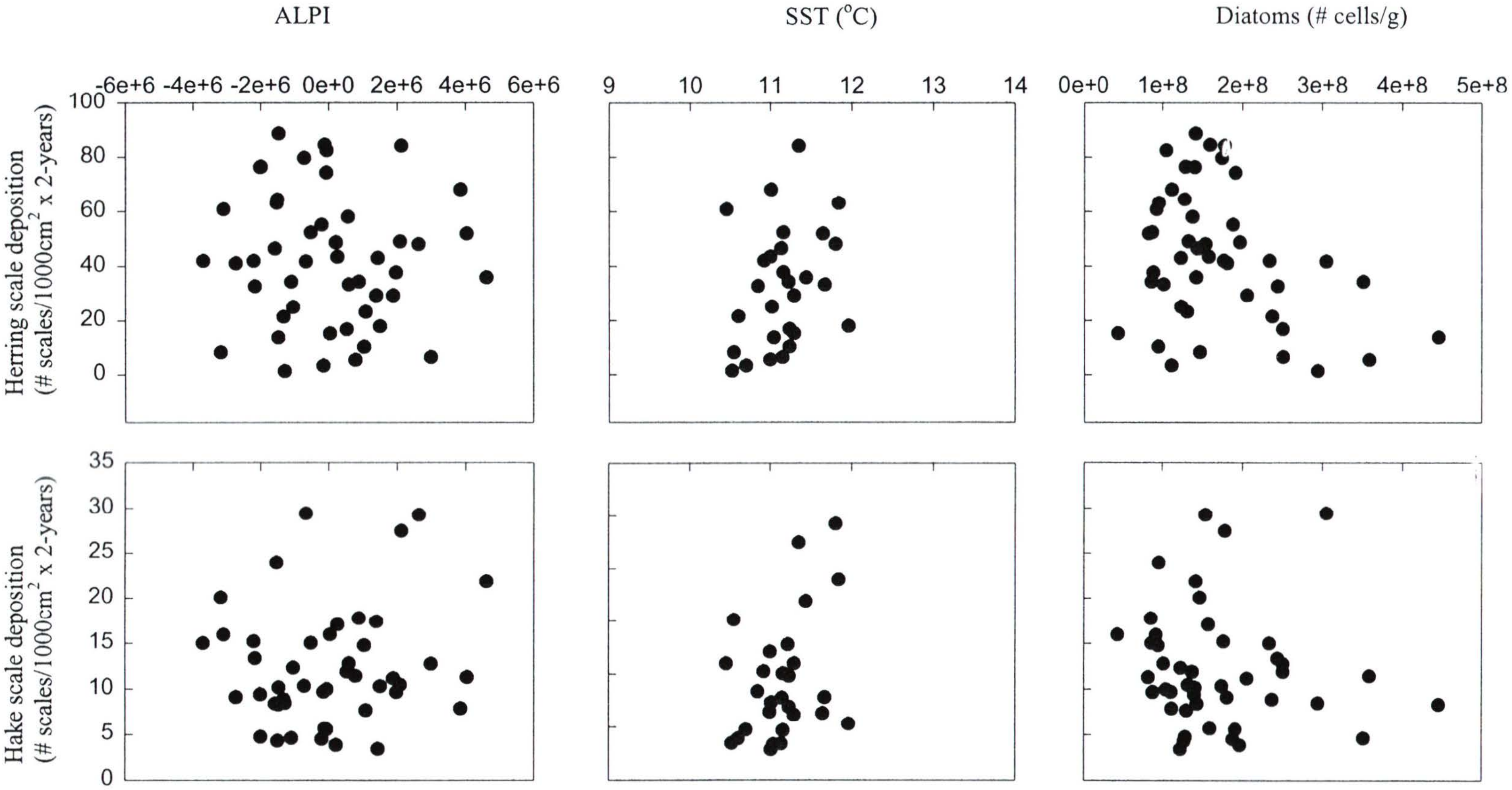


Figure 3.6. Scatterplots of herring and hake scale deposition against environmental parameters.

Figure 3.7i) Cross-spectral output for herring scale deposition and the ALPI dataset. 95% confidence intervals are indicated **A)** herring periodogram, **B)** ALPI periodogram, **C)** herring scale deposition and ALPI cross-spectral coherency: significant peaks are indicated by 95% confidence bars, **D)** herring scale deposition and ALPI phase spectrum.

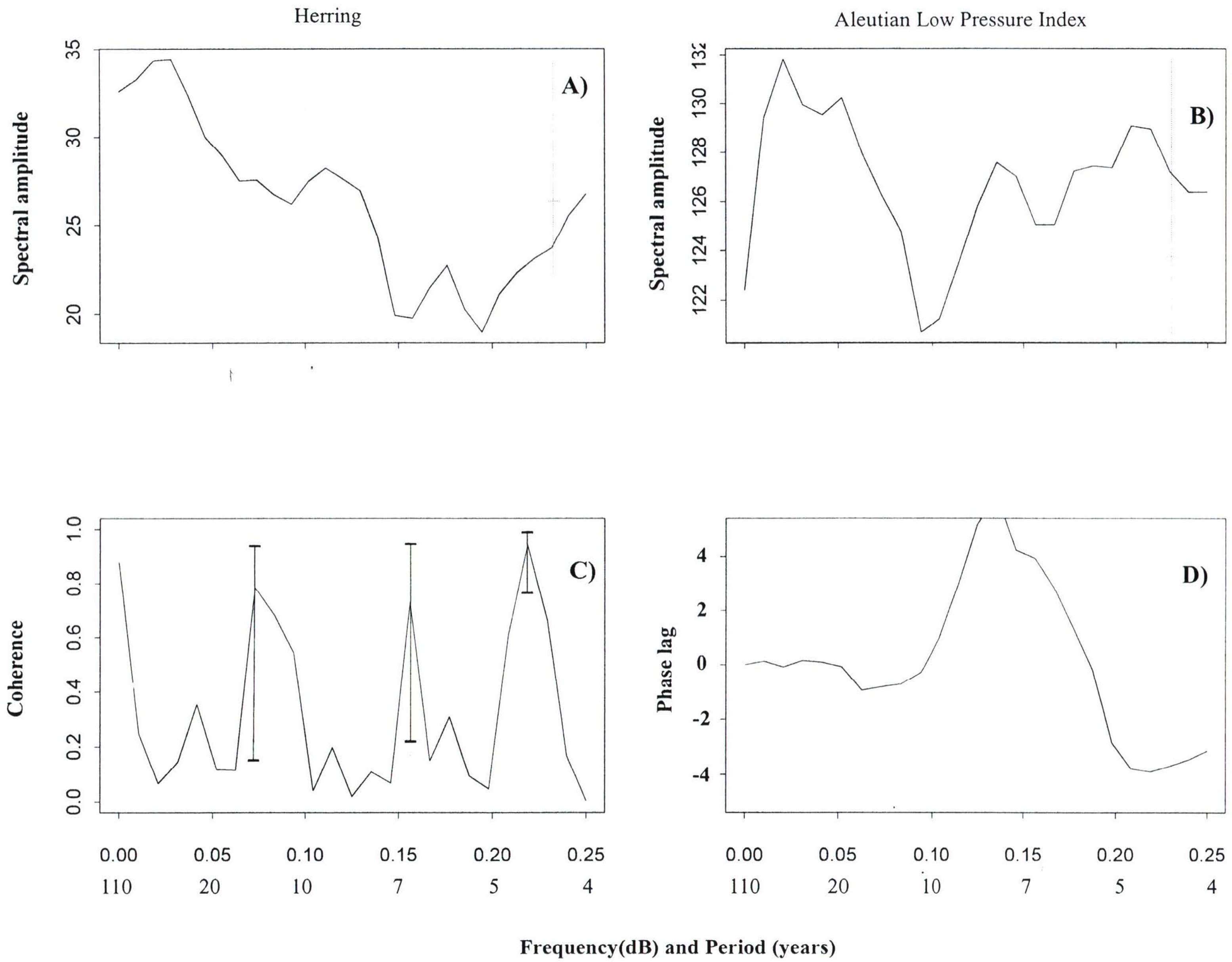

Herring
Aleutian Low Pressure Index
A)
B)
C)
D)
Spectral amplitude
35
30
25
20
132
130
128
126
124
122
Coherence
1.0
0.8
0.6
0.4
0.2
0.0
Phase lag
4
2
0
-2
-4
0.00 0.05 0.10 0.15 0.20 0.25
110 20 10 7 5 4
Frequency(dB) and Period (years)

Figure 3.7ii) Cross-spectral output for herring scale deposition and the SST dataset. 95% confidence intervals are indicated. **A)** herring periodogram, **B)** SST periodogram, **C)** herring scale deposition and SST cross-spectral coherency: significant peaks are indicated by 95% confidence bars, **D)** herring scale deposition and SST phase spectrum.

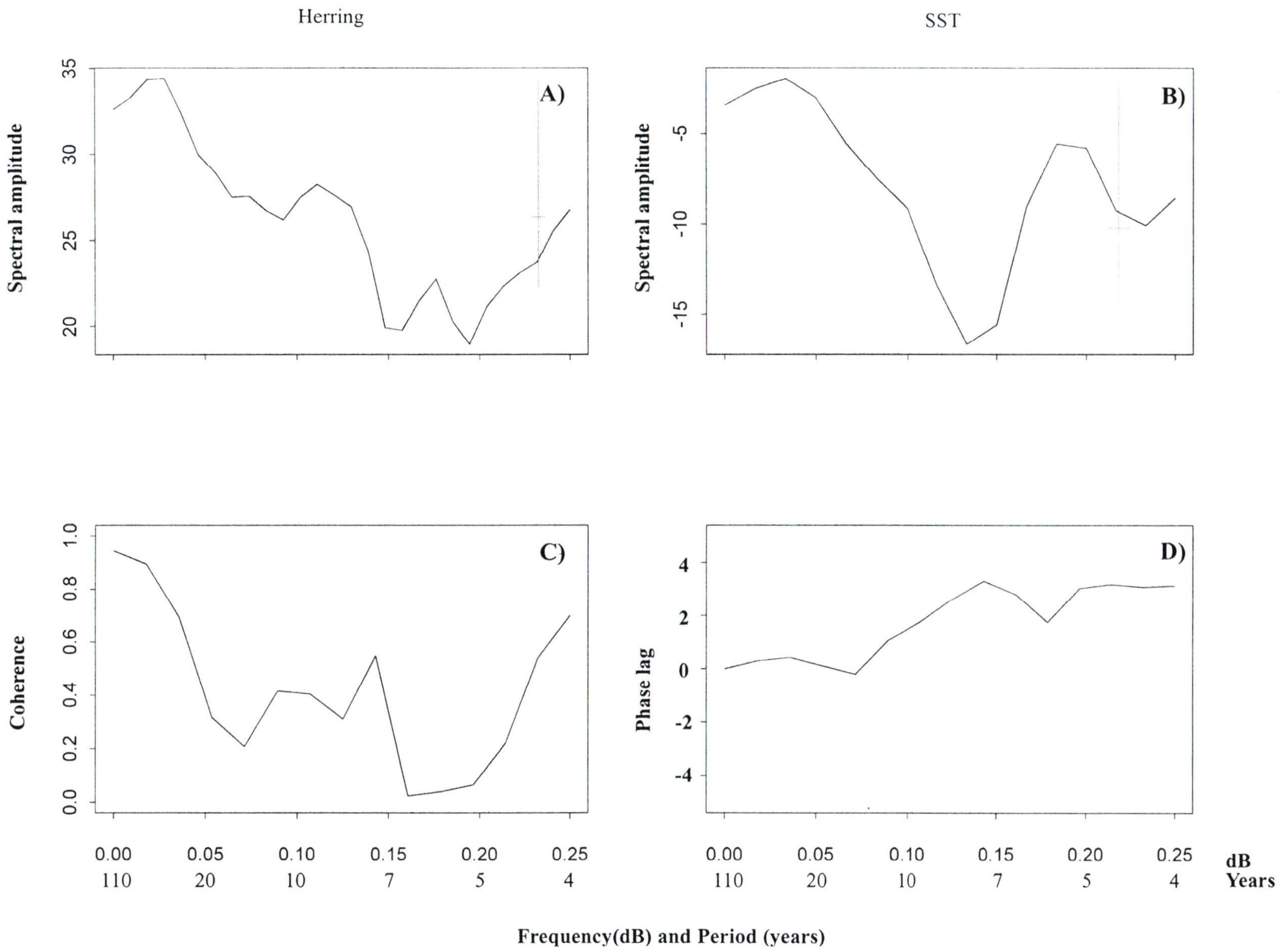

Herring
SST
A)
B)
C)
D)
Spectral amplitude
35
30
25
20
Spectral amplitude
-5
-10
-15
Coherence
1.0
0.8
0.6
0.4
0.2
0.0
Phase lag
4
2
0
-2
-4
0.00 0.05 0.10 0.15 0.20 0.25
110 20 10 7 5 4
0.00 0.05 0.10 0.15 0.20 0.25 dB
110 20 10 7 5 4 Years
Frequency(dB) and Period (years)

Figure 3.7iii) Cross-spectral output for herring scale deposition and the diatom dataset. 95% confidence intervals are indicated. **A)** herring periodogram, **B)** diatom periodogram, **C)** herring scale deposition and diatom cross-spectral coherency: significant peaks are indicated by 95% confidence bars, **D)** herring scale deposition and diatom phase spectrum.

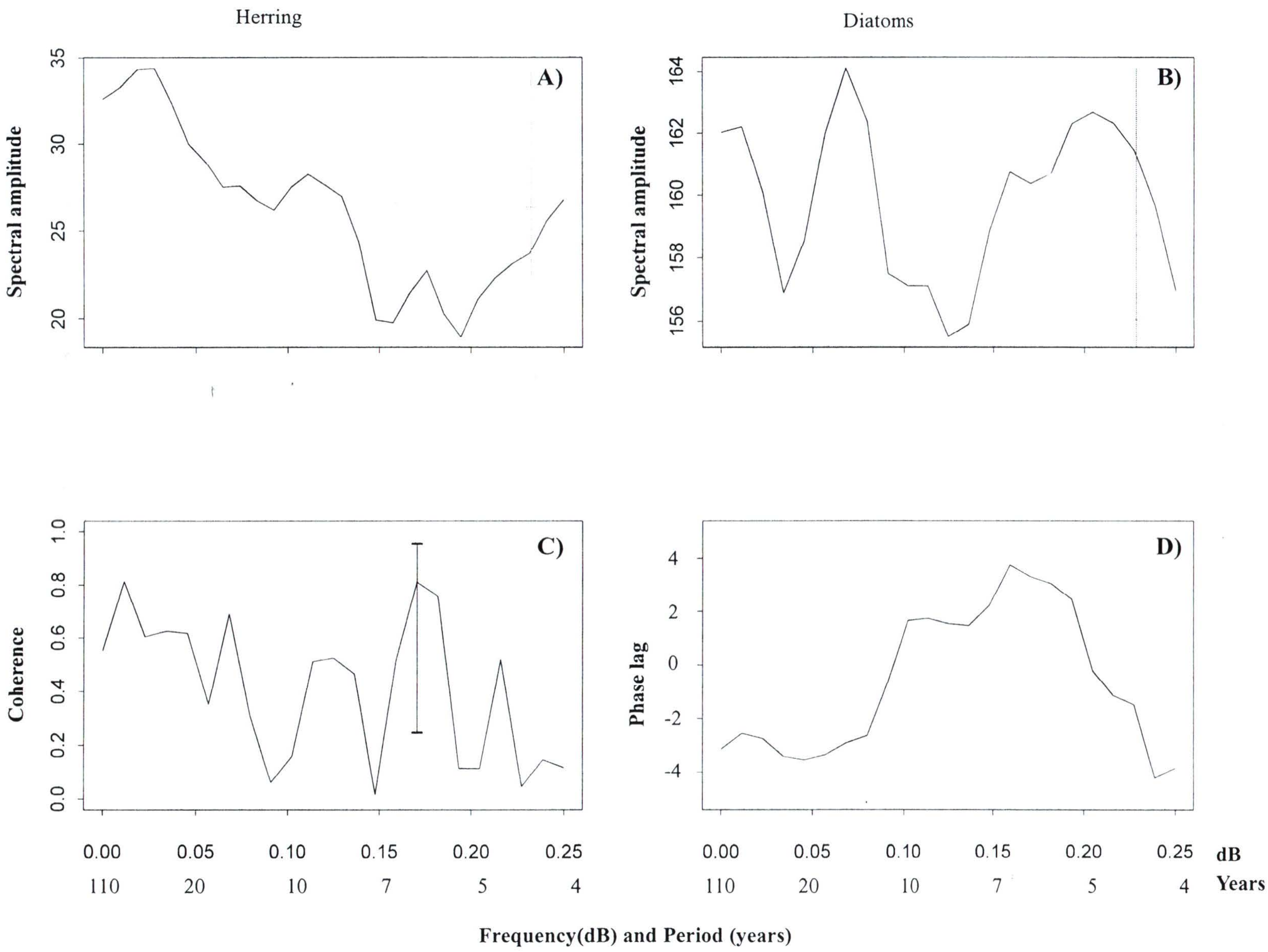

Herring
Diatoms
Spectral amplitude
35
30
25
20
A)
Spectral amplitude
164
162
160
158
156
B)
Coherence
1.0
0.8
0.6
0.4
0.2
0.0
C)
Phase lag
4
2
0
-2
-4
D)
0.00
0.05
0.10
0.15
0.20
0.25
dB
110
20
10
7
5
4
Years
Frequency(dB) and Period (years)

Figure 3.8i) Cross-spectral output for hake scale deposition and the ALPI dataset. 95% confidence intervals are indicated. **A)** hake periodogram, **B)** ALPI periodogram, **C)** hake scale deposition and ALPI cross-spectral coherency: significant peaks are indicated by 95% confidence bars, **D)** hake scale deposition and ALPI phase spectrum.

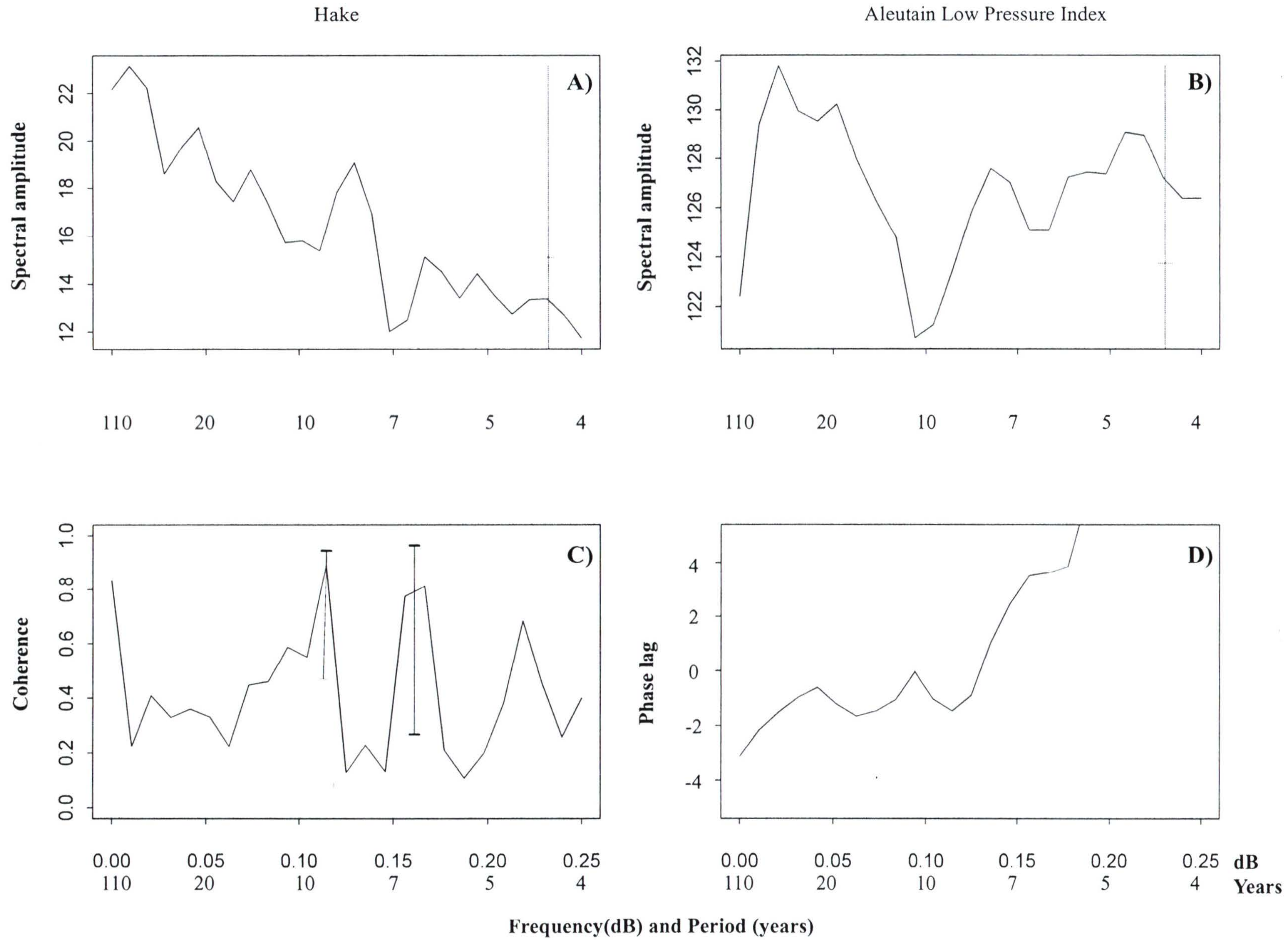

Hake
Aleutain Low Pressure Index
A)
B)
C)
D)
Spectral amplitude
Spectral amplitude
Coherence
Phase lag
12
14
16
18
20
22
122
124
126
128
130
132
0.0
0.2
0.4
0.6
0.8
1.0
-4
-2
0
2
4
110
20
10
7
5
4
0.00
0.05
0.10
0.15
0.20
0.25
dB
Years
Frequency(dB) and Period (years)

Figure 3.8ii) Cross-spectral output for hake scale deposition and the SST dataset. 95% confidence intervals are indicated **A)** hake periodogram, **B)** SST periodogram, **C)** hake scale deposition and SST cross-spectral coherency: significant peaks are indicated by 95% confidence bars, **D)** hake scale deposition and SST phase spectrum.

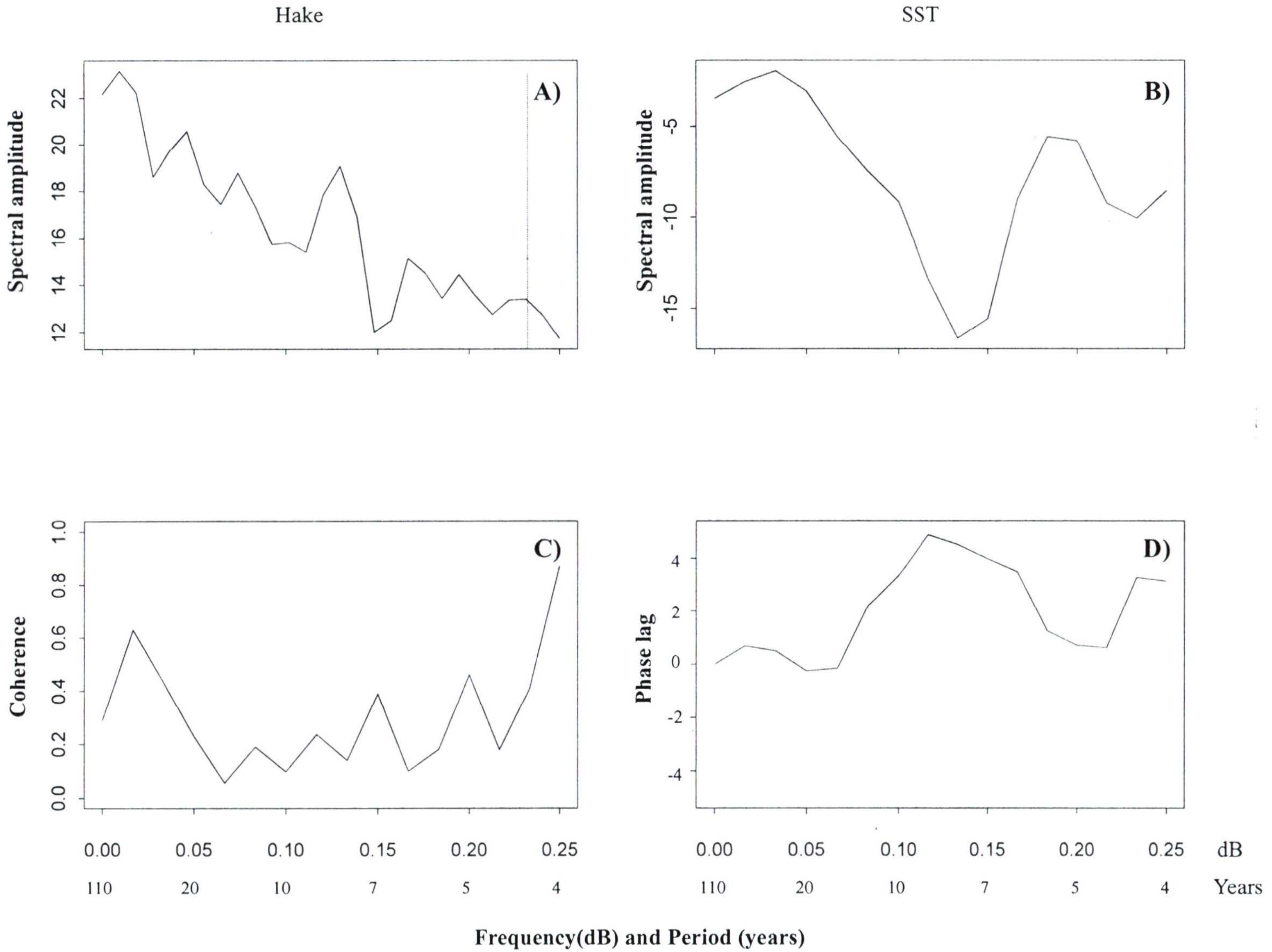
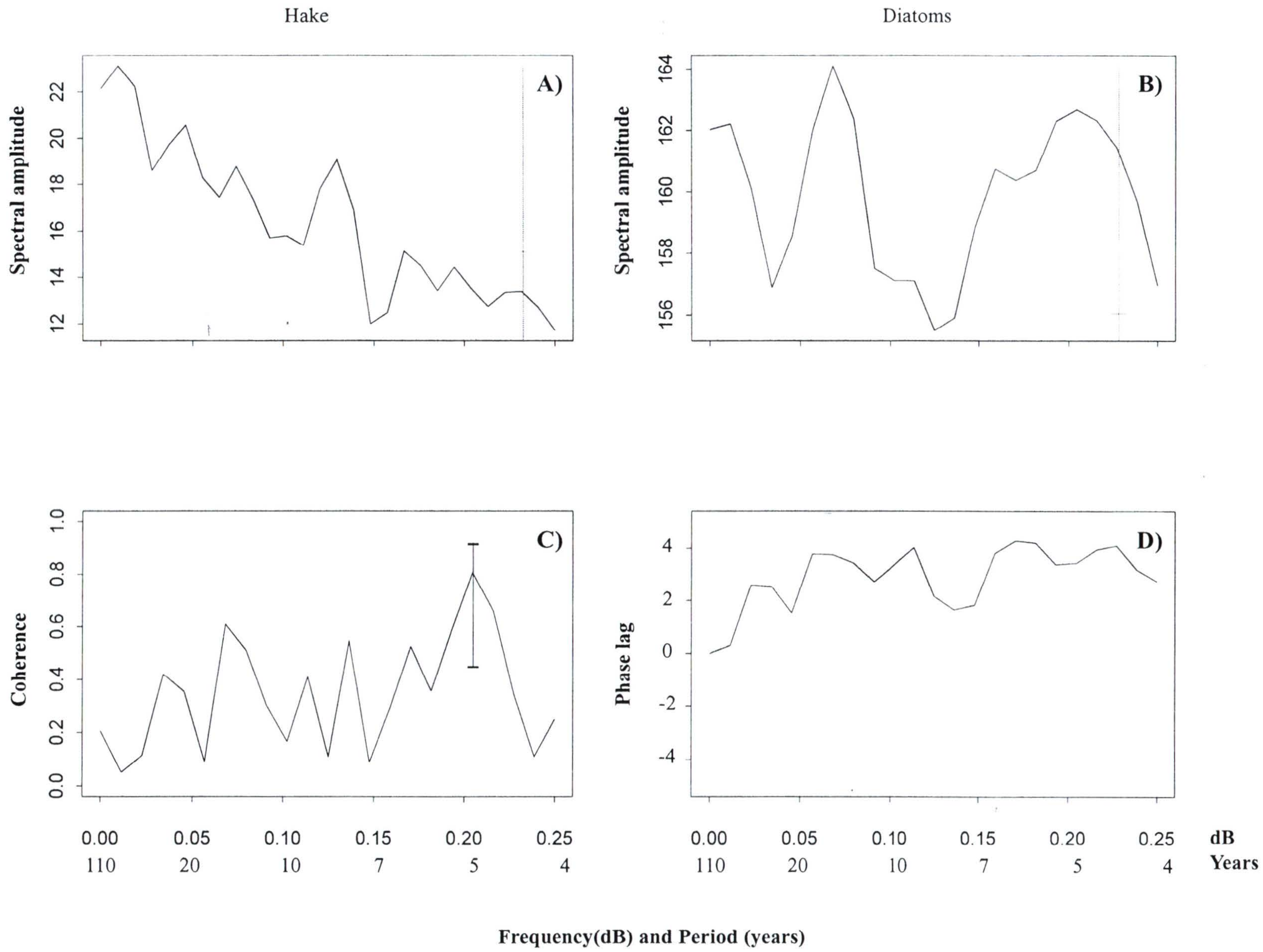

Hake
SST
A)
B)
C)
D)
Spectral amplitude
12
14
16
18
20
22
Spectral amplitude
-15
-10
-5
Coherence
0.0
0.2
0.4
0.6
0.8
1.0
Phase lag
-4
-2
0
2
4
0.00
0.05
0.10
0.15
0.20
0.25
dB
110
20
10
7
5
4
Years
Frequency(dB) and Period (years)

Figure 3.8iii) Cross-spectral output for hake scale deposition and the diatom dataset. 95% confidence intervals are indicated. **A)** hake periodogram, **B)** diatom periodogram, **C)** hake scale deposition and diatom cross-spectral coherency: significant peaks are indicated by 95% confidence bars, **D)** hake scale deposition and diatom phase spectrum.


Hake
Diatoms
Spectral amplitude
22
20
18
16
14
12
A)
Spectral amplitude
164
162
160
158
156
B)
Coherence
1.0
0.8
0.6
0.4
0.2
0.0
C)
Phase lag
4
2
0
-2
-4
D)
0.00 0.05 0.10 0.15 0.20 0.25
110 20 10 7 5 4
0.00 0.05 0.10 0.15 0.20 0.25 dB
110 20 10 7 5 4 Years
Frequency(dB) and Period (years)

For ease of comparison, significant coherence and phase for the scale and environmental data cross-spectral analyses are summarized in Tables 3-2 and 3-3.

Table 3-2. Significant coherence and phase lags for cross-spectral analyses of herring scale deposition and environmental datasets. Positive phase lags indicate the environmental parameter leads scale deposition, negative phase lags indicate scale deposition leads the environmental parameter. Due to the amount of averaging required for each parameter, and the width of the confidence intervals, there is uncertainty associated with these results.

Environmental Parameter	**Coherent Frequencies**	**Phase Lag**
ALPI	12	In-phase
	7	+ 4
	5	- 4
SST	-	-
Diatoms	6	+ 4

Table 3-3. Significant coherence and phase lags for cross-spectral analyses of hake scale deposition and environmental datasets. Positive phase lags indicate the environmental parameter leads scale deposition, negative phase lags indicate scale deposition leads the environmental parameter. Due to the amount of averaging required for each parameter, and the width of the confidence intervals, there is uncertainty associated with these results.

Environmental Parameter	**Coherent periods (years)**	**Phase Lag (years)**
ALPI	9	- 1
	6	+ 4
SST	-	-
Diatoms	5	+ 4

III - FISHERIES DATA

Low-frequency peaks – Smoothed fisheries datasets

Total biomass: Total biomass estimates show a slight peak in the early 1940s and a maximal peak in approximately 1953. Soon after, estimated biomass declines to an all time low in the mid-to-late 60s. Biomass subsequently recovers to peak at a late century high after 1976, declines in the early eighties, and appears to be equilibrating into recent years (Figure 3-9).

Scatterplot – herring and fishery data

Herring scale deposition increases with increasing fishery biomass estimates (Figure 3-10).

High-frequency peaks - Spectral analysis

The periodogram generated from the total biomass dataset shows that a high proportion of the variance in the dataset is concentrated in low frequency peaks. Specifically, 10-30 and four-year peaks explain much of the variance in the dataset (Figure 3-11B). A 25-year oscillation is dominant.

Cross-spectral analysis - herring and fisheries data

The coherency spectrum of herring scale deposition and fisheries biomass estimates shows relatively low coherency at all frequencies (Figure 3-11C) however, although it is not significant, the four and 6-8 year peaks are worth discussing.

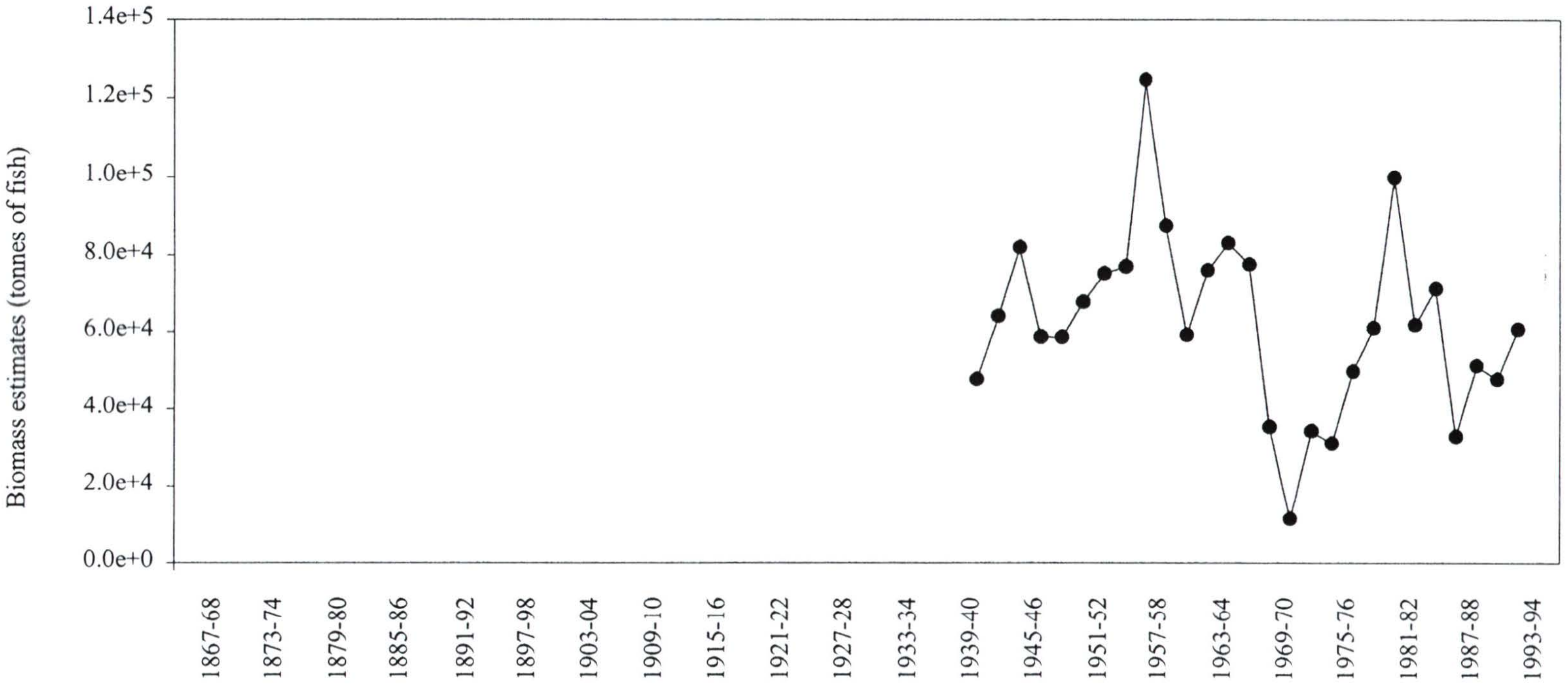


Figure 3-10. Time series of herring fisheries biomass estimates.

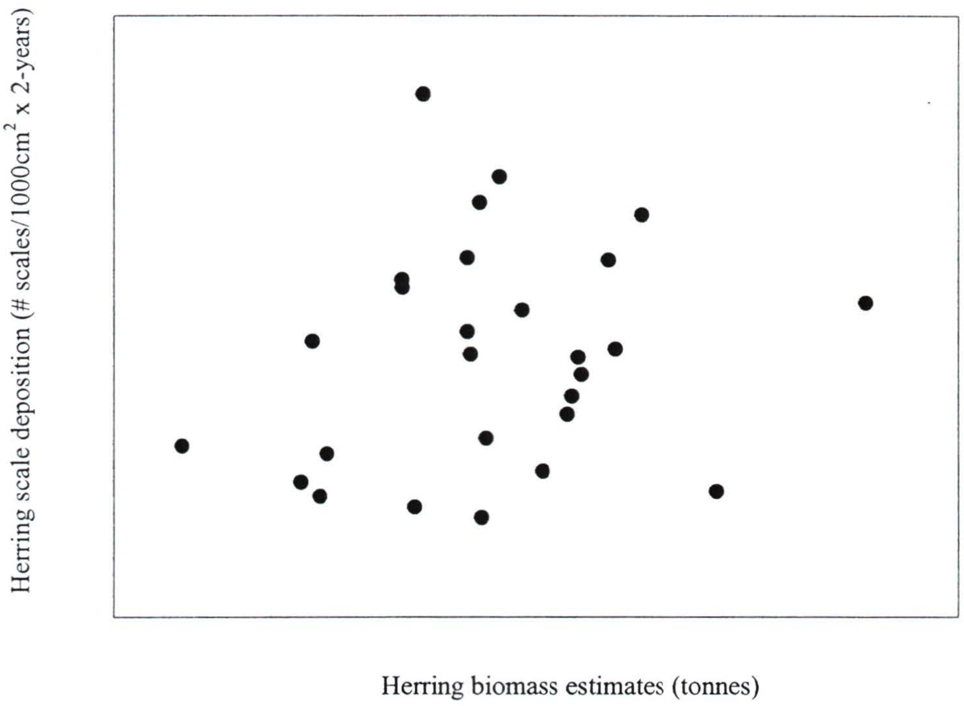
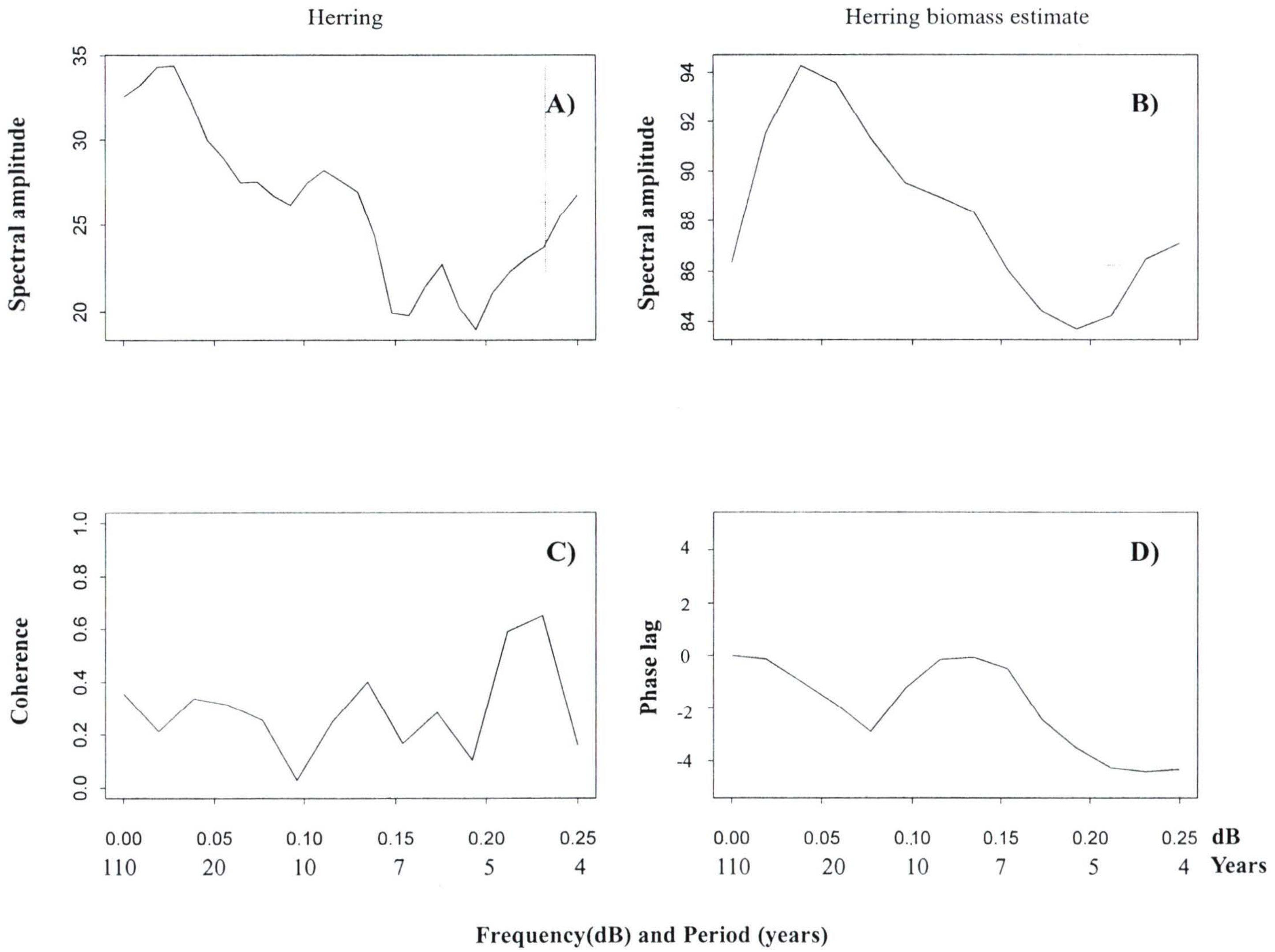


Figure 3.10. Scatterplot of herring scale deposition and herring fishery biomass estimates.

Figure 3.11) Cross-spectral output for herring scale deposition and the fisheries biomass estimates. 95% confidence intervals are indicated. **A)** periodogram for herring scale deposition, **B)** periodogram for herring biomass estimates, **C)** herring scale deposition and biomass estimates cross-spectral coherency: significant peaks are indicated by 95% confidence bars, **D)** herring scale deposition and biomass phase spectrum.


Herring
Herring biomass estimate
Spectral amplitude
35
30
25
20
A)
Spectral amplitude
94
92
90
88
86
84
B)
Coherence
1.0
0.8
0.6
0.4
0.2
0.0
C)
Phase lag
4
2
0
-2
-4
D)
0.00 0.05 0.10 0.15 0.20 0.25 dB
110 20 10 7 5 4 Years
Frequency(dB) and Period (years)

DISCUSSION

1. THE FISH

Pacific herring

Herring scales are the most abundant fish remains deposited in Saanich Inlet anoxic sediment cores (Chapter 2). Pacific herring have been in Saanich Inlet since deglaciation (~11 000 years before present) (Chapter 4) and are one of the predominant temperate pelagic species in the North Pacific Ocean. Like other clupeoid fishes, herring are deciduous schooling fish that form large populations with biomass in the millions of tons (Schweigert 1988; Schweigert 1993). Thus, their dominance in the remains record is not surprising (Chapter 2).

Herring scale deposition over the last 110 years in Saanich Inlet (Figure 3-2A) reflects the characteristic "boom and bust" nature of clupeoid dynamics (Lasker 1985; Lasker and MacCall 1983; Lluch-Belda et al. 1992; MacCall 1996; Smith and Moser 1988). Further, shifts in herring populations documented for the Pacific herring populations worldwide are resolved in the scale deposition record (Kawasaki 1991; Steele 1995) (Figure 3-2A). There is some indication of low frequency peaks in the herring scale data but due to the length of the dataset, discussion of their true periodicity is limited. There is certainly evidence of documented cycles and changes in scale deposition through time in the scale record, and these will be discussed with respect to predator numbers (especially hake), climate forcing, and prey density which are said to influence herring population characteristics (Ware 1991; Zebdi and Collie 1992; Zheng et al. 1993).

Pacific hake

Hake are the most abundant resident pelagic fish in the Strait of Georgia and their scales are also numerous and consistently present in Saanich Inlet sediments. Hake, like herring, have been in Saanich Inlet since deglaciation (Chapter 4) and are deciduous. Their remains are less common than herring remains in the sedimentary record but they outnumber any other fish's remains. From what little information is available, it has been determined that the strong year classes associated with well-studied west coast hake are not synchronous with Strait of Georgia hake (McFarlane and Beamish 1983; McFarlane and Beamish 1985). From recent fisheries records, it appears that hake abundance in the Strait has increased since the 1970s due to a succession of strong year-classes relative to the 1960s (M. Saunders, personal communication). The scale deposition record reflects this post-1970 increase (Figure 3-2B). According to McFarlane and Beamish (1985), the reason for the relative success and abundance of hake in the Strait of Georgia remains to be identified and periodicity in these stocks is as yet undescribed.

Herring and Hake – Predator prey relationship

Herring and hake scale deposition does not show a strong relationship across the 110-year record (Figure 3-3). For much of this century, irrespective of herring, hake scale deposition steadily increases (Figure 3-2). Explanation requires further consideration; however, it is postulated that in some cases, increases in hake (predators) contribute to the declines seen in herring (prey) numbers.

Predator-prey relationships are driving forces behind population dynamics in many ecosystems (Ricklefs 1990). In the North Sea, declines in herring abundance are strongly associated with increases in gadoid fishes (Rothschild 1995). A negative correlation has also been found to exist between herring recruitment and the estimated food ration consumed by hake in Canadian waters in the summer (Zebdi and Collie 1992; Ware 1991). The diet of adult Pacific hake in the Strait is composed mainly of pelagic and semi-pelagic animals. Hake are voracious predators and although euphausiids constitute most of their diet, they also feed heavily on small pelagic fishes such as herring (Livingston and Bailey 1985; McFarlane and Beamish 1985; Tanasichuk et al. 1991). Observations made during a series of cruises in 1981 indicated that about 15% of Strait of Georgia hake were feeding exclusively on herring (McFarlane and Beamish 1983). Although the relationship between herring and hake scale deposition in Saanich Inlet is not obvious (Figure 3-2, Figure 3-3) a closer look at analyses in the frequency domain (Figure 3-4) does suggest that herring and hake in Saanich Inlet interact as predator and prey.

Hake and herring scale deposition over periods of seven to eight years is in-phase (Figure 3-4). This suggests that both species of fish are responding to some forcing at the seven-year period as they are responding in-phase. As will be discussed, this seven-year period corresponds to strong fluctuations in ALPI/ENSO. Coherence is also significant at a 4-year period with herring leading hake by five years. This suggests that at higher frequencies (i.e. interannual scale) hake may actually exhibit a numerical response to herring numbers. On a four-year time scale, trophic interactions may influence relative abundances in these populations. Some hake are migratory to the West Coast of Vancouver Island and therefore during favourable years (i.e. warm period beginning in 1976), more hake have migrated to this area. In the last half of this century, few migratory hake have entered the Strait of Georgia (the Strait supports a resident population) however, some Strait of Georgia herring summer off the west coast of Vancouver Island so they may be impacted by hake predation in that area as well as the Strait (D. Ware, Personal communication).

II - THE ENVIRONMENT AND FISH

Aleutian Low Pressure

Wooster and Hollowed (1995) and Ware (1995) confirm that a significant amount of Northeastern Pacific variability is forced by changes in the strength and position of the Aleutian Low Pressure system. Changes in atmospheric and oceanic circulation appear to be coupled and Wooster and Hollowed (1995) further postulate there are two general categories of conditions: type A and type B. The relationships between herring and hake scale deposition and the ALPI are not strong (Figure 3-6A and B) and each shows a different association with this parameter. Herring scale deposition tends to increase when ALPI is negative, that is, when Aleutian Low Pressure is below average (Type A). Hake scale deposition, conversely, increases when the ALPI is more positive, indicating a strong Aleutian Low (Type B).

TYPE	REGIME	ALEUTIAN LOW	ALASKA GYRE	ENSO	FISH
A	Cool	Weak, west	Weak	No	Herring
B	Warm	Strong, east	Strong	Yes	Hake

Modified from (Wooster and Hollowed 1995).

According to the literature, and supported by the ALPI dataset used in this study, the Aleutian Low Pressure System was above average between 1925-45, below average to average between 1946-76, and above average again between 1977-89 (Figure 3-5A). For the period between 1925-45, herring scale deposition declines as expected (Robinson and Ware 1994; Schweigert 1995; Whitehead 1985). Also as expected, hake scale deposition tends to increase through this period (Bailey and Francis 1985; Bailey et al. 1982; Beamish and McFarlane 1985).

The period of below average intensity in Aleutian Low pressure between 1946-76 coincides almost exactly with the period leading into and during a major decline in herring scale numbers, and hake scale numbers remain steady through this period. Neither of these trends is expected, which may indicate something is interfering with expected ALPI responses. As will be discussed in more detail below, this period coincides with the beginning of intense fishing of herring stocks in the Strait of Georgia (Ketchen et al. 1983). Hake in the Strait were not yet heavily harvested at this time.

The strong ALPI years after 1977 show an increase in herring and hake scale deposition. Hake scale deposition is expected to increase during this period in response to the very strong ALPI, however, the return of herring scales from near zero values is not expected as the ALPI conditions are not optimal for herring. A point of major change in all time series is 1976. The abrupt change in climate in 1976 is summarized in Ebbesmeyer et al. (1991) but generally, this shift is associated with a strong phase of the Aleutian Low, high SST, and increased precipitation along the coast (Hayward 1997). Also, zooplankton abundances increased significantly across the Northeastern Pacific Ocean (Brodeur and Ware 1992; Trenberth and Hurrell 1995). Many of these changes favour high fish production, and the period from 1976-78 was exceptionally good for fish recruitment in the North Pacific Ocean (Beamish and Bouillon 1995; Hollowed and Wooster 1995). Outside of optimal ALPI conditions, it is not surprising that herring and hake both proliferate during the 1976 regime shift because many other conditions may have become favorable (i.e. food availability). Thus, where optimal conditions for one parameter are not met, perhaps others compensate. This regime shift will be revisited throughout the paper.

The favourable ALPI conditions for hake during the late 1970s coincide with the establishment of the hake fishery in 1978. Interestingly, the hake fishery is thought to contribute to increased hake recruitment. Since hake are formidable predators and are notoriously cannibalistic, fluctuations in marine fish can result from the influence of older individuals on the mortality in young (Botsford and Wickham 1979). The Strait of Georgia hake fishery focuses on removals of the large adults, which make up a significant proportion of the cannibals. Thus, more young hake survive to recruit under these circumstances, increasing hake population abundances, and subsequently impacting herring populations (C. Walters, personal communication 1998).

Herring and hake both become adults and recruit to their respective fisheries at age four (Schweigert 1995). Cross-spectral analyses indicate that, with respect to ALPI, herring and hake scale deposition are coherent at a period of six to seven-years (Figure 3-7i and 3-8i) and that these peaks are out of phase with the ALPI leading herring and hake scale deposition by four years. Since year-class strength is determined during juvenile life-stages, and abundance changes that occur due to climate may not be evident until affected recruits enter the spawning population or the fishery (Beamish 1995), ALPI effects should leave a lag signature as evident in the scale deposition record. Bulatov (1989) found a significant relationship between walleye pollock abundance and environmental factors similar to ALPI three to four years earlier, thus lending credence to this proposition.

Because of atmospheric coupling, the six to seven-year ALPI cycles can also be linked to El Nino Southern Oscillation (ENSO) events (Wooster and Hollowed 1995). The ENSO phenomenon is a cyclic warming event in the equatorial Pacific that develops every three to seven years (Philander 1983). ENSO related warming reduces ecosystem productivity and alters fish stocks. Specifically, hake migration to northern waters increases during ENSO years and herring numbers are characteristically low (Ware 1995). Moreover, cross-spectral results indicate that herring scale deposition and ALPI are in-phase at a 13-year periodicity. Ware (1995) suggests that interactions of ENSO and SST result in a pattern of alternating warm and cool climate states. Since 1850, he counts warm periods that occur with an 11.4-year periodicity (approximates the 13 year period). Thus, these two linked periodicities are convincing evidence that herring and hake stocks are driven in part by strong Aleutian Low Pressure/ENSO.

Sea Surface Temperature

Since transitions from warm to cool sea surface temperature states are associated with the coupled dynamics of ENSO and Aleutian Low Pressure (Wooster and Hollowed 1995), herring and hake scale data should show similar relationships to SST as to the ALPI. According to the SST literature, herring are more numerous during cooler years whereas hake proliferate in warmer years (Bailey and Francis 1985). Hake scale deposition and SST show this expected relationship (Figure 3-6D) however, herring scale deposition tends to increase with increased SST (Figure 3-6C). Despite the coupling of ALPI and SST, the relationship between scale deposition and SST is not straightforward.

The major SST changes through the last half of the century are roughly summarized as follows: 1958-64 was a warm period, 1965-69 mixed, 1971-76 cool, and 1977-84 warm again (Hollowed and Wooster 1995) (Figure 3-5B). Overall, herring scale deposition oscillates but declines through these first three stages of warm, mixed and cool conditions, and increases through the late century warming (Figure 3-2A). Most studies indicate that herring abundances are negatively correlated to temperature so the decline in herring number from 1958-65 is in keeping with the literature (Schweigert 1995; Tester 1948; Ware 1991). However, in other studies of herring in the Northeastern Pacific, this negative correlation finds exception. For example, Stocker et al. (1985) found Strait of Georgia herring stocks to be maximized at intermediate temperatures, and Hollowed and Wooster (1995), stated that many commercially exploited fish for which long-term records exist (e.g. herring) exhibit aperiodic fluctuations in relation to temperature. The cross-spectrum between herring scale deposition and SST shows no significant strong coherence (Figure 3-7ii) thus, although this is in keeping with some literature, SST is not postulated to have a very strong influence on Saanich Inlet/Strait of Georgia herring stocks.

Hake scale deposition declines or remains steady through the warm and mixed periods from 1958-1976 (Figure 3-2B). Although hake scale deposition does not show dramatic changes in much of the record, earlier than 1958 deposition increases through most warming and cooling phases (Figure 3-2B). This is not expected from the literature on West Coast hake populations and may be a unique characteristic of Strait of Georgia hake (Bailey and Francis 1985; Bailey et al. 1982; Beamish and McFarlane 1985; McFarlane and Beamish 1985; Ware and McFarlane 1995). Further, the cross-spectrum between hake scale deposition and SST shows no significant strong coherence.

Reasons for the inconsistent correspondence between high-frequency peaks in herring and hake scale deposition and SST may have much more to do with the SST dataset than the actual behaviour of the fish in response to this parameter. The SST data are from Entrance Island near Nanaimo, B.C.. This region is influenced greatly by Fraser River discharge. Fraser River freshwater is less dense than seawater and thus, ouflow from the river will flow above the denser ocean water. Sea surface temperatures in this blanket of brackish water may be different from those temperatures important to fish at greater depths. This dataset was chosen because diatom populations in Saanich Inlet were found to respond to Entrance

Island SST (McQuoid 1995). Further, monthly data averaged to 2 years may mask the response of fish to temperature, thereby decreasing the apparent response. In the future, studies should look at seasonal time series of temperature data.

Primary production- Diatoms

Trophic interactions among phytoplankton, zooplankton and fish are complicated as they are dependent on interactions in space and time (Steele 1995). As such, the relationship between primary production and fish has often been described as complex and non-linear (Cury and Roy 1989; Mann 1993; Robinson 1994). Herring and hake scale deposition decrease with increasing diatom cell numbers (Figures 3-6E and 3-6F). This relationship is not strong but a closer look at the details of the system may help to explain this association. Simplified, diatom growth is influenced by water temperature, light and nitrogen levels. Zooplankters such as copepods eat diatoms and are subsequently eaten by euphausiids. Herring and hake both eat euphausiids and hake further supplement their diet with small pelagic fish such as herring (Robinson and Ware 1994). Diatom to fish transfer efficiencies for the west coast modeled by Robinson and Ware (1994) are low and highly variable (between 0.5% - 1.2%). Upon consideration of the trophodynamic pathway and the number of intermediate factors that could disrupt this food chain, diatom productivity may not necessarily reflect fish populations. Primary production changes very quickly in response to the environment but secondary production does not respond as rapidly (Robinson 1994; Ryther 1969). Robinson (1994) suggests that in the Northeastern Pacific, diatom production is correlated to current abiotic conditions, whereas euphausiid production is more highly correlated to last season's abiotic conditions. Further, diatoms are most abundant in the late winter-early spring, euphausiids are numerous come summer and fish are in the Inlet year round. The intermediate in the food chain is thus a season and at least one trophic level removed from primary production.

Cross correlation analysis indicates that the herring and diatom datasets are coherent at a six to seven year period with diatom production leading scale deposition in herring and hake by approximately four years (Figures 3-7iii and 3-8iii). These cycles are similar to those seen with the ALPI. ALPI (and ENSO) affects water column stability, which may be an important and influential parameter in phytoplankton production (Gargett 1997). Further, zooplankton time series for southern British Columbia (west coast of Vancouver Island) indicate that zooplankton tend to vary with ALPI: when ALPI is strong, zooplankton populations are also strong (Mackas 1995). The four-year lag between diatoms and scale deposition supports the contention that climate affects fish recruitment but a cohesive and consistent explanation is still uncertain. It is interesting to note that all environmental variables examined in this study, ALPI, SST (although SST was not significant) and primary production showed coherency at a six to seven year periodicity, with environment leading fish scale deposition by four years (Tables 3-2 and 3-3).

III - FISHING

Herring scale deposition is positively related to herring biomass estimates (Figure 3-10). Comparing scale deposition rates to biomass estimates, and determining that these two records are reflective of one another confers a certain degree of credence to using scale deposition rates as proxies for fish fluctuations. The relationship is not strong and it may be that both fisheries data and scale deposition data must be regarded with caution; biomass estimates may not be reflective of true abundance but rather of measurable abundance (Beamish 1995; Isaacs 1975) and scale deposition may also be inaccurate. Further, the biomass estimates are from the Strait of Georgia and the scale record from Saanich Inlet; although these are within the same larger-scale ecosystem, abundance comparisons at these two very different orders of magnitude may be difficult.

Low-frequency peaks in the Saanich Inlet herring scale record mirror the evolution of the herring fishery in the Strait of Georgia. Before fishing, fluctuations in abundance presumably were due to natural causes. Herring scale numbers record typical, abrupt "boom and bust" dynamics through the first 60 years of the scale record (Figure 3-2A). Early century information on Strait of Georgia herring populations derives from anecdotal and uncertain fisheries records. The consensus, though not specifically quantitative, is that herring abundances were higher pre-1920 as seen in the scale record (Ketchen et al. 1983). An exploration of the fishery as presented in the literature points to over-exploitation of herring as a potential driving factor for the major decline in herring numbers (and scale numbers) seen in the late 1960s to mid-1970s (Schweigert 1993).

The first commercial fishery was reported in 1877 using drag or beach seining (Hourston and Haegele 1980). In 1905 drift gill nets were employed, and by 1910 purse seines were widely used. Early century catches ranged from 130-650 tons (Ketchen et al. 1983). The 1904-1934 fishery primarily catered to the dry salted market and production peaked at 42 000 tons but was reduced to 13 000 tons due to unsettled market conditions in 1932 (Ketchen et al. 1983). A major boom in exploitation occurred from 1935-1967 for the reduction (meal and oil) market. This fishery took place over the late fall and winter months, taking adults and juveniles alike and thus decreasing numbers of March spawners and recruits. Although catch quotas were introduced, there were frequent extensions and by the mid-1950s, catches were up around 70 000 tones (Ketchen et al. 1983). This fishery expansion coincides with the beginning of the decline recorded in the scale deposition record in Saanich Inlet.

The reduction fishery continued to grow, and by the 1960s the rate of removal was at an all-time high. Spawning escapement in 1965 fell to half of what it was in 1964 and to only 10% in the succeeding 3 spawning seasons (Ketchen et al. 1983). Nonetheless, catches remained high due to new technologies and massive catches. In 1967-68 due to poor recruitment of successive weak year-classes, high fishing efficiency, and underestimation of the declining size of spawning escapements in the 1960s, the Strait of Georgia fishery was closed (Ketchen et al. 1983). The crash in herring scale numbers in Saanich Inlet is not synchronous with the crash in the Strait of Georgia stocks however, this lack of synchronicity is within the range of the estimated geochronological error (+/- 5 years – Chapter 2).

In the early 1970s, the fishery was reopened and took on a new character: the roe herring era had begun. This fishery takes place in March before spawning and does not exploit juvenile fish. The recovery of Strait of Georgia stocks is reflected in the Saanich scale record. In addition to the change in the character of exploitation, recovery of the stocks is thought to have been a response to the major environmental regime shift in 1976 in the North Pacific.

Cross-spectral analysis of herring scales and biomass estimates shows a non-significant peak at 7-8 years (Figure 3-11). The 7-8 year cycle is now familiar and likely relates to ALPI/ENSO conditions. Interestingly, the two time series are in-phase, which suggests the fish may be driven by climate, while the fishery is responding exactly to fish fluctuations. Fishery estimates should track fish numbers from year to year and this direct correspondence (Figure 3-11 D) suggests that for major herring fluctuations fisheries estimates mirror scale deposition to a reasonable degree.

SUMMARY

Scale deposition rates do record significant changes in fish populations. Overall, pre-exploitation data (pre-1920s) are explained by straightforward responses in terms of fish interactions and environmental conditions (ALPI). After the 1920s, such relatively straightforward environmental relationships become strained. Although the true role fishing plays in driving herring populations is still speculative, results from this study suggest that in the Strait of Georgia ecosystem between 1946 and the closure of the fishery in 1969 heavy fishing thus led to the crash in Pacific herring populations in the late 1960s.

Fishing is an obvious source of mortality to fish but studies of fluctuations in fish populations have not yet come to any definitive conclusion as to the degree fishing effects any clupeoid collapse (Lasker and MacCall 1983). Other paleoecological studies have indicated that there is little question that there are natural fluctuations of high magnitude in fish populations due to factors other than fishing (Baumgartner et al. 1992; DeVries and Pearcy 1982; Holmgren-Urba and Baumgartner 1993; Shackleton 1986; Soutar and Isaacs 1974). Such data support the presence of major fluctuations in herring populations beyond human influence; in addition, these results support Ketchen et al. (1983) that suggest high fishing efficiency and underestimation of the declining size of spawning escapements resulted in the crash in Strait of Georgia herring populations of the 1960s.

Clupeoid stocks are susceptible to overfishing (Cushing 1982; Cushing 1971). The 1940-1960 herring fishery was the largest in British Columbia (Ketchen et al. 1983) and during this time, environmental responses seen in pre-exploitation herring scale deposition break down. Also, the replacement of the characteristic abruptness of clupeoid booms and busts with an overall decrease in amplitude in the scale deposition record suggests that during the period of highest exploitation, herring populations were adversely affected. Anoxic sediment cores and commercial fishing data have revealed that many pelagic fish populations alternate abruptly between periods of low and high abundance (Collie and Spencer 1993; Cushing 1982; Francis and Hare 1994). Thus, "natural" declines and recoveries are said to be abrupt and the hypothesis is that these populations have both high and low abundance equilibria and that the transitions between low and high are caused by low-frequency environmental variations (Collie and Spencer 1993). Moreover, once fishing pressure abated, stocks reestablished themselves almost immediately. After the 1968 fishery closure, the fishery re-opened but the character of the fishery changed dramatically. The result was recovery of the stocks.

The role of the environment in driving fish populations should not be discounted. To the contrary, pre-fishing dynamics are explained in part by expected environmental responses, ALPI/ENSO elicit strong responses, and the signature left in the sediments by the mid-1970s regime shift is remarkable. Perhaps if a longer record of scale deposition were collected, equally remarkable changes in fish scale deposition would be seen in response to regime shifts like that of 1976 (Mantua et al. 1997). Thus, as in other paleoecological investigations of pelagic fish remains (Baumgartner et al. 1992; DeVries and Pearcy 1982; Holmgren-Urba and Baumgartner 1993; Soutar and Isaacs 1974), there is evidence in Saanich Inlet of fluctuations with causes other than over-exploitation.

Causation is not easy to address in any environment and confounding the issues in marine systems are their notoriously high dimensionality. The significant coherent variation at typical ENSO periodicities (Philander 1983) seen in herring and hake scale fluctuations, ALPI, and diatoms, all lend support to the postulation that ENSO plays a significant role in driving interannual variation in herring and hake stocks. The consistency of the phase lag of 4 years - led by environment and followed by scale deposition - further supports that ENSO events affect recruitment as this is manifested in the sedimentary record 4 years later at maturation (Figure 3-12).

The objective of this project was to assess if variations in the scale deposition record in Saanich Inlet B.C. could be used to determine what controls variations in herring and hake population sizes. Using paleoecology, it may indeed be possible to develop an understanding of historical relations of biological response to physical changes in Saanich Inlet and the Strait of Georgia. Explainable temporal variability in the scale records exists. Little can be done about the timing and effects of climate change but a better understanding of climatic impacts and interactions with anthropogenic impacts on aquatic ecosystems will provide otherwise unavailable information to resource managers to factor into their programs. Because

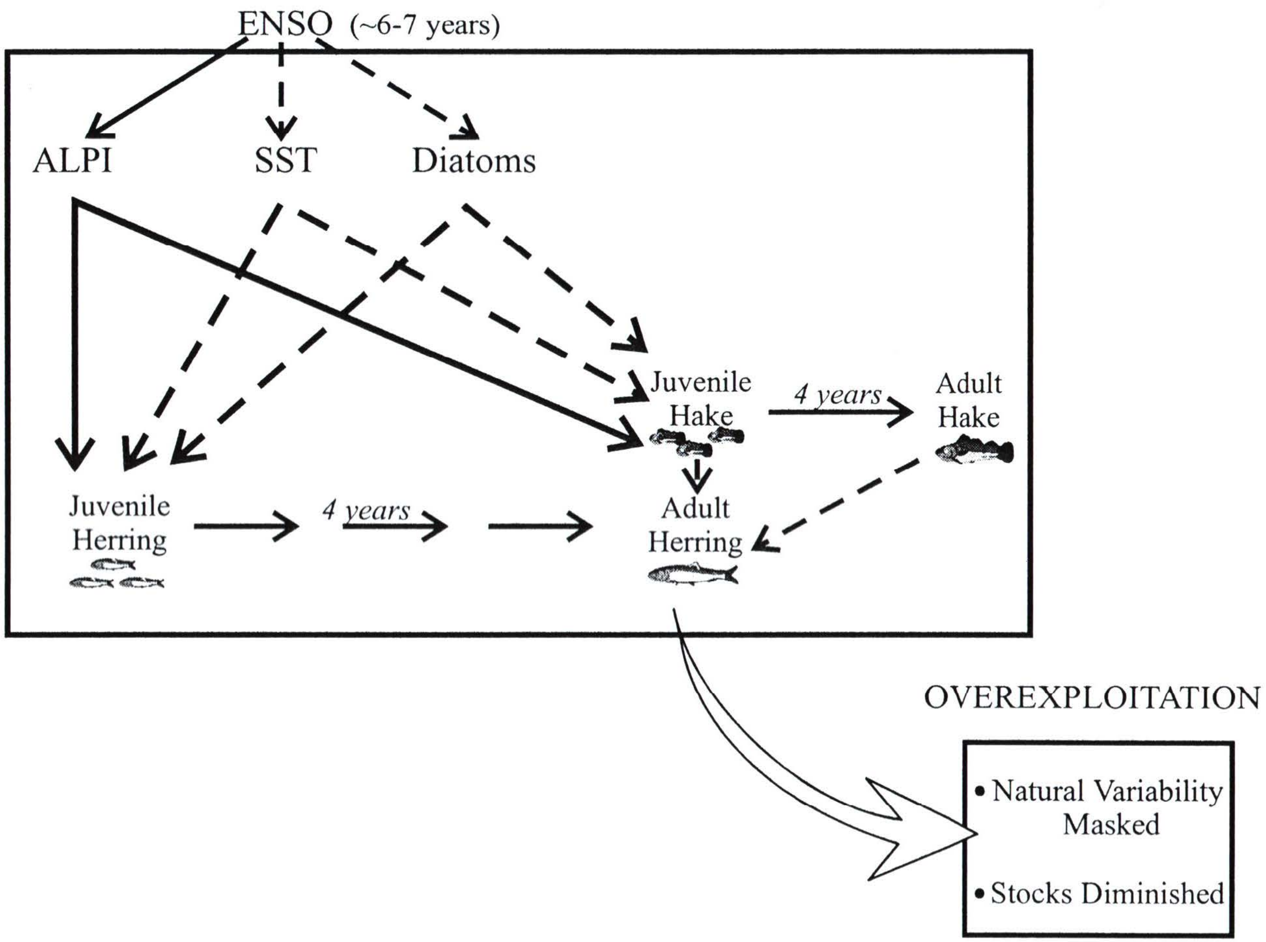


Figure 3.12. Generalized cartoon of major parameters driving herring population dynamics in Saanich Inlet.

sedimented fish debris does seem to chronicle past environmental and fish stock variability, taking longer cores may retrieve records may indicate if there is cyclicity to any of the trends seen in this short-duration data.

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CHAPTER 4: A Holocene Record of Marine Fish Remains from the Northeastern Pacific

V. Tunnicliffe, J. M. O'Connell, M. R. McQuoid

ABSTRACT

Ocean Drilling Program Leg 169S retrieved a complete sequence of Holocene sediments from Saanich Inlet, British Columbia, Canada. Fish remains and diatom skeletons were extracted from sediments at Site 1034. Very small bones, teeth and scales were present throughout the core except in the lowermost glacio-marine clays; scales degraded with depth. About a quarter of the remains were identifiable to species; Pacific herring contributed, by far, the greatest proportion of remains with Pacific hake and cartilaginous fish yielding significant fractions. A reconstructed record from samples every 50 years shows great variability much of which is a function of the small sample size constrained by the core area. A smoothed abundance curve highlights two periods of maximal abundance at about 1500 and 6500 years Before Present. Abundances in the last 1000 years are lower than the rest of the record. A correlation of this curve with abundances of seven phytoplankton species is significant; diatoms explain about a third of the variance. Fish remains appear in the record just before 12000 BP but greater diversity does not occur until about 6000 BP.

INTRODUCTION

The coastal marine ecosystem of northwestern North America was created after the last ice age. Examination of late Pleistocene through Holocene sedimentary strata provides a picture of an emerging assemblage of organisms subject to a variety of climate conditions in these centuries. The Cordilleran Ice Sheet retreated from the lower Vancouver Island area about 13400 BP (Booth 1987; Thorson 1980). Shortly afterwards, the effects of summer perihelion in the Earth's orbit resulted in a warming trend from about 11000 to 7000 BP characterized by higher summer temperatures and lower rainfall resulted (Heusser et al. 1985). A thermal maximum existed in southern B. C. from about 9000 to 7500 BP exceeding current mean annual temperatures by 2 to 4°C (Clague and Mathewes 1989; Hebda 1995). The cooler, wetter conditions of the later Holocene, after 5000 BP, are reflected in the vegetation shifts recorded in pollen from sediment cores (Hebda 1995; Leopold et al. 1982).

British Columbia had a highly changeable coastline as the glaciers rapidly retreated. Sea-level shifted as both isostatic and eustatic adjustments occurred with rapid changes between 11000 and 6000 BP (Luternauer et al. 1989; Friele and Hutchinson 1993). As the shelf ice retreated, the animals invaded. Most information on fish assemblages derives from piecemeal records from archaeological sites (summarized in Hebda and Frederick 1990). These authors do find a variety of fish reported from middens dating between 5000 and 6500 BP when well-established human populations were exploiting the fish of the British Columbian coast.

Saanich Inlet, on Vancouver Island (Figure 4-1), was the site of a mini-leg of the Ocean Drilling Program in August 1996. The drilling objective was to extract a complete Holocene sedimentary sequence that would penetrate to glacial sediments. Our sub-project was designed to examine the history of the fish assemblage through the Holocene from the time of glacial retreat. As sediments were required for other studies, our samples are restricted to only 8.3 cm^2 of sediment surface. Although the surface area is minimal, the very fine vertical sequence allows precise annual sampling for much of 12,000 years. Studies of fish remains in recent sediments mostly are undertaken where sediment layers are relatively undisturbed and pelagic fish stocks are sufficiently high to make substantial contributions to the sediments. These tend to be continental margin upwelling areas. In two anoxic basins off California, fish remains were first used to discern fluctuations in sardine, northern anchovy and Pacific hake abundances (Soutar 1966; Soutar and Isaacs 1969). Baumgartner et al. (1992) use additional cores in this area to create a remarkably consistent history of population cycling in sardine, hake and northern anchovy from AD270 to AD1970. DeVries and Pearcy (1982) describe a Holocene sequence of fish remains with large time gaps from the Peru margin. Shackleton (1986b) reconstructs a record of Namibian pilchard and anchovy over a 100-year period.

Use of fish remains in sediments is attractive because of the potential to discern long-term patterns in fish stocks. However, there are many problems in interpretation because of mechanisms of transfer of the remains to the sediments, preservational biases and reworking (DeVries and Pearcy 1982) (Shackleton 1988), For example, clupeoid fish (anchovies, herring, sardines) lose scales very easily compared to other species; relative contributions must be considered when using scales to interpret stock fluctuations (Shackleton 1988) (O'Connell, Chapter 2).

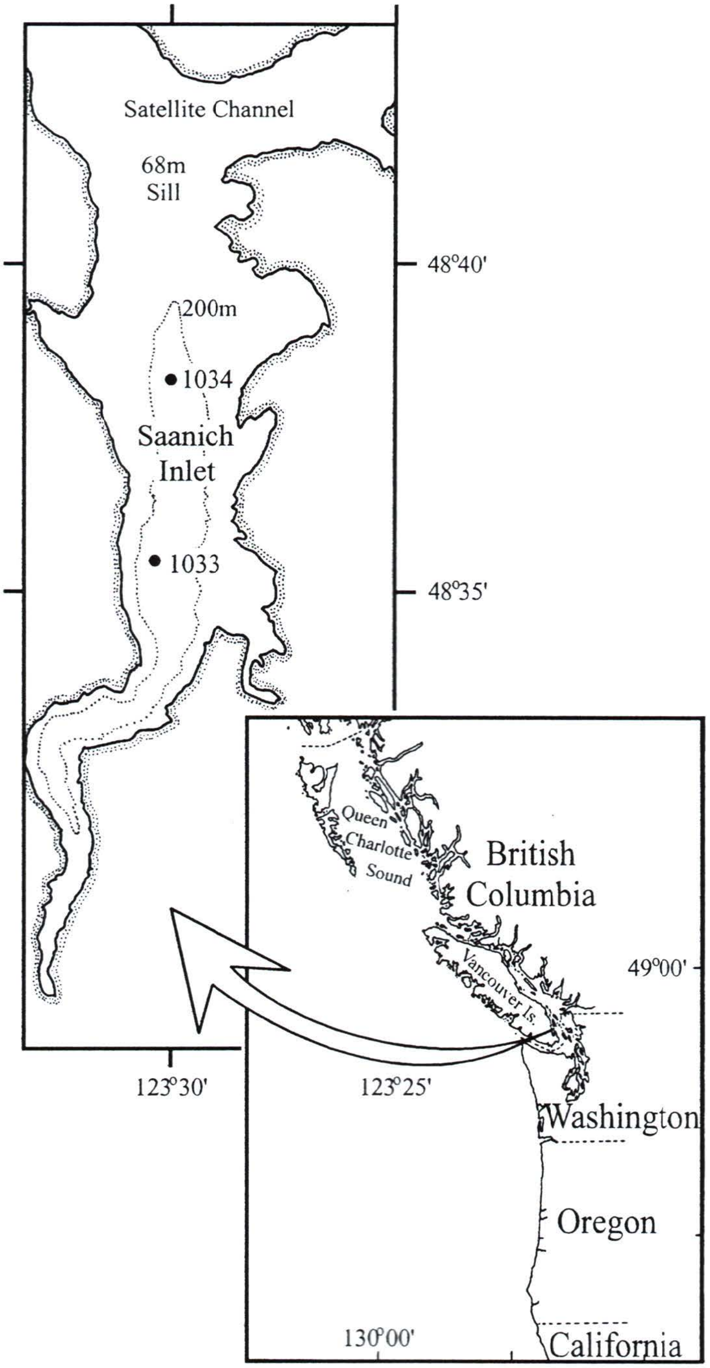

Figure 4.1. Location of Saanich Inlet on Vancouver Island, western Canada and the locations of the two ODP drill sites: 1033 and 1034. This study was conducted on sediment from 1034

Nonetheless, timing of appearance and overall abundance patterns are instructive in the construction of the history of the marine assemblage. Here, we take a further step to see if abundance patterns of fish remains have any relation to those of the Holocene diatom sequence.

METHODS

Study Site

The attraction of Saanich Inlet as a site for detailed historical studies lies in the nature of sediment deposition. The bottom waters of Saanich are hypoxic, if not anoxic, through much of the year. Sediments are undisturbed by bioturbation and thus record annual deposition in the couplet varves. Spring diatom blooms are light while the sediments laid down in the rest of the year are dark (Gross et al. 1963; McQuoid and Hobson 1997). Occasional massive layers from slumping disrupt the layered sequence but, otherwise, it is possible to sample known time intervals down to a single year. This condition has lasted for most of the past 10,000 years; unlaminated sediments mostly glacial in origin underlie this sequence. A shallow sill at the northern end restricts circulation in Saanich Inlet. The major source of terrigenous sediments is a river northwest of the sill; there is little sediment delivery from drainage directly into the Inlet.

Coring, extraction and handling during the ODP Leg 169S (August 20 1996) are described elsewhere (Bornhold et al. 1997b). Our work uses cores from Hole 1034 in mid-inlet at 48°38.00'N, 123°30.00'W and water depth 215m (Figure 4-1). We present information from a composite of three holes at one site (1034B, 1034D and 1034E) that are separated by 10m in an L-pattern. Hole 1034B, the major source for this study, penetrated 118.2 mbsf into Pleistocene clays. Radiocarbon dating techniques are described by Bornhold (1997b). The Mazama Ash layer (7645 BP) shows well at about 55m below sea floor in 1034B.

Sample Processing

Cores were retrieved in liners of 6.25 cm internal diameter. The cores were split and only half was sampled. The sample half was split again: fish remains were extracted from one side whereas corresponding laminae were sampled for diatoms (Figure 4-2). Samples were taken at 25 year intervals where year counts could be made and at 50 cm intervals in slumped or non-laminated sediments.

Hole 1034E (2 samples) and Hole 1034D (31 samples) overlapped the top of Hole 1034B (288 samples). To obtain adequate volume for fish remains we took 10 years of sediment; occasional holes due to prior sampling for other studies required additional laminae above and below the center of the sample. Sample volume was measured. Diatoms were retrieved from one lamina that corresponded to the middle of the fish sample.

Sediments were kept cold and processed within 18 months of drilling. Samples averaged 68.34 cm^3 in volume and over 75% came from well-laminated sediment that yielded year counts. For fish remains, sediments were very gently washed through 250μm and 125μm sieves and the residues retained in alcohol. The remains were picked and identified by comparison to reference scale and bone collections at University of Victoria. Samples for diatom analysis were cleaned with glacial acetic acid and peroxide (McQuoid 1995) . Aliquots were then dried onto 18mm diameter cover slips and mounted as permanent slides in Naphrax (Battarbee 1986). Diatoms were counted about every 50 years while fish remains were assessed for every 25 years. As not all diatoms in a year's sediments could be counted, flux was calculated using an estimate of sediment density for each layer.

RESULTS

Sediments

The holes at Site 1034 were correlated using distinctive horizons; appearance of the cores are described by Bornhold (1997b). Except for the top of 1034B which was disturbed during collection and the occasional massive interval, it was possible to discern annual laminations down to about 8000 BP. The underlying sediments down to about 10200 BP are (about 70mbsf) are variably laminated, sometimes indistinctly. This upper part of the hole, called Unit I, is generally composed of diatomaceous stilts. The dense, silty clays of the lower Unit II are interpreted as glaciomarine in origin (Bornhold et al. 1997b).

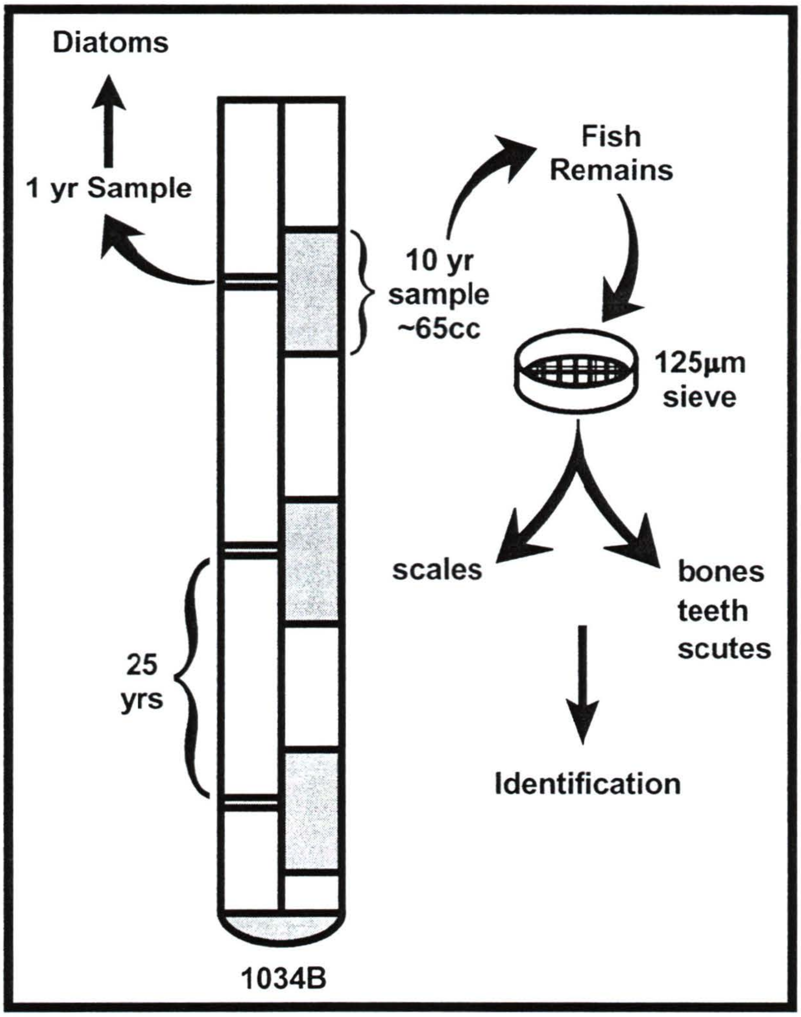

Figure 4.2. Sampling protocol. Half of each core is archived with ODP. The sampling half was split again with diatom and fish samples removed from matching horizons. A 10-year sample for fish remains was extracted every 25 years; where laminations were not present, a 10 cm section was taken for every 25 cm depth.

We could measure the thickness of a determinate number of years (between 8 and 14) for 237 samples: average annual laminae thickness between about 1100 BP and 10200 BP is 0.70 cm. Compaction does occur and the sampled volume decreases gradually with depth (Figure 4-3).

Unit II clays were difficult to process and yielded little material on the sieves; only a few samples in the bottom quarter of 1034B (below about 11300 BP) were examined.

Preservation biases

Fish scales are composed of microcrystalline apatite in a collagen-ichthylepidin matrix (Wallin 1957) and are susceptible to degradation. Examination of the scale:bone ratio suggests there is a preservational loss in scales as the scale to bone ratios diminish dramatically down-core (Figure 4-4). Other studies in Saanich Inlet indicate that recent sediments (last 130 years) have scale:vertebrae ratios above 1 (O'Connell, Chapter 2.). The ODP core has scale:bone ratios consistently well below 1 (average 0.15) and we believe scales are not well preserved in this lengthy Holocene record. Hole D also appears to have quite a different ratio than the equivalent depth in Hole B emphasizing variations in relative losses.

We examined sediment phosphate records to assess potential for dissolution of fish remains in the ODP cores. The solid phase phosphate shows no major peaks that relate to our fish data in Site 1034 (G. Filippelli, personal communication). At Site 1033, further up-inlet, the peak in solid phosphate values occurs deep in the core corresponding to the 60-70m horizon in Figure 4-5 (S. Calvert, personal communication) For dissolved phosphate (Bornhold et al. 1997a), there is a peak that is shifted down-core from the peak in ichthyoliths (Figure 4-5). This off-set profile combined with the solid phosphate information leaves the question of dissolution bias unresolved. It is probably occurring to some extent but there may be another phosphate source involved. Suess (1981) notes that the situation in Peru where fish debris contributes significantly to the phosphate nutrient pool is unusual and that, under normal conditions, other organic matter is the primary source for phosphate. Thus, we present the data on fish remains with the caution that there may be relatively higher dissolution in the lower core. Because of the uncertainty in dissolution, the changing scale:bone ratios and small sample sizes, scales are used only in a qualitative fashion to add information on fish identities. All quantitative results are based on enumeration of bones, scutes and teeth but should still be taken only as generalizations.

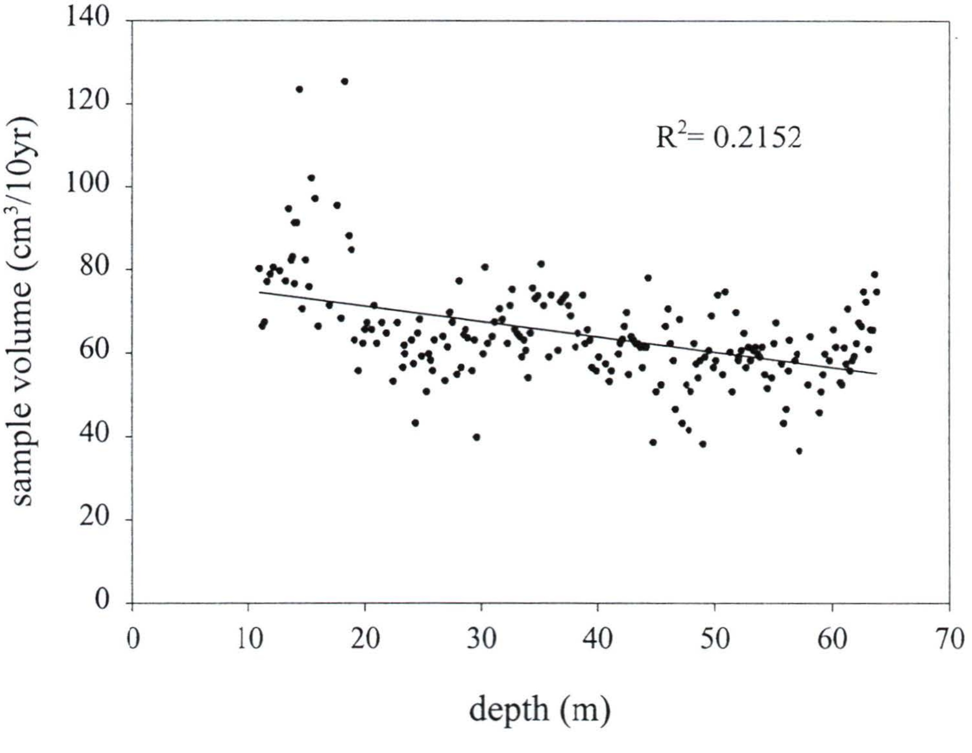

Figure 4.3. Sampled volume versus depth in Hole 1034B. For this presentation, only samples with countable annual varves and measurable volumes were used. The plot illustrates the decreasing volume of sediment sampled with depth apparently due to compaction of sediments.

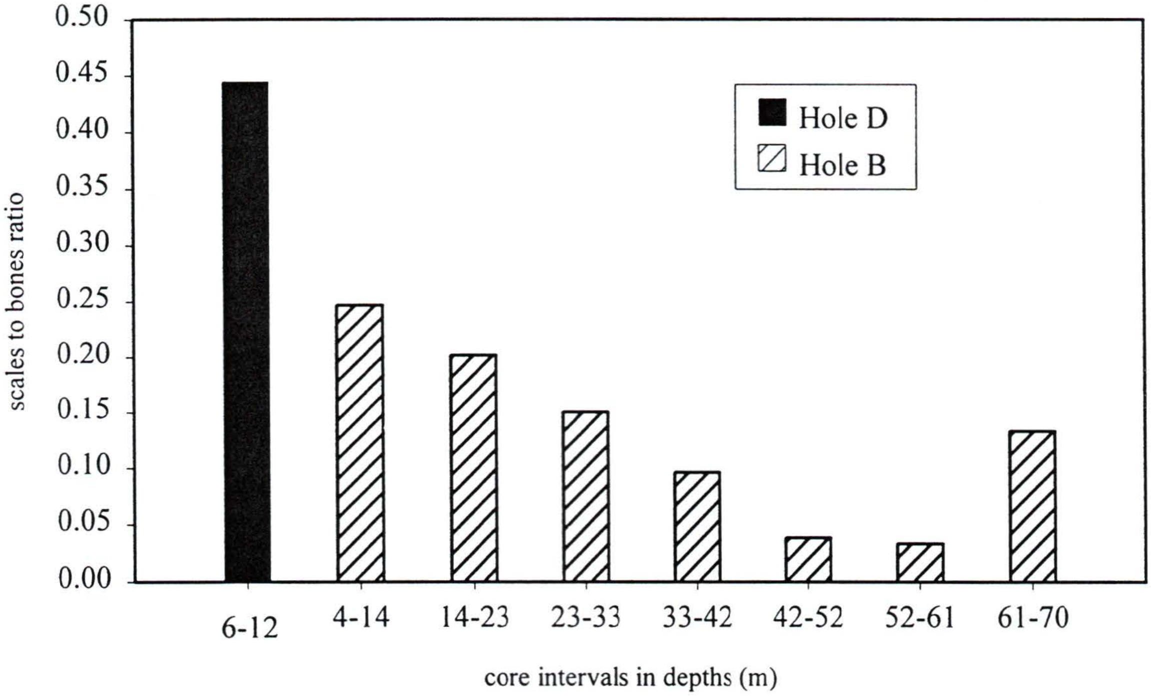

Figure 4.4 Scale to bone ratios in 10 m depth intervals in holes 1034D and 1034B. The profile strongly suggests a great loss of the scale record with respect to the less susceptible bones both between holes and with increasing depth. Scale counts are not used in construction of subsequent figures. Depth intervals are those calculated for the discreet core sections within each hole; amalgamated Site correlations result in some overlap between cores.

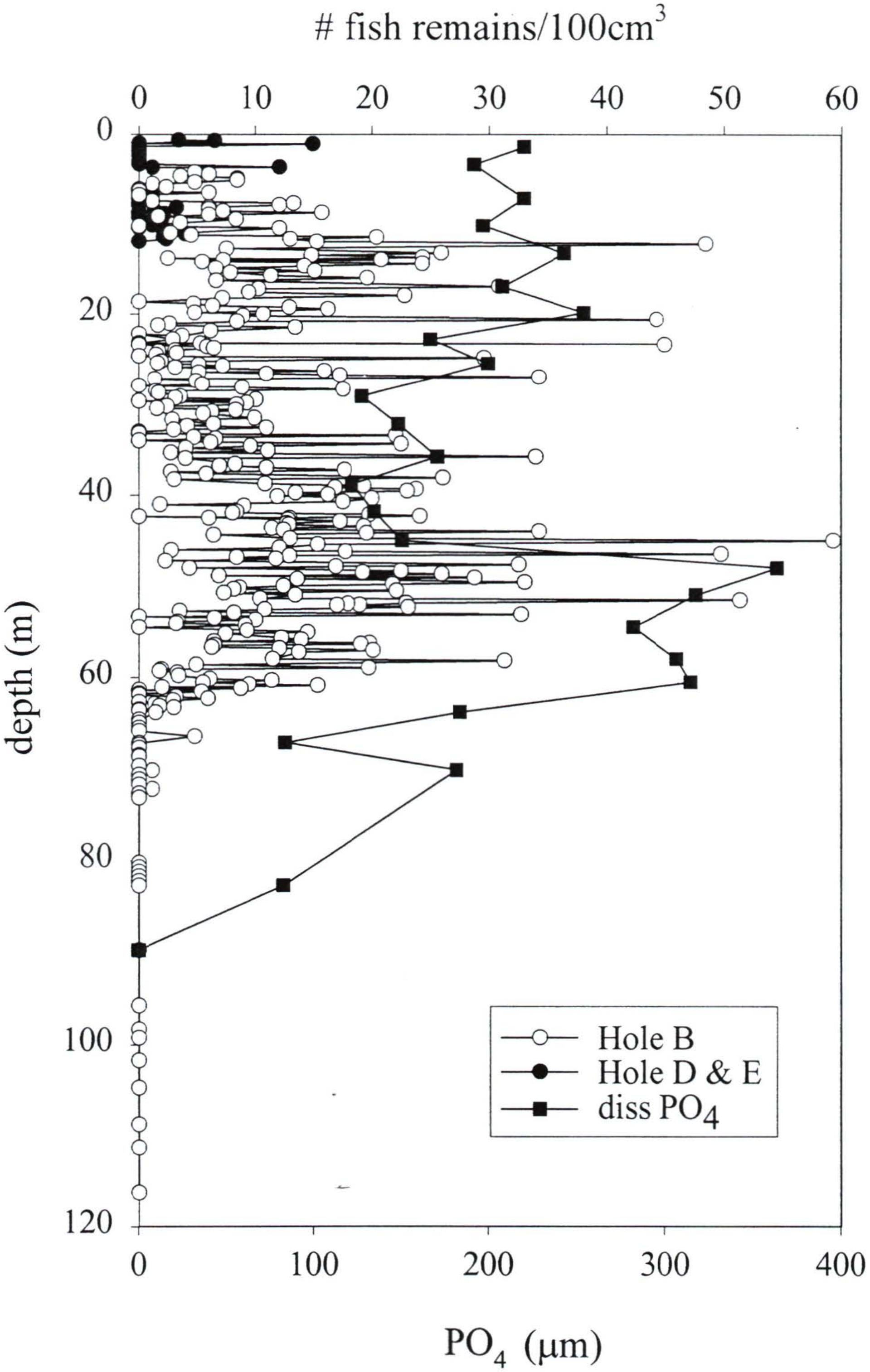

Figure 4.5. Abundance of fish remains (bones, teeth, and scutes) adjusted to a sample size of 100 cm^2. The filled circles are samples from 1034D and E; most of the samples (open circles) are from 1034B. The filled squares connect measurement of dissolved phosphate made on interstitial water extracted upon core recovery (data from Bornhold et al. 1997). Approximate radiocarbon ages are provided from AMS dates on material from core 1034B.

Ichthyolith Character

A total of 2,077 hardparts that appeared to derive from fish were picked from the sediments. Over 90% of the remains were held in the 250 μm sieve and ranged up to centimeter-sized vertebrae. Most fish parts were bones and teeth; scales accounted for about 10% of the count. Small unidentifiable bone fragments were present but the majority of bones were whole elements from very small fish. Early juveniles likely supplied the poorly calcified vertebrae that were not yet fully formed. Fin rays and ribs could rarely be identified to species whereas gill rakers, dermal bones, vertebrae and head parts were most diagnostic. Teeth usually could be identified although herring teeth are possible to confuse with other undifferentiated species. We believe most of the herring (*Clupea harengus pallasi*) identifications to be accurate, but there is a possibility of some confusion with sardine (although not with anchovy). Herring were clearly present in abundance and represented 53% of the identifiable bones (Table 4-1). No indisputable sardine bone was found except for the report by Casteel (1975) who records a single sardine operculum from Saanich sediments. The skate identification is accompanied by a question mark (Table 4-1) because a positive match with bone collections could not be made despite the abundance of these ichthyoliths. These "scutes" were very small and we have no juveniles in our collection for comparison. They all derive from the same cartilaginous fish – likely skate but definitely not dogfish.

The majority of the bones recovered in the sediments were teeth, scutes, vertebrae, ribs, fin rays and gill rakers. On the whole, there were few head parts found. Fish have an enormous number of tiny articulating bones in their heads that are unlikely to be diagnostic and subject to degradation. The mean number of diagnostic features in fish varies and skeletal elements rarely have been assessed probably because of the extensive reference collection and expertise required to identify the structures (Wheeler 1978). Many elements remain unidentifiable: only 37% of the recovered remains were taxonomically distinguishable (Table 4-1).

Fish scales recovered were 99% taxonomically identifiable although they made up only 10% of all fish remains extracted from the core. Relative species abundances do not reflect those of the bones.

Table 4.1. From a total of 2077 fish remains, 770 hardparts (37%) were identified to species; 568 of the identified hardparts were bones and 202 were scales. Herring and cartilaginous fishes dominated the 16 identified species. Of the unidentified remains, there were 201 teeth and scutes, 2 scales and 1104 bones. First appearance of a species is the deepest depth observed (* = scale evidence). The time of first appearance of each species is estimated from sparse radiocarbon dates (see (Bornhold et al. 1997a). Sardine record# is from Casteel (1975); this study located sardine scales at about 9000 BP.

Species	**Relative abundance** (bone remains)	**Depth of first appearance** (meters below sea floor)	**Time of first appearance** (years before present)
Pacific hake	3.5	71.21*	12000 – 13000
Pacific herring	52.6	70.20	12000 – 13000
Rockfish	0.2	63.81	~10050
surf perch	0.5	57.19	~7370
Dogfish	3.0	56.30	7300 – 8000
skate(?)	10.0	54.81	7300 – 8600
Sandlance	0.9	49.93	6400- 7300
Sculpin	0.7	47.60	~6500
Salmonid	0.9	45.99	4400 – 4800
Pacific cod	scales only	42.66*	~6300
Shark	0.2	20.80	~2000
Northern anchovy	0.5	19.08*	~2000
sardine#	operculum	N/A	~8850-9850

Hake scales were 40% as abundant as herring scales whereas hake bones were only 6% as abundant as herring bones. A hake scale is thicker and thus less susceptible to degradation (O'Connell, Chapter 2). In a record of this length, bones appear more reliable for relative abundance assessments.

Distribution of Fish Remains

An average of seven remains were retrieved in raw samples with range from zero to 36. The clay sediments of Unit II below 68.4mbsf yielded few ichthyoliths although extensive shell hash from molluscs was present in the upper part of this unit. We found no fish remains below 70.2m in 1034B, a depth that dates to between 12000 and 13000 BP. Many other characters of the core such as organic carbon, sulfur and ammonia decrease markedly below 70m (Bornhold et al. 1997a). In contrast, nearly all samples above these base layers yielded remains. Another region of low recovery was in the upper 12m, especially from Hole 1034D (Figure 4-5). There is a possible artefact as these cores were shipped to the ODP repository in Texas and sampled 15 months after recovery (8 months after processing 1034B). Nonetheless, 1034B samples are also depauperate in the upper layers and confirm the relatively low recovery in this region compared to the rest of the core.

The signal of abundances shown in Figure 4-5 is noisy. A five-sample running mean is presented for the upper 80m in Figure 4-6. Here, two distinct regions of high abundances are evident: around 12m and between 45 and 53m depths. Other features include a sharp initial increase at 60m and a mid-point low. Figure 4-7 presents some of these data converted to flux. Flux could be calculated only for those samples where annual couplets were distinct. The abundance peak around 45m is lower than in the concentration plot (Figure 4-6) due to sediment compaction: 100 cm^3 sediment in the lower strata comprises more years. While these values are a better reflection of real sediment input, they require both excellent lamination and pristine cores untouched by preceding workers (many adjustments for 'sampling holes' had to be made).

Relation to Diatoms

Diatom counts per gram dry weight sediment were converted to numbers per volume using densities measured on the adjacent lamina; the profile of direct counts is very similar to the converted counts shown in Figure 4-8.

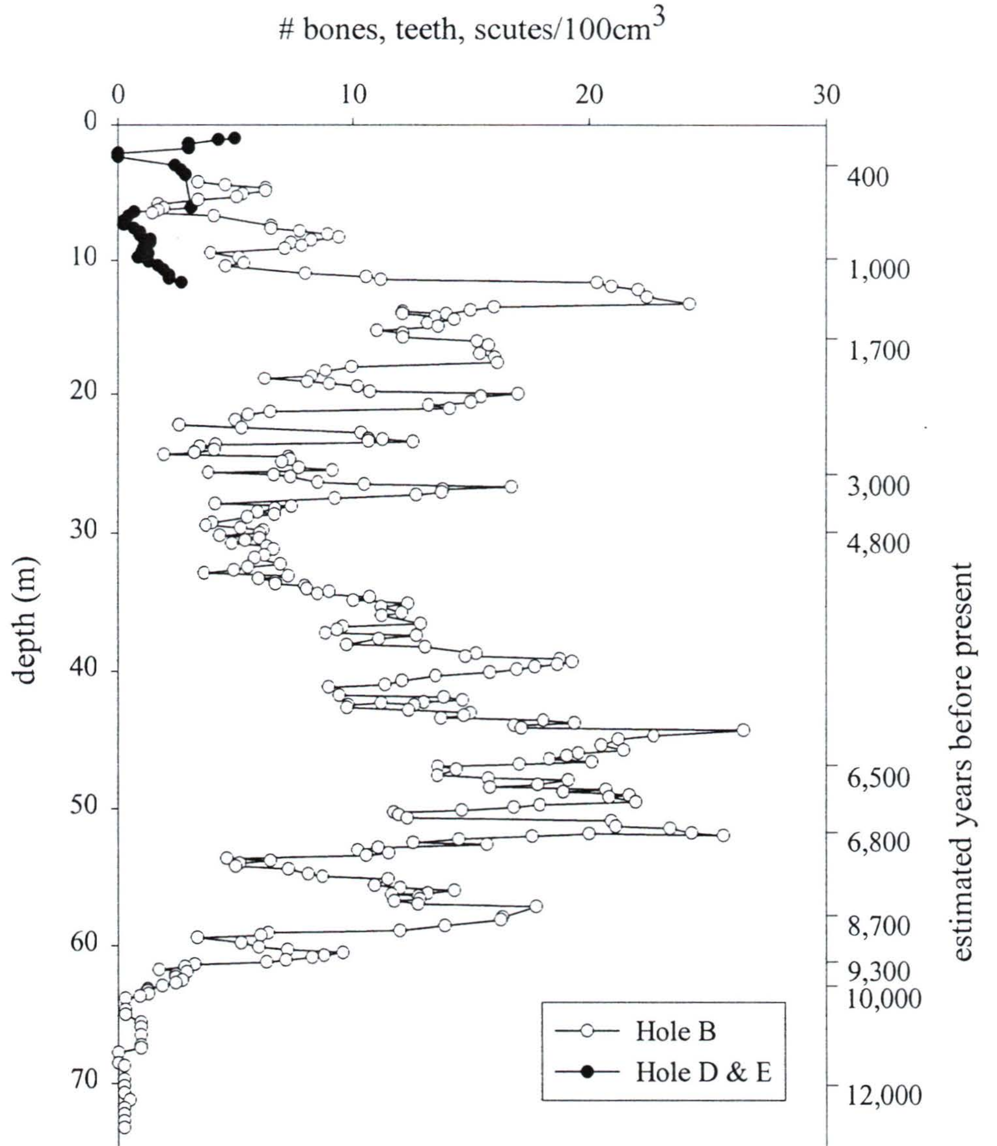

Figure 4.6. Five-sample running mean of concentration of fish remains; replotted from Figure 5 to reduce noise.

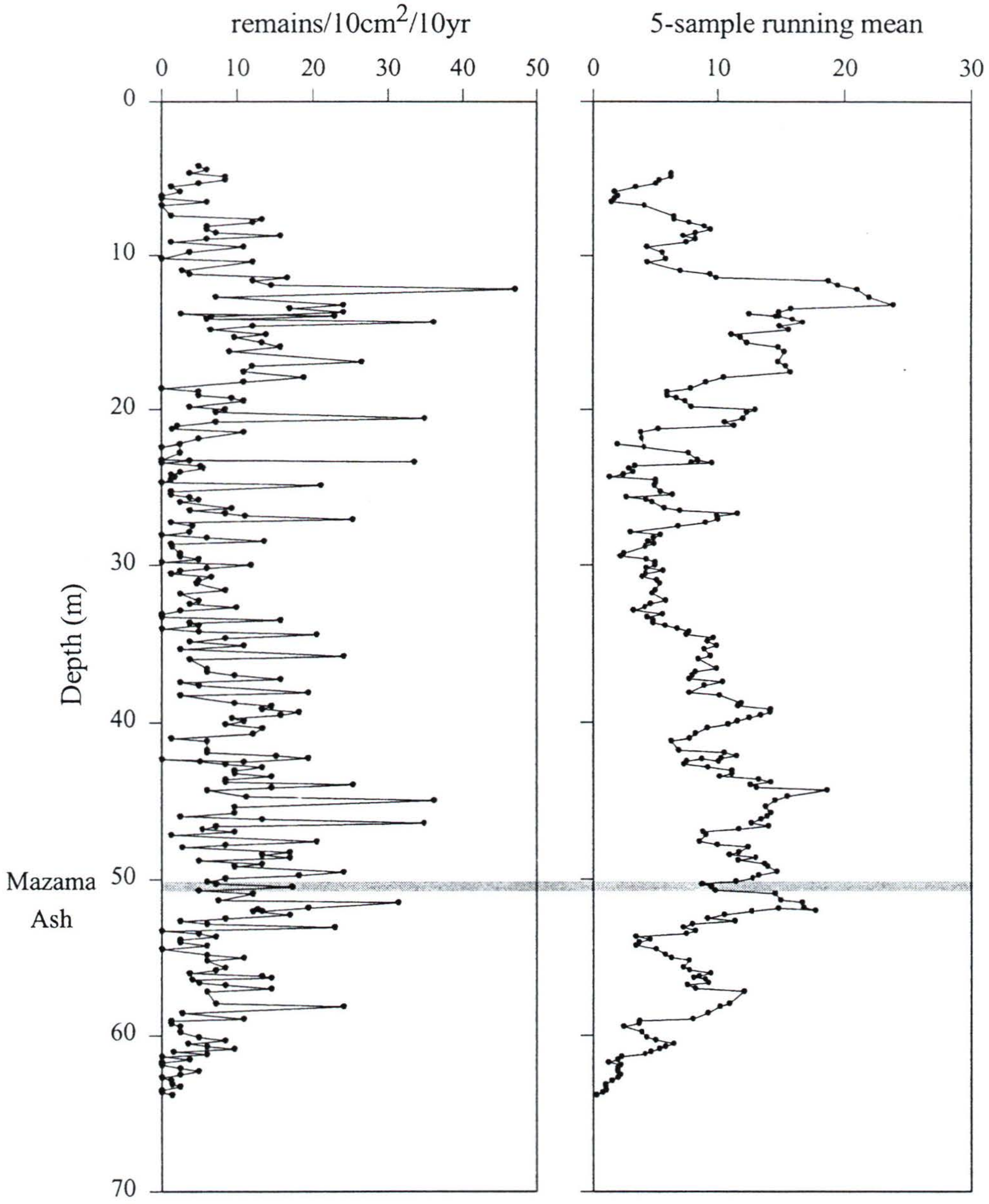

Figure 4.7. Flux of fish remains plotted as remains per 10cm2 sediment surface per 10-year interval. A is each sample while B is five-sample running mean. Laminae were not distinguishable in the uppermost (due to sampling) and lowermost (disturbed sedimentation regime) sections of the core so these intervals are not represented.

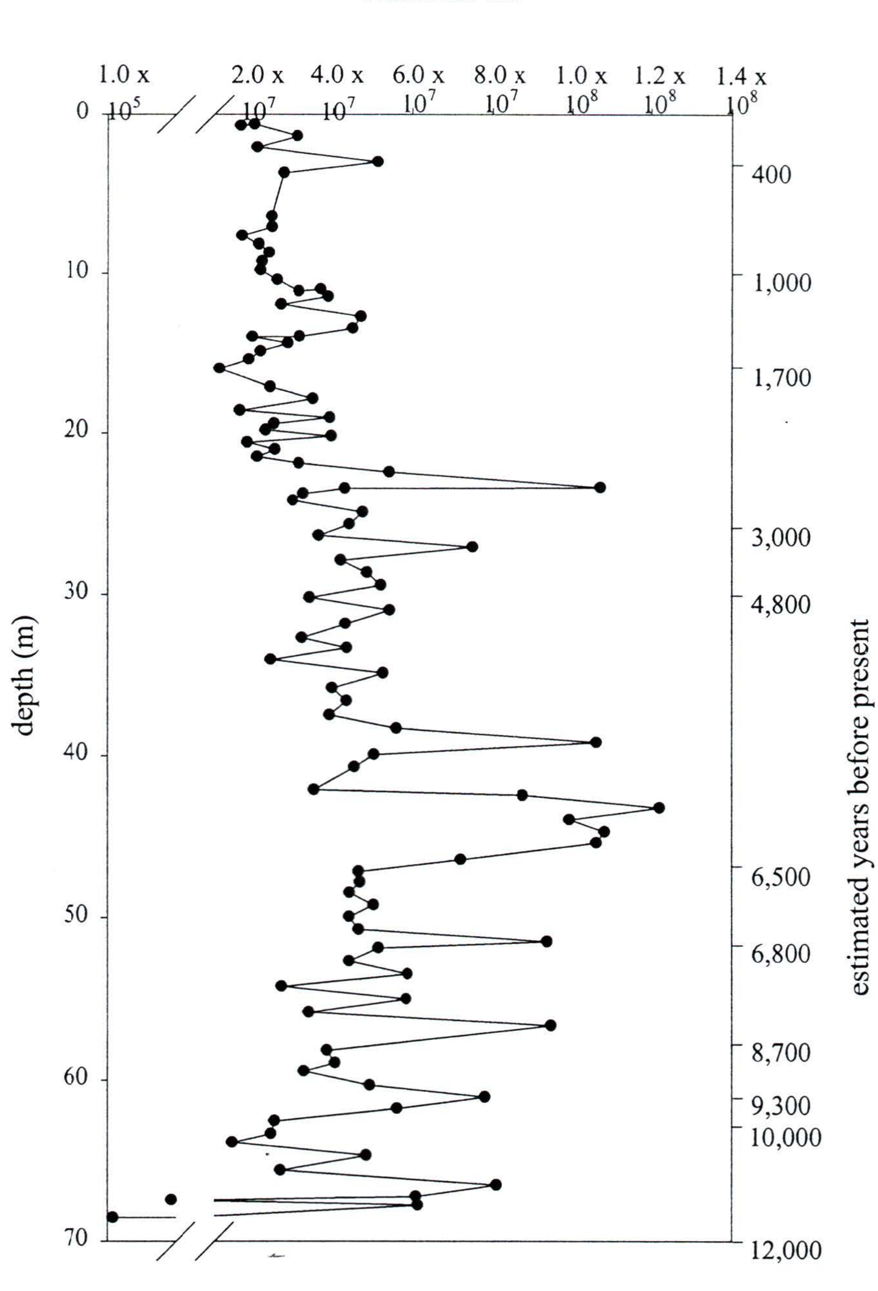

Figure 4.8. Concentrations of diatoms in Site 1034B. One-year samples were taken to match the middle of the 10-year fish remains samples at about every 50 years. Samples were examined for six diatom and one silico-flagellate species.

Diatoms appear in abundance a few meters below fish remains. No diatoms were present in exploratory smear slides below 70m. There is a distinct 40 - 50 m peak that is narrower than that of the fish profile. The low diatom concentrations in the upper 20m may be due to less sediment compaction but variability is much lower as no high concentrations are encountered.

High frequency variability is a feature of both fish and diatom records. For examination of long-term relationships, use of smoothed records yields a more realistic result (O'Connell, Chapter 2). We used a five-point moving average to examine relationships among abundances of plankton species and fish remains.

Fish abundance correlates with diatom abundance significantly with a multiple r-squared value of 0.33 (df=94; p<<0.01). The following diatom species make the greatest contribution to the significant relationship: *Skeletonema costatum*, *Thalassiosira gravida*, *Thalassionema nitzschioides, Chaetoceros* spores and *Paralia sulcata.*

DISCUSSION

Large volumes of sediment are required to derive adequate numbers of macrofossils for quantitative analysis. The constraints imposed by available ODP core material are such that we cannot assess comparative abundances of species through time. The use of long cores to interpret fish histories is attractive but it does assume a faithful translation of living populations to the sediments. Many sources of variability exist including varying preservation potential with time, effects of a single fish death nearby, bone breakage, differential preservation of the species (O'Connell, Chapter 2). Some identification of remains is possible when adequate reference collections covering the diversity of scales and bones in a fish are available. Over 60% of bone identifications were impossible in this study as some bones - especially from juveniles - were not diagnostic or were in poor condition.

We see scale degradation down-core. This artefact appears to be a phenomenon of these older sediments. In a complementary high-resolution study on Saanich sediments from the last 130 years, scales were numerous and showed no degradation; they were more useful than vertebrae in reconstruction of abundances through time (O'Connell, Chapter 2 and 3). Other studies spanning up to 2000 years also used scales with no comment on degradation (Soutar and Isaacs 1969, Soutar and Isaacs 1974; Shackleton 1986a; Baumgartner et al. 1992; Holmgren-Urba and Baumgartner 1993). DeVries and Pearcy (1982) examined remains in cores from coastal Peru that encompassed earliest and latest Holocene with a large discontinuity; they note a marked decline in scale to vertebrae ratio and diminished preservation in greater water depths. Basin-specific geochemistry and the length of the record likely determine the utility of the scale record. Work on bacterial abundances in Hole 1034B documents the presence of microbes in high numbers at 40 to 60 m in depth (K. Juniper, personal communication) that may contribute to continued degradation with time.

Because scales contain apatite and bones are phosphatic, sediment geochemical profiles, such as dissolved phosphate, may reflect dissolution of these remains in the sediments (Baumgartner et al. 1992; DeVries and Pearcy 1982; Soutar and Isaacs 1974). Suess (1981), determined that dissolution of phosphatic fish debris represents a mechanism for remineralization of phosphate. His study of anoxic sediments under the Peru upwelling zone suggests that fish bones and scales supply three times more phosphorus to the nutrient pool than other organic matter (Suess 1981). The chemical behaviour of phosphate remains poorly understood and we cannot determine whether downcore dissolution of bones was occurring in Saanich; the evidence from phosphate levels is not strong. At worst, dissolution would reduce the lower abundance peak in Figure 4-6.

The record of fish remains from Saanich Inlet fluctuates widely. Our study focuses on such a tiny piece of the Inlet floor that the details of Figure 4-5 are probably irrelevant. Variability between holes is very high. Fish remains in shallow box cores spanning the last 130 years of Saanich history also showed great variability but consistent low-frequency patterns arose after data smoothing (O'Connell, Chapter 2). The high sampling regularity of the ODP cores within such fine stratigraphic control gives reasonable confidence that Figures 4-6 and 4-7B reflect the historical trends of some of the Inlet fish. Preservation and representation factors discussed above caution against focus on the fine details of this record.

The fish remains in the ODP core are mostly from pelagic schooling species. Few of the bottomfish such as lingcod, rockfish or flatfish presently known in the Inlet are recorded from this central basin site; similar low recovery was seen in the shallow cores (O'Connell, Chapter 2). Clupeoid fish dominate the Saanich record as they do in the above-cited studies of fish records. Most bone and scale remains are herring (*Clupea harengus pallasi*) with some possible sardine (*Sardinops sagax*). Until recently, Saanich Inlet was a well-known area for pre-spawning aggregations of herring that spawn in the adjacent Strait of Georgia (D. Hay, personal communication).

The predominance of herring, hake (*Merluccius productus*) and dogfish (*Squalus acanthias*) remains in the sediments of Saanich Inlet is not surprising as these fish all shed scales, teeth and scutes easily. They are the most numerous pelagic/hemipelagic fish around Vancouver Island (McFarlane and Beamish 1983; Ware and McFarlane 1986; Tanasichuk et al. 1991). Herring is prey for both hake and dogfish. Off western Vancouver Island, euphausiids and herring constituted 93% of hake diet while euphausiids, herring and hake were 87% of dogfish diet (Tanasichuk et al. 1991). These fish are trophodynamically linked and their continued presence in the sedimentary remains record suggests this dynamic has been in place for millennia.

Sediment records are not useful in assessing past salmon histories. In this study only four likely salmonid elements were identifiable in among over 2000 remains. Similar poor return was experienced in the shallow box cores (O'Connell, Chapter 2). Currently, there are strong chum runs in Saanich and major runs of other salmonids in Cowichan River just west of the mouth of Saanich. This fish does not shed scales easily and the bones are poorly ossified; they likely degrade before they can be transported from the rivers after spawning. Salmon are known from the Columbia River, Oregon by 8000 BP (Hebda and Frederick 1990) so, presumably also inhabited the Inlet region at this time.

The Saanich sediment record yields information on the timing of fish appearances in the Inlet and, presumably, the surrounding waters. From 14000 to 12000 BP, Saanich received glacial outwash as a large bay open to the Haro Strait. We find no fish remains in this interval; either deposition conditions did not foster preservation or there were few fish in the Inlet. Closed fjord conditions occurred after 12000 BP when laminated sediments appear in the sediment cores (Figure 4-9). We have several occurrences of herring bones in the 13000 to 12000 BP time. Pacific herring is a cool-water fish presently found north to the Beaufort Sea. During the 13500- 11000BP interval, shallow water foraminiferal and

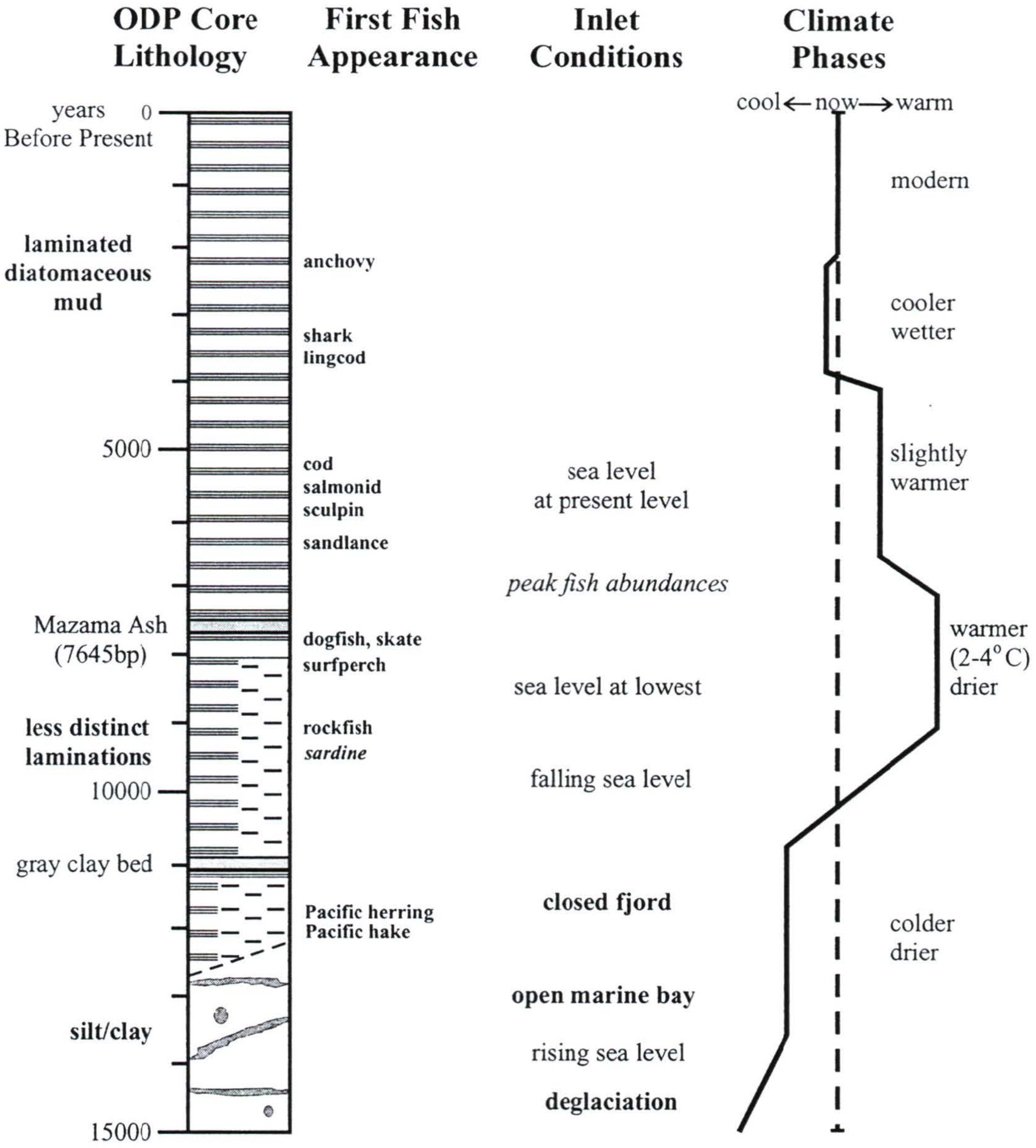

Figure 4.9. Chronology of events around Saanich Inlet throughout the Holocene. Vertical axis is time, not core depth. Gray clay bed is interpreted to be an outwash event from a large glacial lake on the mainland of British Columbia. Estimated time of first fish appearances is indicated. The sardine record is from Casteel (1975). Climate condition is adapted from Hebda (1995).

molluscan assemblages in the Strait of Georgia area are characterized as Arctic-Alaskan; Balzarini (1983) suggests a modern equivalent latitude of 60°N. Patterson et al. (1995) interpret foraminiferal assemblages between 11000 and 10000 BP in Queen Charlotte Sound (Figure 4-1) to reflect significant water mass differences offshore from those seen today. They propose year-round (not seasonal) dominance by the Aleutian Low pressure cell which would block upwelling of nutrients and northward flow of warmer water. Similar influences likely existed off Vancouver Island (R. Thomson, personal communication). Influx of warmer water fishes to the Strait of Georgia and Saanich Inlet may have required the seasonal Aleutian Low conditions that occurred later in the Holocene to present.

Huntley et al. (1998) postulate that isostatic rebound caused a low relative sea level stand at 9000 to 8000 BP thus altering circulation over the northern sill to a restricted water body. A greater diversity and abundance of fish is encountered after 9000 BP when the majority of fish species appear (Figure 4-9). Preservation conditions might have been better but, in addition, warmer and drier conditions prevailed in lower British Columbia at this time (Hebda 1995; Heusser et al. 1985; Mathewes and Heusser 1981). After sea level rise of the middle Holocene, present oceanographic conditions were established. Records of marine fish exploitation by indigenous peoples increase greatly in the 6500-5000 BP interval; most of the species recorded in our samples are known from middens on Vancouver Island and lower British Columbia at this time (Hebda and Frederick 1990). This time interval corresponds to the lower abundance peak of Saanich Inlet fish remains (Figures 4-5 & 4-6). Populations of local peoples may have increased at this time in response to ample fish resources. Alternatively, relative use of fish species increased.

Perhaps the most striking observation is that the abundances of fish remains in the last 1000 years are among the lowest recorded in the Inlet's marine history. There are no major changes in composition in the upper core but abundance and flux peak between 1000 and 2000 BP then decrease markedly to present. A similar decrease occurred in the northern anchovy (also a clupeoid) records from Santa Barbara Basin sediment cores (Soutar and Isaacs 1969). These authors estimate anchovy numbers at 1500 BP to be four to five times greater than present while we see about a three to four-fold difference. The lower amplitude and variability of the diatom record of the last millennium in Saanich Inlet may reflect an overall decline in productivity.

The relationship between primary production and fish is complex and non-linear (Cury and Roy 1989; Mann 1993; Robinson 1994). We see significant correlations between abundances of some diatoms species and fish remains. Most biomass transfer between plankton and fish is thought to occur via the "traditional pathway": from diatoms to meso/macro-zooplankton to fish (Cushing 1982; Kiorboe 1993; Mann 1993; Robinson 1994). Diatom to fish transfer efficiencies for the west coast of Vancouver Island are highly variable (between 0.5% - 1.2%) (Robinson and Ware 1994). As most larval and juvenile fish depend on secondary production by zooplankton rather than primary production as a source of food (Robinson 1994), it can be difficult to estimate fish production from primary production. That a clear long-term relationship exists between these trophic levels in the Saanich record suggests a consistent response of fish to diatoms and, perhaps, both biotic groups to climate factors (O'Connell, Chapter 3).

Under the exceptional preservation conditions of an enclosed basin it is possible to reconstruct biotic histories from the macro-remains in ODP cores. Interpretation is qualitative but a consistent history does arise. Herring and hake remains dominate the record as they do under current conditions. There was a period of maximal abundance of both fish and diatom remains about 6000 to 7000 BP. Warmer climate conditions likely influenced overall production in and around the Inlet. Ongoing work on other aspects of these cores - geochemical, palynological, and sedimentological - may reveal possible causes of the decrease in fish abundances in the last millennium.

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CHAPTER 5: Synopsis

The goals of this project were to investigate, apply and discuss paleoecological analyses of fish remains from ocean sediments. Chapter 1 introduces the format of the thesis. In this chapter, a short synopsis and summary of major results and interpretations is presented to put the three sub-projects (presented as the three main chapters) into concurrent context.

Chapter 2 focuses on obtaining, managing and interpreting sedimented fish remains data. The findings from this study are applied in the next two chapters (Chapters 3 and 4). Overall, in order to use fish remains in paleoecological studies of fish populations:

- The study site must have the necessary conditions to permit the preservation of delicate fish remains, and to permit the chronological preservation of sedimentary strata.

- The experimental design must be set up to ensure adequate replication, and these experimental units must be aligned with care. There must be some indication of the degree of uncertainty associated with alignment and geochronology.

- Large sample sizes (and thus large volumes of sediment) must be obtained for fish remains work because of the uncertainties associated with the origins of the remains and because these are macro-remains. Large volume corers (i.e. box corers) are recommended.

- Proper identification of remains in the sediment is an important factor when attempting to use faunal material in paleoecological reconstructions. As such, attention to ensure an adequate reference collection covering the diversity of remains in a fish is imperative.

- The sedimentary record of fish remains does not act as a presence/absence record and in Saanich Inlet, as in other studies, only deciduous pelagic fish are represented in quantifiable abundance.

- There must be some thought to issues of preservation in the sediments. If there is evidence of significant degradation through time in the record, the feasibility of using remains from that core for paleo-reconstruction may be questioned. Further, different remains preserve differentially; in upper Saanich Inlet sediments, scales were found to be more numerous and more consistently represented than vertebrae through time.

- Autocorrelation in sedimentary time series is not unusual and appropriate data management, standardization and analysis are required to minimize misinterpretation and violation of statistical assumptions.

- Because of the uncertainty in the means whereby scales are contributed to the sediments, careful attention to outliers and unusual samples is cautioned. Removal of outliers will alleviate many of the problems deriving from anomalous or "pulse" scale contributions due to carcasses settling to the sea floor. An acknowledgement of the variety of means for remains to arrive in the sediments will assist in interpretations.

- Data smoothing facilitates interpretations of low-frequency peaks through time and spectral analyses and cross spectral analyses in the frequency domain act to decipher high-frequency peaks, coherence and phase structure in two autocorrelated datasets.

Chapter 3 takes the methods and insights of Chapter 2 and applies them in a paleoecological analysis of herring and hake populations in Saanich Inlet British Columbia. A composite dataset of scale accumulation rates traces the dynamics of these pelagic fish through the past 110 years in the inlet. Predator-prey interactions, response to environmental parameters, and effects of fishing are all interpreted. Overall:

- Scale deposition rates do record significant changes in fish populations: pre-exploitation data (pre-1920s) are explained by straightforward responses in terms of fish interactions and environmental conditions. After the 1920s, when anthropogenic pressures intensify in the Strait of Georgia ecosystem, these environmental relationships become strained.

- Aleutian Low Pressure and the teleconnected El Nino Southern Oscillation are postulated to be the most significant environmental driving factors for high-frequency variation in the herring and hake datasets. Predator-prey interactions, sea surface temperature, and primary production also explain some variation; their dominant periodicities are contiguous with ALPI/ENSO dynamics, and it is postulated that most of their effects are driven by this dominant atmosphere-ocean system. From the scale record, the effects of ALPI/ENSO appear to affect juvenile fish survival and recruitment.

- Herring stocks in the Strait of Georgia are susceptible to anthropogenic influences. As seen in the scale record, heavy fishing in the Strait of Georgia ecosystem between 1946 and the closure of the fishery in 1969 altered fish responses to environment and is postulated to be a primary cause of the crash in Pacific herring populations in the late 1960s.

- The increase in marine productivity of the late 1970s documented in the literature was seen in both the herring and hake records.

- This study confirms the feasibility of using paleoscience to help investigate dynamics of herring and hake in Saanich Inlet as they relate to predator-prey, environmental and anthropogenic driving factors.

Chapter 4 uses modifications of the methods developed and used in Chapters 2 and 3 and applies them to a sedimentary record spanning the entire Holocene since deglaciation in Saanich Inlet. A diatom record obtained from the same paleo-sedimentary matrix is examined in conjunction with the fish record to investigate whether these methods can be used to derive a long-term link between primary and tertiary production the Strait of Georgia ecosystem.

- There are peaks in abundance of fish remains through the sedimentary record although the number of remains is quite low due to the limited material available for study and, thus quantifications are tentative.

- Bones are more numerous than scales through this long record but due to the difficulty in identifying bone remains species identifications can only be used qualitatively.

- When smoothed, peaks in diatom counts are correlated to fish remains abundance and a relationship between past primary production and fish is suggested.

- Pacific herring and Pacific hake have populated Saanich Inlet since deglaciation and the development of marine conditions over 10 000 years ago.

- Most other species represented in the record appear less than 8000 BP. This coincides with the timing of climatic moderation to conditions like those at present. Isostatic and eustatic adjustments are stabilizing and Saanich Inlet is becoming fjord-like. Also at this time, diatom abundances peak and sediments are becoming varved.

Climate factors are major contributing factors in fish-resource productivity. Fish populations exhibit a wide array of distributional patterns reflecting their sensitivities to environmental factors and it has been confirmed here that it is possible to correlate seasonal and interannual fluctuations in the distribution of fishes with changing hydrographic conditions. Through paleoecological studies of fish remains, a greater understanding of general fish ecology may be achieved as the complex information archived in the sediments may help elucidate relationships and dynamics that would be poorly resolved using conventional techniques.

Canada's marine resources support an important part of the nation's food supply, sustain the economies of many coastal communities, and in British Columbia, commercial fishing is the fourth largest primary industry. As the human population is expanding, the increasing demand for high quality protein and other marine resources has focused attention on the present stocks of commercial marine species and on the feasibility of increasing or at least maintaining the present harvest. The sensitivity of pelagic stocks to fishing pressure has been demonstrated. The results of this project can make a contribution to fisheries management by examining the past production history of several exploited species to aid in the appropriate initiation of harvest and protection protocols specific to the fish in question.

All paleoecological research has its limitations as the conclusions are drawn from proxy information and may incorrectly represent past realities. Non-linear relationships between fish and the environment are hard to explain and in the case of a paleoecological study when environmental parameters are chosen *a priori*, a lack of understanding of causal mechanisms may lead poor choice of environmental variables for investigation. Because the time series of scale deposition examined in this study are either short in relation to major climatic regime shifts (Chapter 3), or sample sizes are small so as to limit interpretations (Chapter 4), stand alone statistical proof of solid links between parameters driving fish population fluctuations remain speculative. Still, the benefit of using long-term paleo-records is demonstrated; this method allows a look at the responses of fish populations over long time scales that are greater than the lifetimes of their components. Overall, a paleoscience approach to investigation of pelagic fish population fluctuations and dynamics shows promise.

APPENDIX 1: Fish taxa in scale reference collection

Fish taxa in scale reference collection

Alosa sapidissima	American shad
Anopoploma fimbria	Sablefish
Atheresthes stomias	Arrowtooth flounder
Clupea harengus pallasi	Pacific herring
Cymatogaster aggregata	Shiner perch
Embiotoca lateralis	Striped seaperch
Engraulis mordax	Northern anchovy
Gadus macrocephalus	Pacific Cod
Glyptocephalus zachirus	Rex sole
Hexagrammos decagrammus	Kelp greenling
Hexagrammos lagocephalus	Rock greenling
Hexagrammos stelleri	Whitespotted greenling
Hippoglossoides elassodon	Flathead sole
Hippoglossus stenolepis	Pacific halibut
Onchorhynchus gorbuscha	Pink salmon
Onchorhynchus keta	Chum salmon
Onchorhynchus kisutch	Coho salmon
Onchorhynchus nerka	Sockeye salmon
Onchorhynchus tshawytscha	Chinook salmon
Ophiodon elongatus	Lingcod
Parophrys vetulus	English sole
Pleuronichthys coenosus	C-O sole
Psettichthys melanostictus	Sand sole
Rhacochilus vacca	Pile perch
Sardinops sagax	Pacific sardine
Sebastes auriculatus	Brown rockfish
Sebastes borealis	Shortraker rockfish
Sebastes brevispinis	Silvergrey rockfish
Sebastes caurinus	Copper rockfish
Sebastes flavidus	Yellowtail rockfish
Sebastes maliger	Quillback rockfish
Sebastes nigrocinctus	Tiger rockfish
Sebastes paucispinis	Bocaccio
Sebastes pinniger	Canary rockfish
Thaleichthys pacificus	Eulachon

APPENDIX 2: Raw scale and vertebra deposition data from all box cores

Box Core Scale Deposition Data

CORE	DATE	herring	hake	sardine	salmon	anchovy	lingcod	rockfish	eulachon	P. cod	perch	mackerel	?? scale
1A	1891-92	3	8										
1A	1893-94	8	4					1					
1A	1895-96	1	3										
1A	1897-98												
1A	1899-1900	1	6										
1A	1901-02	10	15										
1A	1903-04	4	4					1					
1A	1905-06	7	2	5	15								
1A	1907-08	7											
1A	1909-10	15	1										
1A	1911-12	15	1										
1A	1913-14	16	2					1					
1A	1915-16	15											
1A	1917-18	4											
1A	1919-20	15	2										
1A	1921-22	15	5										
1A	1923-24	10											
1A	1925-26	2	4					1					
1A	1927-28	8	2										
1A	1929-30	10	4										
1A	1931-32	3	2										
1A	1933-34	15	2										
1A	1935-36	3	1										
1A	1937-38	2	1										
1A	1939-40	12	1										
1A	1941-42	10	4	2									
1A	1943-44	9	4										
1A	1945-46	8	1										
1A	1947-48	8	1										
1A	1949-50	3	3										
1A	1951-52		2										
1A	1953-54	1	5										

Box Core Scale Deposition Data

CORE	DATE	herring	hake	sardine	salmon	anchovy	lingcod	rockfish	eulachon	P. cod	perch	mackerel	?? scale
1A	1957-58		3										
1A	1959-60	6											
1A	1961-62	3	3										
1A	1963-64	4	39										
1A	1965-66	3	28				1						
1A	1967-68	2	8										
1A	Top 17 2/2		5										
1A	Top 171/2		9										
1B	1935-36	3	2										
1B	1937-38	4		8									
1B	1939-40	11	3	2									
1B	1941-42	6	2										
1B	1943-44	7	4										
1B	1945-46	2	1										
1B	1947-48	2	4			1		1					
1B	1949-50	1	1										
1B	1951-52	12	4				1	1					
1B	1953-54	295	4										
1B	1955-56	11	2										
1B	1957-58	8	3										
1B	1959-60	3	2										
1B	1961-62	4	5										2
1B	1963-64	2	2										
1B	1965-66												
1B	1967-68	2	4	2									
1B	1969-70		3									2	
1B	1971-72	3	8	2				1				11	
1B	1973-74	1	1					1					
1B	1975-76		1									2	
1B	1977-78	3	4					1					
1B	1979-80	5	4					2					

Box Core Scale Deposition Data

CORE	DATE	herring	hake	sardine	salmon	anchovy	lingcod	rockfish	eulachon	P. cod	perch	mackerel	?? scale
1B	1981-82	3	3	2							2		
1B	1983-84	12	2	2									1
1B	1985-86	27	18	2									
1B	1987-88	10	4										
1B	1989-90	20	6	1									
1B	1991-92	5	2										
1C	1861-62	14	4			1				1			
1C	1863-64	12	3										
1C	1865-66												
1C	1867-68	9	1					2					
1C	1869-70	1				2				1			
1C	1871-72	1		4		1	1						
1C	1873-74	5		2		1							
1C	1877-78	6	1										
1C	1879-80		1			1							
1C	1883-84	50	2			7		2					
1C	1885-86	19	1			2		2					
1C	1887-88	13	2	1		4		1					
1C	1889-90	11	2			3							
1C	1891-92	8	1			9							
1C	1893-94	7	1			1							
1C	1895-96	3				5							
1C	1897-98	3	1		1	2				1			
1C	1899-1900	3	7	1									
1C	1901-02	1											
1C	1903-04	10	3										
1C	1905-06												
1C	1907-08	13	1										
1C	1909-10	17	1										
1C	1911-12	11	3										
1C	1913-14	8	1										

Box Core Scale Deposition Data

CORE	DATE	herring	hake	sardine	salmon	anchovy	lingcod	rockfish	eulachon	P. cod	perch	mackerel	?? scale
1C	1915-16	11		1				1					
1C	1917-18	11	2										
1C	1919-20	11	2										
1C	1921-22	8											
1C	1923-24	26	1							1			
1C	1925-26	24	3								1		
1C	1927-28	12	1										
1C	1929-30	5	2										
1C	1931-32	11	3										
1C	1933-34	20	1										
1C	1935-36	15	1				1						
1C	1937-38	25	1					1					
1C	1939-40	11	2										
1C	1941-42	12	2										
1C	1943-44	5											
1C	1945-46	11	1	2									
1C	1947-48	21	6	3		1							
1C	1949-50	27	2	1									
1C	1951-52	7						1					
1C	1953-54	4	1										
1C	1955-56	5	1			1							
1C	1957-58	13	2										
1C	1959-60												
1C	1961-62												
1C	1963-64												
1C	1965-66	1	4	3		3							
1C	1967-68												
1C	1969-70												
1C	1971-72												
1C	1973-74												
1C	1975-76	1		2		1							

Box Core Scale Deposition Data

CORE	DATE	herring	hake	sardine	salmon	anchovy	lingcod	rockfish	eulachon	P. cod	perch	mackerel	?? scale
2A	1913-14	33	1	1			1						
2A	1915-16	13	4				1						
2A	1917-18	26	3			1							
2A	1919-20	43	2	18		18	1	2		2			
2A	1921-22	28	1	4		5	4						
2A	1923-24	9											
2A	1925-26	7	1										
2A	1927-28	8	1	6									
2A	1929-30	5	3	3	1								
2A	1931-32	8	3	5									
2A	1933-34	4		4									
2A	1935-36	5											
2A	1937-38	10	4	11									
2A	1939-40	8	4	4				2					
2A	1941-42	13	6										
2A	1943-44	1	8	4		2		3					
2A	1945-46	5	5	1									
2A	1947-48	2	5										
2A	1949-50	4	4	1									
2A	1951-52		4	1									
2A	1953-54	3	4	2		1	1						
2A	1955-56	16	7	2		1							
2A	1957-58	9	4						1				
2A	1959-60	8	10										
2A	1961-62	7	9					1					
2A	1963-64	3	5	1									
2A	1965-66		15										
2A	1967-68		2		1								1
2A	1969-70	3	2										4
2A	1971-72	6	8										
2A	1973-74	1	7										
2A	1975-76		5										

Box Core Scale Deposition Data

CORE	DATE	herring	hake	sardine	salmon	anchovy	lingcod	rockfish	eulachon	P. cod	perch	mackerel	?? scale
2A	1977-78	3	7		1								
2A	1979-80	12	6	1									3
2A	1981-82	6	9			1							
2A	0-2 cm	3	13										
2A	3-4 cm	6	11						1				
2A	5-6 cm	13	11			1							
2A	7-8 cm	7	5	1									
2A	9-10 cm	3	3	1									
2A	11-12 cm	6	2										
2B	1883-84	21	10				1						
2B	1885-86	14	13			1		1					
2B	1887-88	25	5			3							
2B	1889-90	27	3			8							
2B	1891-92	21	5	2		10							
2B	1893-94	40	5		1	6		2		1			
2B	1895-96	13	5			4				3			
2B	1897-98	18	5			2		1		1			
2B	1899-19	12	13					1					
2B	1901-02	15	3							1			
2B	1903-04	23	5	2				1					
2B	1905-06	54											
2B	1907-08	67	7				1						
2B	1909-1910	26	2				1						
2B	1911-12	30	2										
2B	1913-14	27	1					1				1	
2B	1915-16	25								2			
2B	1917-18	39	4										
2B	1919-20	25											
2B	1921-22	32	3					1					
2B	1923-24	21	2										
2B	1925-26	27	2										

Box Core Scale Deposition Data

CORE	DATE	herring	hake	sardine	salmon	anchovy	lingcod	rockfish	eulachon	P. cod	perch	mackerel	?? scale
2B	1927-28	16											
2B	1929-30	33	1										
2B	1931-32	17	3					1		1			
2B	1933-34	11								1			
2B	A	5	3					1					
2B	B	20	1										
2B	C	24											
2B	D	16					1						
2B	E	11											
2B	F	9		1				1					
2B	G	11	1										
2B	H	14	3									1	
2B	I	19	5				1	2					
2B	J	11	2										
2B	K	4	2										
2B	L	15	5										
2B	M	5	3										
2B	1955-56	14	9	1									
2B	1957-58	15	5							1			
2B	1959-60	8	3										
2B	1961-62	22	3				1						
2B	1963-64	10	2										
2B	1965-66	11											
2B	1967-68	13	3										
2B	8-9cm	3	2										
2B	6-7cm		4					2					
2B	4-5cm												
2B	2-3cm	1											
2B	0-1cm	1	2										

Box Core Bone Deposition Data

		Vertebrae										Otolith			
Core	**DATE**	**herring**	**hake**	**sandlance**	**anchovy**	**rockfish**	**sculpin**	**flatfish**	**? gunnel**	**?gadid**	**un-i.d.**	**herring**	**sandlance**	**?gunnel**	**?gadid**
1A	1891-92	1	2	3			3								
1A	1893-94	1	2	21			1					2			
1A	1895-96	2													
1A	1897-98														
1A	1899-1900														
1A	1901-02														
1A	1903-04	2													
1A	1905-06	4	3	10											
1A	1907-08	86	1									3			
1A	1909-10														
1A	1911-12	2													
1A	1913-14														
1A	1915-16	2													
1A	1917-18	4													
1A	1919-20	25		4											
1A	1921-22														
1A	1923-24	6	1									2			
1A	1925-26	6													
1A	1927-28														
1A	1929-30	7													
1A	1931-32	4	2												
1A	1933-34	3													
1A	1935-36	4	2	1											
1A	1937-38	3													
1A	1939-40														
1A	1941-42	4													
1A	1943-44	11	1	1											
1A	1945-46	28	2												
1A	1947-48														
1A	1949-50	6													
1A	1951-52	3									1				

Box Core Bone Deposition Data

		Vertebrae										Otolith			
Core	DATE	herring	hake	sandlance	anchovy	rockfish	sculpin	flatfish	? gunnel	?gadid	un-i.d.	herring	sandlance	?gunnel	?gadid
1A	1953-54														
1A	1955-56	10													
1A	1957-58	4										2			
1A	1959-60	4													
1A	1961-62	5		2											
1A	1963-64	1													
1A	1965-66	1		1											
1A	1967-68														
1A	Top 17 2/2	4													
1A	Top 171/2	5	1												
1B	1935-36	3													
1B	1937-38	1										1			
1B	1939-40	1		1											
1B	1941-42														
1B	1943-44	7		1								1			
1B	1945-46	3													
1B	1947-48	3													
1B	1949-50	108		2											
1B	1951-52	4										1			
1B	1953-54	5		3											
1B	1955-56			1											
1B	1957-58														
1B	1959-60														
1B	1961-62														
1B	1963-64														
1B	1965-66	1		1											
1B	1967-68	4													
1B	1969-70	1													
1B	1971-72	1	2									1			
1B	1973-74	1										1			

Bone Deposition Data

		Vertebrae										Otolith			
Core	**DATE**	**herring**	**hake**	**sandlance**	**anchovy**	**rockfish**	**sculpin**	**flatfish**	**? gunnel**	**?gadid**	**un-i.d.**	**herring**	**sandlance**	**?gunnel**	**?gadid**
1B	1975-76	1										1			
1B	1977-78	4													
1B	1979-80	1													
1B	1981-82	2													
1B	1983-84	1													
1B	1985-86		1								1	2			
1B	1987-88	1													
1B	1989-90														
1B	1991	1													
1C	1861-62	1													
1C	1863-64	3													
1C	1865-66														
1C	1867-68														
1C	1869-70														
1C	1871-72														
1C	1873-74	1													
1C	1877-78														
1C	1879-80														
1C	1883-84														
1C	1885-86														
1C	1887-88														
1C	1889-90														
1C	1891-92														
1C	1893-94											1			
1C	1895-96	1													
1C	1897-98														
1C	1899-1900														
1C	1901-02														
1C	1903-04	1	1								1				
1C	1905-06										1				

Box Core Bone Deposition Data

		Vertebrae										Otolith			
Core	DATE	herring	hake	sandlance	anchovy	rockfish	sculpin	flatfish	? gunnel	?gadid	un-i.d.	herring	sandlance	?gunnel	?gadid
1C	1907-08	2													
1C	1909-10														
1C	1911-12	3													
1C	1913-14	1													
1C	1915-16														
1C	1917-18														
1C	1919-20	3													
1C	1921-22		1												
1C	1923-24														
1C	1925-26	2									1				
1C	1927-28	41	2								1	1			
1C	1929-30	11													
1C	1931-32	3									1	3			
1C	1933-34	5													
1C	1935-36	6													
1C	1937-38	3	1												
1C	1939-40	3										1			
1C	1941-42	3													
1C	1943-44	1													
1C	1945-46	2	1												
1C	1947-48		1								1				
1C	1949-50	2													
1C	1951-52	2	3												
1C	1953-54														
1C	1955-56	10													
1C	1957-58	3													
1C	1959-60														
1C	1961-62														
1C	1963-64														
1C	1965-66														
1C	1967-68														

Box Core Bone Deposition Data

		Vertebrae										Otolith			
Core	**DATE**	**herring**	**hake**	**sandlance**	**anchovy**	**rockfish**	**sculpin**	**flatfish**	**? gunnel**	**?gadid**	**un-i.d.**	**herring**	**sandlance**	**?gunnel**	**?gadid**
1C	1969-70														
1C	1971-72														
1C	1973-74														
1C	1975-76														
2A	11-12 cm	1	1												
2A	9-10 cm	2													
2A	7-8 cm											1			
2A	5-6 cm	1	2	1								1			
2A	3-4 cm		1												
2A	0-2 cm	2	1								1				
2A	1981-82	3													
2A	1979-80	2	1								1				
2A	1977-78	6													
2A	1975-76	6													
2A	1973-74	2	3												
2A	1971-72	12													
2A	1969-70	2	1												
2A	1967-68	3													
2A	1965-66	2													
2A	1963-64	2	1	2											
2A	1961-62	2	2	1											
2A	1959-60								1		3	1			
2A	1957-58	3	3				1								
2A	1955-56	16	2	1							5				
2A	1953-54	4													
2A	1951-52	2	1												
2A	1949-50	11													
2A	1947-48	2			1						1				
2A	1945-46	8	1												
2A	1943-44	10	5			2					1				

Box Core Bone Deposition Data

		Vertebrae										Otolith			
Core	DATE	herring	hake	sandlance	anchovy	rockfish	sculpin	flatfish	? gunnel	?gadid	un-i.d.	herring	sandlance	?gunnel	?gadid
2A	1941-42	6	2												
2A	1939-40	8	1								1	3			
2A	1937-38	7													
2A	1935-36	18	1					1			1	3			
2A	1933-34	13	1								1	1			
2A	1931-32	14				2						3		1	
2A	1929-30	5	1								1	1			
2A	1927-28	8	1												
2A	1925-26	8										3			
2A	1923-24	5										1			
2A	1921-22	18		2											
2A	1919-20	5	1	10			2				10				
2A	1917-18	6									1				
2A	1915-16														
2A	1913-14	3													
2B	1883-84	3													
2B	1885-86		1												
2B	1887-88	1													
2B	1889-90	3										1			
2B	1891-92	2										2			
2B	1893-94	1													
2B	1895-96	1										1			
2B	1897-98														
2B	1899-1900	1	1	1							1				
2B	1901-02	2	2												
2B	1903-04	1								1		2			
2B	1905-06	3									1				
2B	1907-08	4									1				
2B	1909-1910	6								1	3	1			
2B	1911-12	3		1											

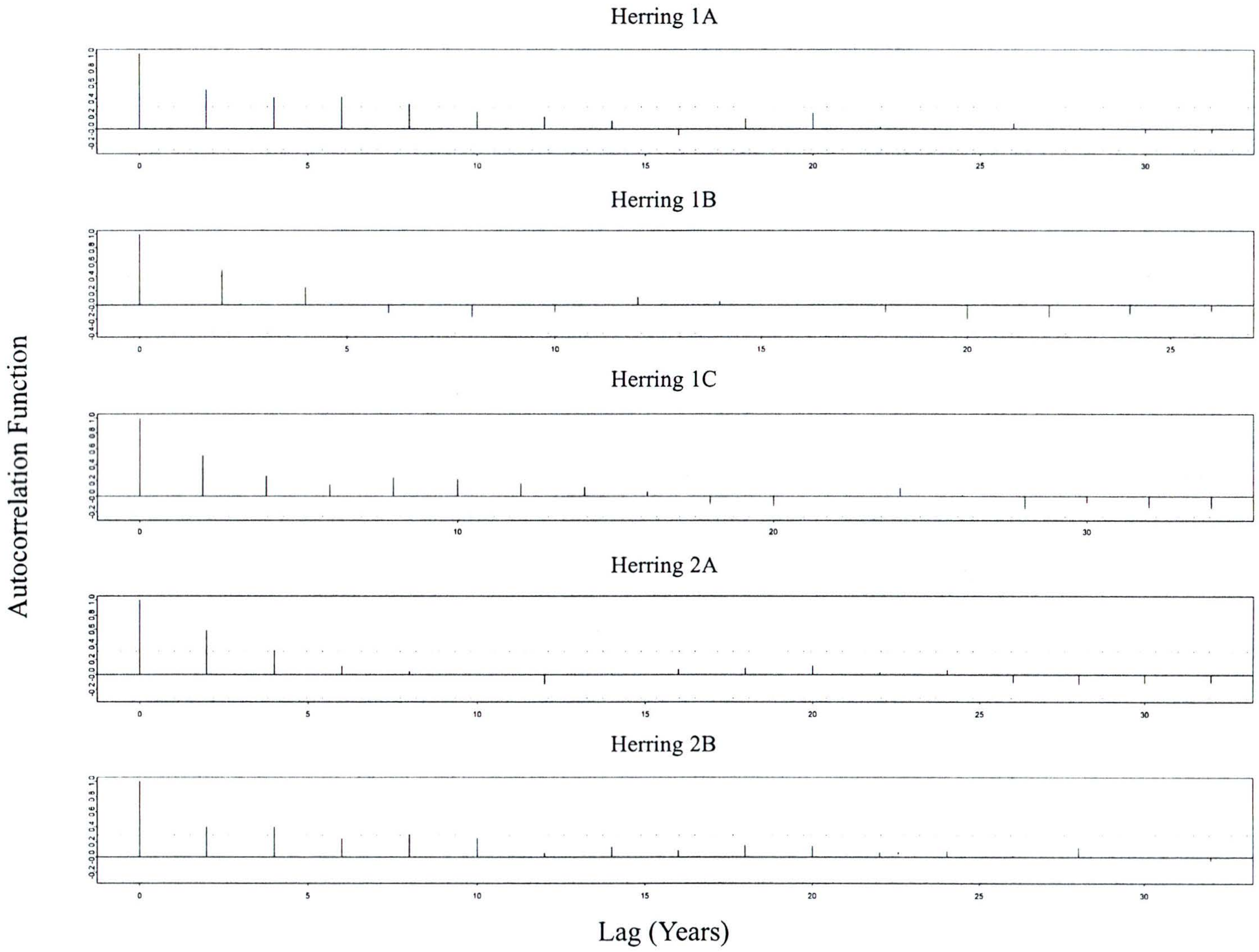
Box Core Bone Deposition Data

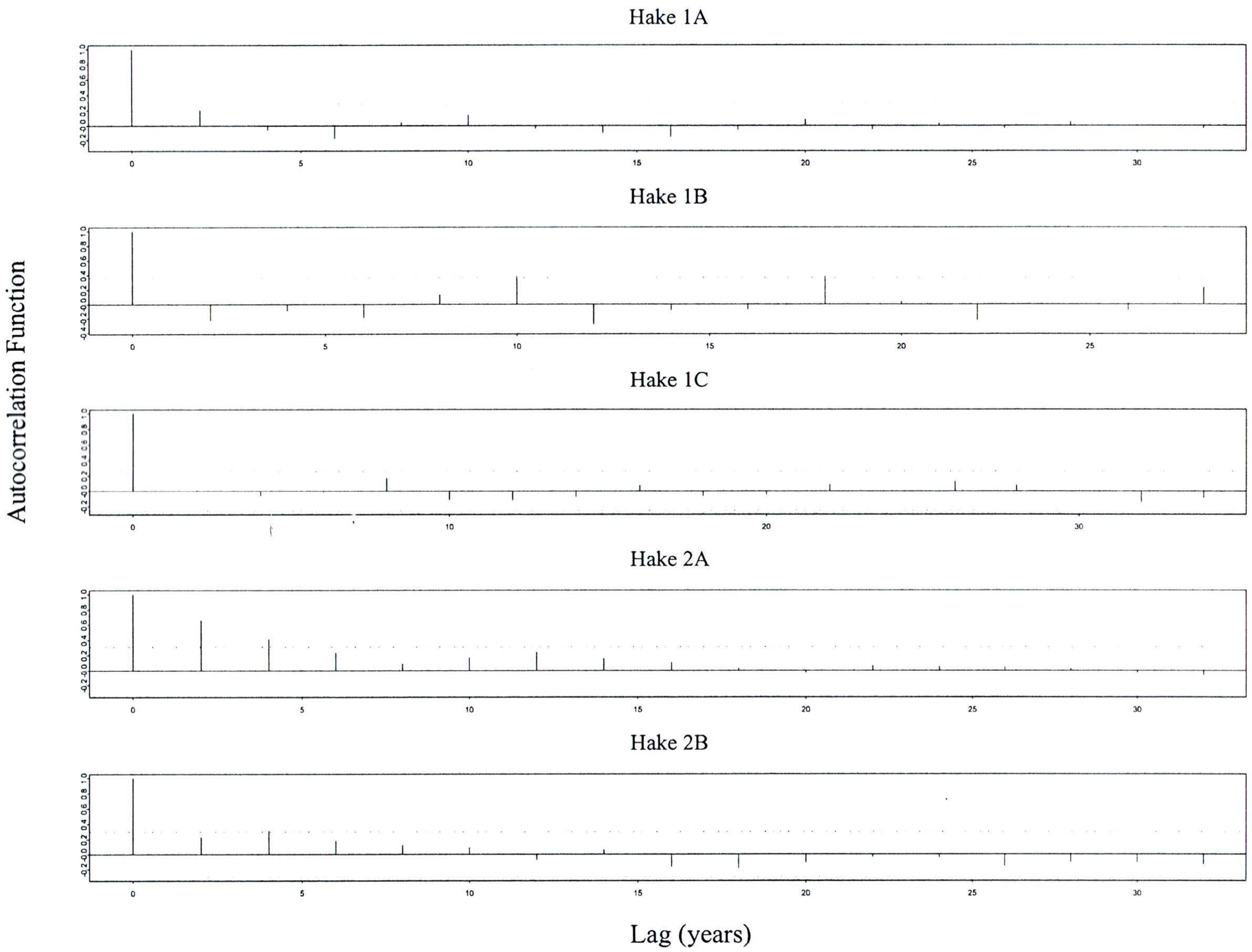
		Vertebrae										Otolith			
Core	DATE	herring	hake	sandlance	anchovy	rockfish	sculpin	flatfish	? gunnel	?gadid	un-i.d.	herring	sandlance	?gunnel	?gadid
2B	1913-14	2													
2B	1915-16	2													
2B	1917-18	2													
2B	1919-20	1													
2B	1921-22	3										1			
2B	1923-24	3													
2B	1925-26	43		2								2			
2B	1927-28	2		2											
2B	1929-30	3		2							2	1			
2B	1931-32	4													
2B	1933-34	2								1			1		
2B	A	3										1			1
2B	B	2		2											
2B	C	3													
2B	D	2													
2B	E	2										1			
2B	F	3	1												
2B	G	6	1												
2B	H	1								1					
2B	I	2		1						2	2				
2B	J	1													
2B	K	3	1	2							1				
2B	L	3													
2B	M	1								2					
2B	1955-56	4	1												
2B	1957-58	4	1	2											
2B	1959-60	5						2		1	2				
2B	1961-62	4	1									1			
2B	1963-64	3	1												
2B	1965-66			1								1			
2B	1967-68	2	1	1											

Box Core Bone Deposition Data

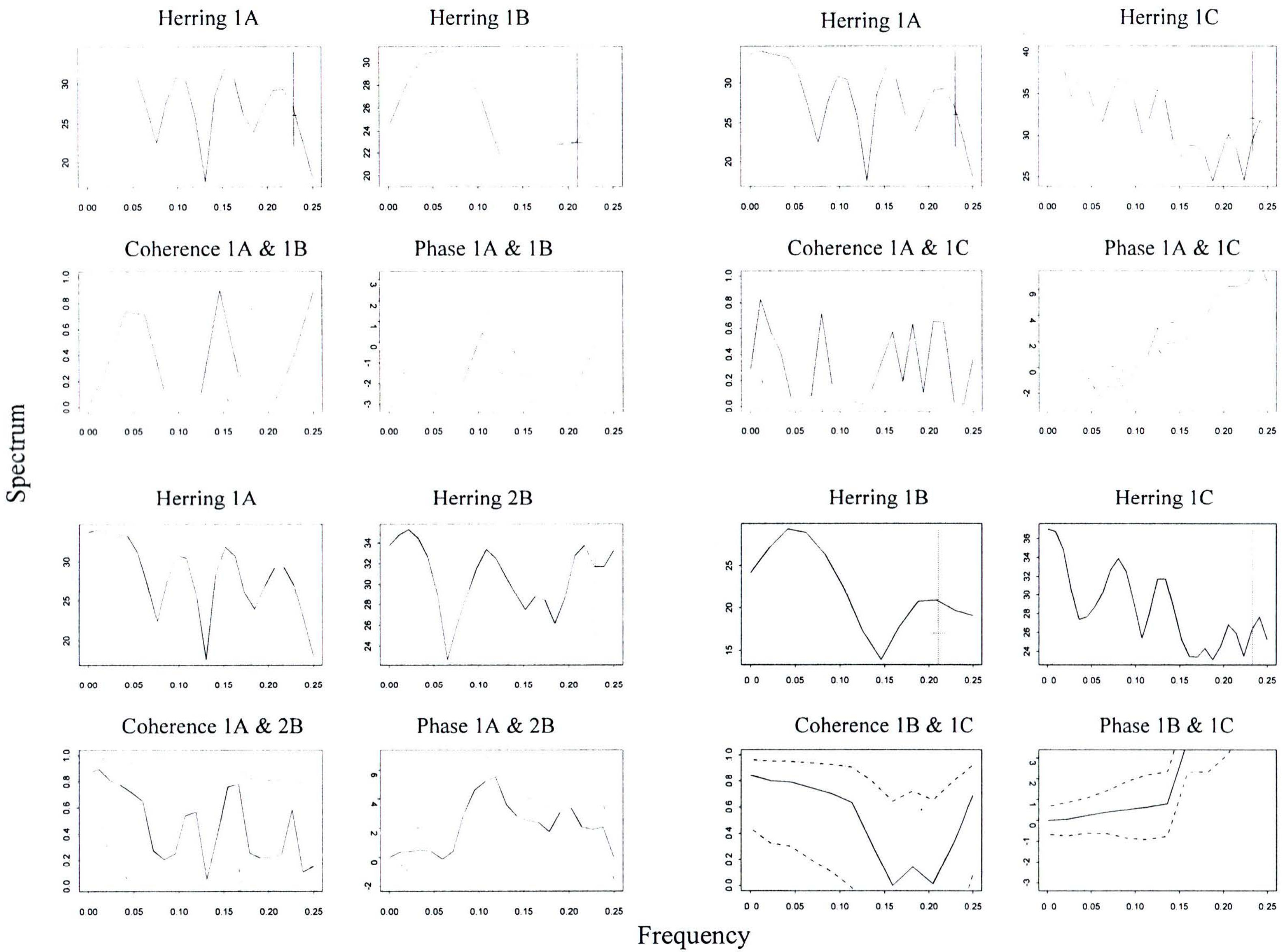
		Vertebrae										Otolith			
Core	DATE	herring	hake	sandlance	anchovy	rockfish	sculpin	flatfish	? gunnel	?gadid	un-i.d.	herring	sandlance	?gunnel	?gadid
2B	8-9cm										1				
2B	6-7cm		1												
2B	4-5cm		1							1					
2B	2-3cm	1								1					
2B	0-1cm														

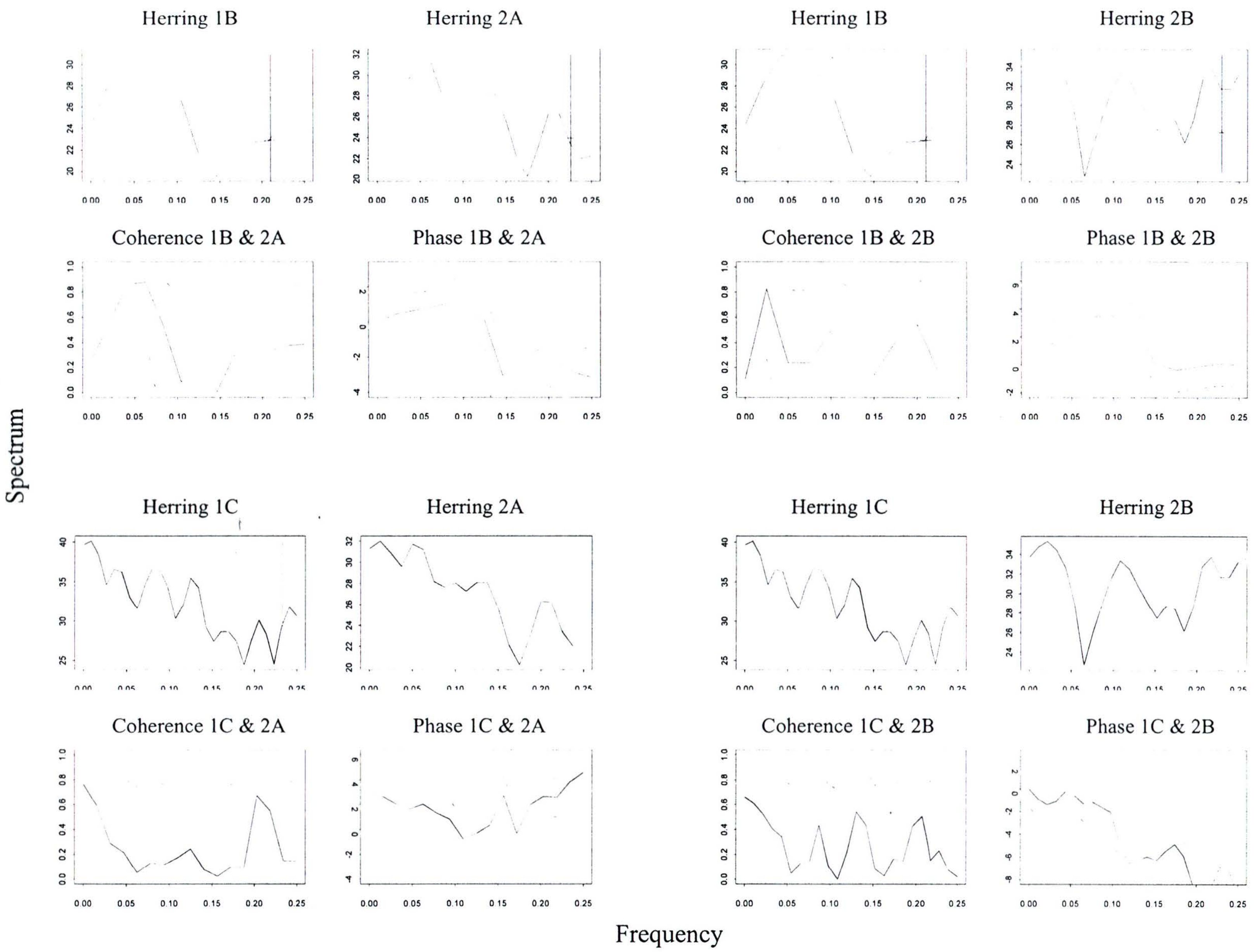
APPENDIX 3: Autocorrelation plots **A)** Herring, **B)** Hake.

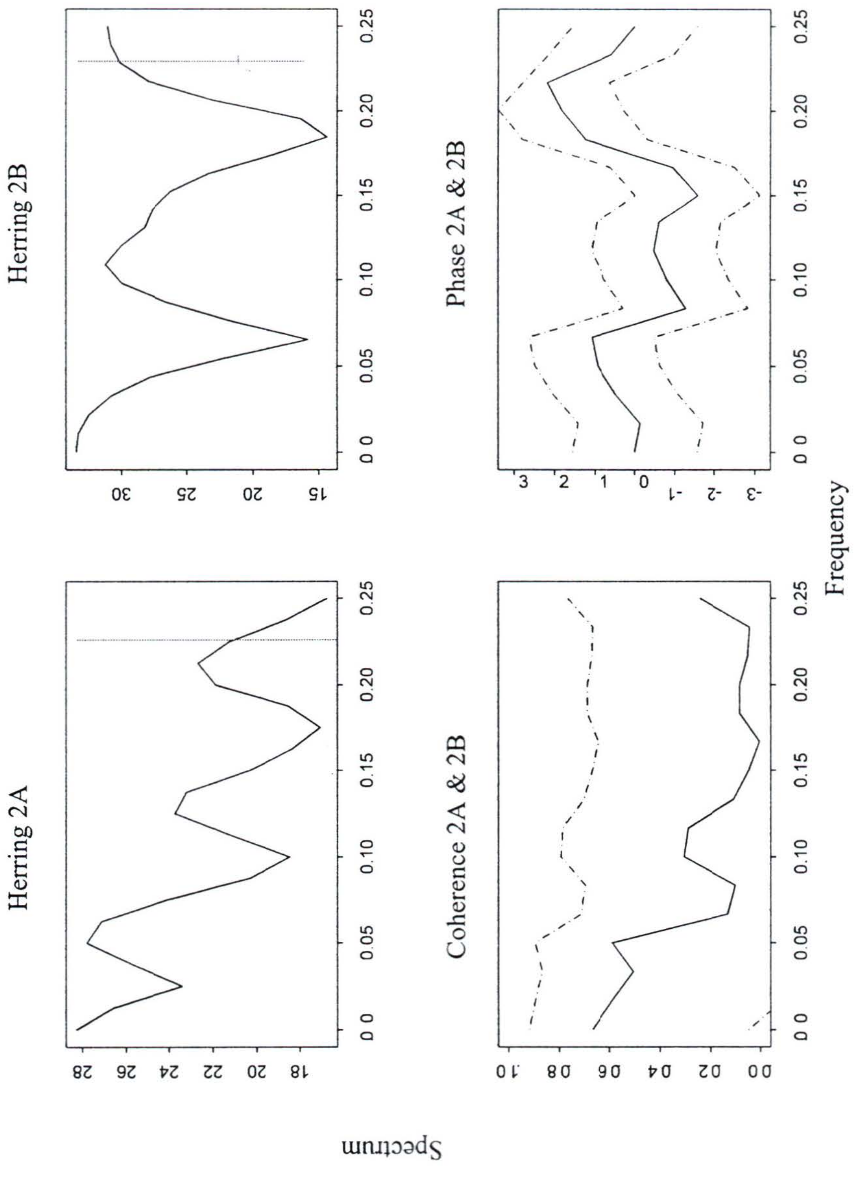

Herring 1A
Herring 1B
Herring 1C
Herring 2A
Herring 2B
Autocorrelation Function
Lag (Years)
-0.2 0.0 0.2 0.4 0.6 0.8 1.0
-0.4 -0.2 0.0 0.2 0.4 0.6 0.8 1.0
0 5 10 15 20 25 30
0 5 10 15 20 25
0 10 20 30

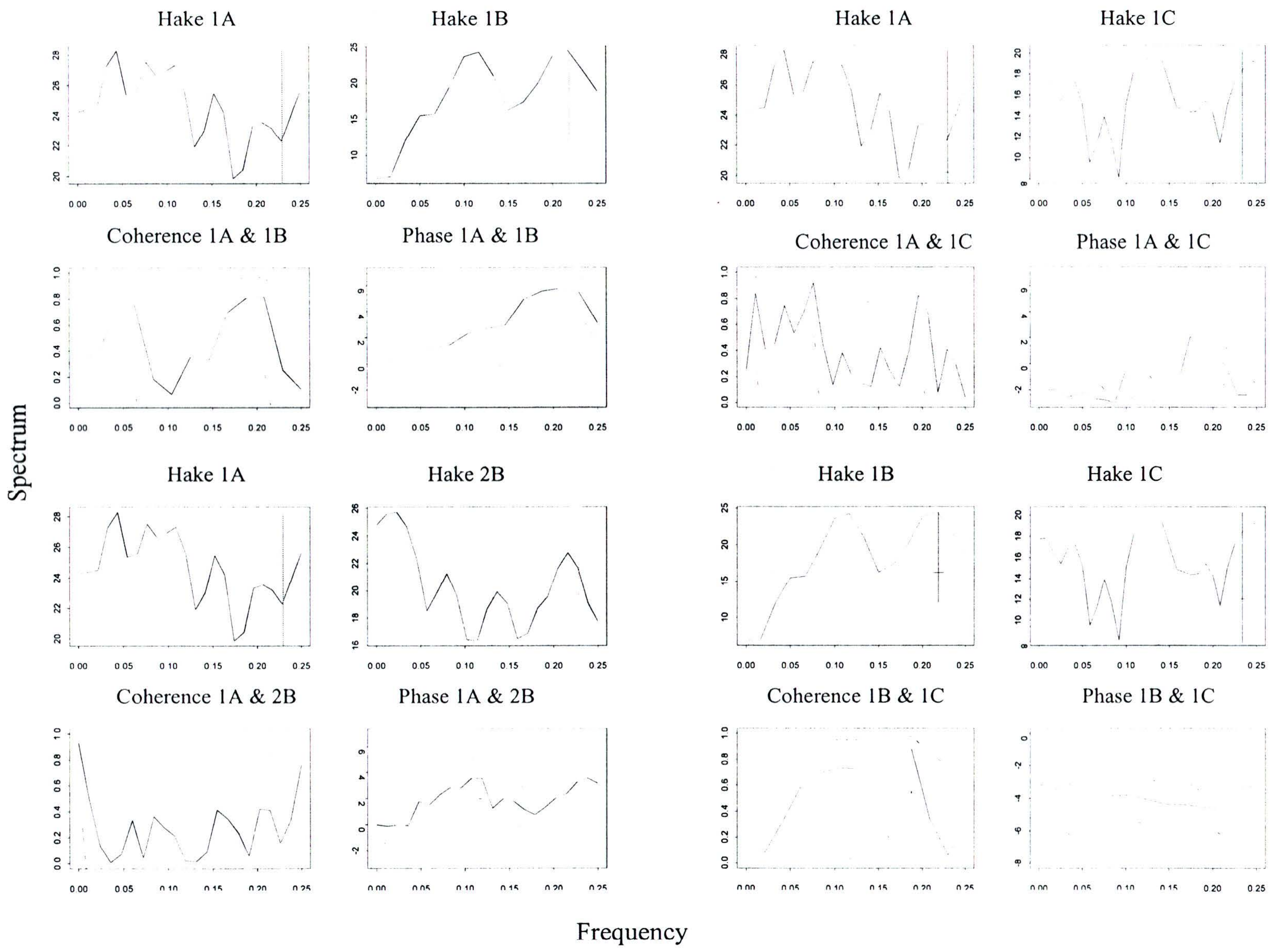

Hake 1A
Hake 1B
Hake 1C
Hake 2A
Hake 2B
Autocorrelation Function
Lag (years)
-0.2 0.0 0.2 0.4 0.6 0.8 1.0
-0.4 -0.2 0.0 0.2 0.4 0.6 0.8 1.0
0
5
10
15
20
25
30

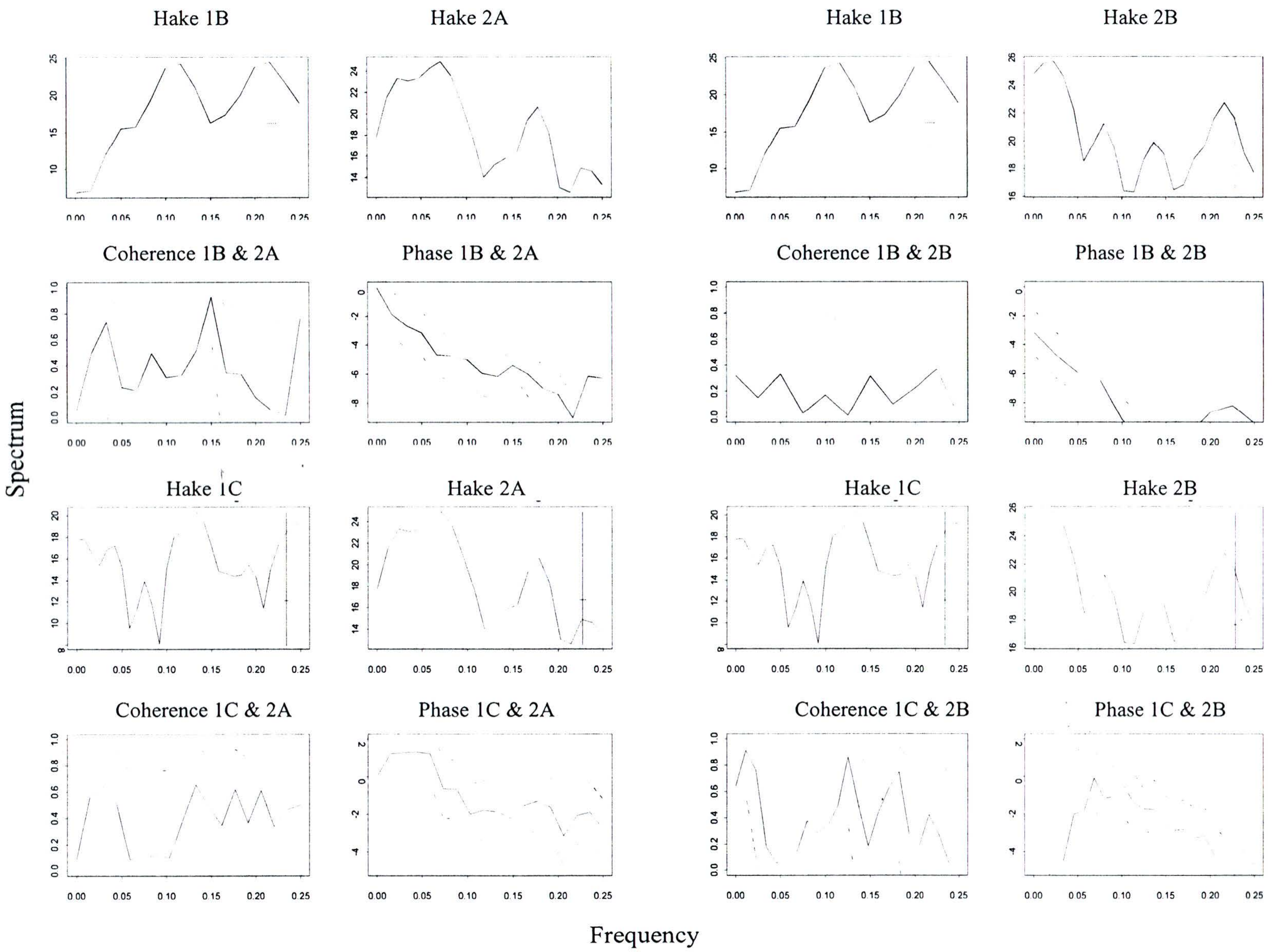
APPENDIX 4: Cross-spectral output between all cores **A)** Herring; **B)** Hake

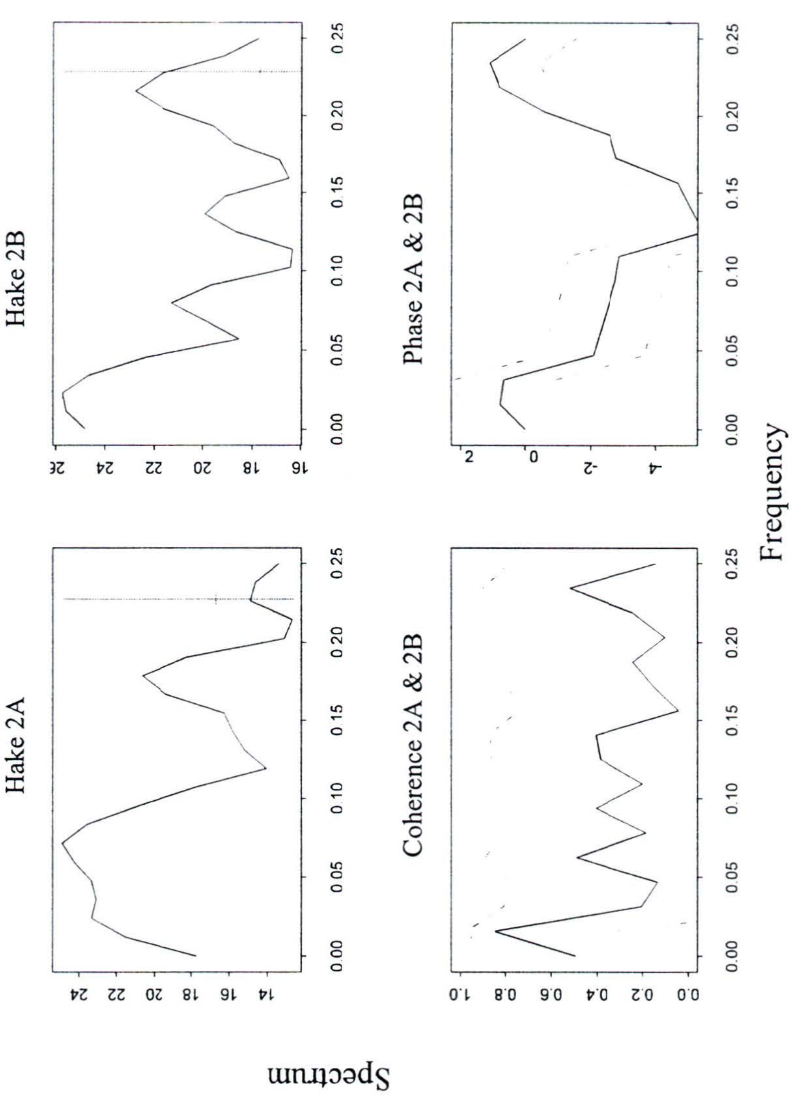

Herring 1A
Herring 1B
Herring 1A
Herring 1C
Coherence 1A & 1B
Phase 1A & 1B
Coherence 1A & 1C
Phase 1A & 1C
Herring 1A
Herring 2B
Herring 1B
Herring 1C
Coherence 1A & 2B
Phase 1A & 2B
Coherence 1B & 1C
Phase 1B & 1C
Spectrum
Frequency
0.00
0.05
0.10
0.15
0.20
0.25


Herring 1B
Herring 2A
Herring 1B
Herring 2B
Coherence 1B & 2A
Phase 1B & 2A
Coherence 1B & 2B
Phase 1B & 2B
Herring 1C
Herring 2A
Herring 1C
Herring 2B
Coherence 1C & 2A
Phase 1C & 2A
Coherence 1C & 2B
Phase 1C & 2B
Spectrum
Frequency
0.00 0.05 0.10 0.15 0.20 0.25
20 22 24 26 28 30 32 34
25 30 35 40
0.0 0.2 0.4 0.6 0.8 1.0
-8 -6 -4 -2 0 2 4 6


Herring 2A
Herring 2B
Coherence 2A & 2B
Phase 2A & 2B
Spectrum
Frequency
0.0
0.05
0.10
0.15
0.20
0.25
18
20
22
24
26
28
15
20
25
30
0.0
0.2
0.4
0.6
0.8
1.0
-3
-2
-1
0
1
2
3


Hake 1A
Hake 1B
Hake 1A
Hake 1C
Coherence 1A & 1B
Phase 1A & 1B
Coherence 1A & 1C
Phase 1A & 1C
Hake 1A
Hake 2B
Hake 1B
Hake 1C
Coherence 1A & 2B
Phase 1A & 2B
Coherence 1B & 1C
Phase 1B & 1C
Spectrum
Frequency
0.00
0.05
0.10
0.15
0.20
0.25


Hake 1B
Hake 2A
Hake 1B
Hake 2B
Coherence 1B & 2A
Phase 1B & 2A
Coherence 1B & 2B
Phase 1B & 2B
Hake 1C
Hake 2A
Hake 1C
Hake 2B
Coherence 1C & 2A
Phase 1C & 2A
Coherence 1C & 2B
Phase 1C & 2B
Spectrum
Frequency
0.00
0.05
0.10
0.15
0.20
0.25


Hake 2A
Hake 2B
Coherence 2A & 2B
Phase 2A & 2B
Spectrum
Frequency
24 22 20 18 16 14
26 24 22 20 18 16
1.0 0.8 0.6 0.4 0.2 0.0
2 0 -2 -4
0.00 0.05 0.10 0.15 0.20 0.25

APPENDIX 5: Scale counts, standard length and weight of 10 *C. harengus pallasi*

# scales	**std. length**	**weight**
523	15.6	35.1
594	17.1	38.9
684	18.2	32.2
614	18.8	40.9
601	19.1	39.9
578	19.1	67.5
665	19.8	48
703	19.8	58.4
788	20.8	74.5
634	21.1	83.4

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Title of thesis:
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6th International Conference on Paleoceanography Student Travel Award	1998
NSERC PGSB	1998

Publications

Jacqueline M. O'Connell, Euan D. Reavie, and John P. Smol. (1997). Assessment of water quality using epiphytic diatom assemblages on *Cladophora* from the St. Lawrence River (Canada). Diatom Research - Volume 12(1): 55-70