

#### Available online at www.sciencedirect.com





Palaeogeography, Palaeoclimatology, Palaeoecology 224 (2005) 367-384

www.elsevier.com/locate/palaeo

# Late Holocene paleofish populations in Effingham Inlet, British Columbia, Canada

C.A. Wright<sup>a,\*</sup>, A. Dallimore<sup>b</sup>, R.E. Thomson<sup>a,c</sup>, R.T. Patterson<sup>d</sup>, D.M. Ware<sup>c</sup>

<sup>a</sup>Institute of Ocean Sciences, Fisheries and Oceans Canada, 9860 West Saanich Road, Sidney, British Columbia, Canada V8M 4B2

<sup>b</sup>Pacific Geoscience Center, Geological Survey of Canada, 9860 West Saanich Road, Sidney, British Columbia, Canada V8M 4B2

<sup>c</sup>Department of Earth and Ocean Sciences, University of British Columbia, 6339 Stores Road, Vancouver, British Columbia, Canada V6T 1Z4

<sup>d</sup>Department of Earth Sciences, 2240 Herzberg Laboratories, 1125 Colonel By Drive, Ottawa, Ontario, Canada, K1S 5B6

Received 7 June 2004; received in revised form 18 March 2005; accepted 18 March 2005

#### Abstract

Paleontological studies of fish remains in laminated sediments provide a proxy relationship between fish populations and ocean climate. This study examines climate variability from approximately 500 y B.P. to 4000 y B.P. as recorded in fish remain abundances (primarily scales) collected from laminated sediments within Effingham Inlet on the west coast of Vancouver Island, British Columbia. The study also discusses technical issues involving fish remains from laminated sediments, including sampling resolution, sediment volume, identification of remains and appropriate abundance considerations.

The dominant species in the assemblage include Northern anchovy and Pacific herring, with lesser percentage-abundances from rockfish, hake, elasmobranches and surfperch. The data indicate that Northern anchovy experienced a shift in scale deposition abundance at approximately 2800 y B.P. with not only a greater total abundance but also a greater consistency of deposition with time. Pacific herring underwent cyclical deposition that changed little through time. Statistical analysis reveals that none of these species is directly responding to climatic signals as indicated in the lithological and palynological record, but that this could have been partially due to the sampling resolution of the piston core. Analysis indicates a lack of correlation between the two dominant species, as might be expected on the basis of their opposing lifestyle strategies with respect to sea surface temperatures.

With appropriate sampling strategies, paleohistorical fish remains from laminated sediments reflect changes in population structure and behaviour for some species, illustrate basic secondary trophic information, and provide potential clues to basin-scale oceanographic/climatological variability.

© 2005 Elsevier B.V. All rights reserved.

Keywords: Marine sediments; Late Holocene; Fish; Palaeoceanography; Palaeoclimatology

<sup>\*</sup> Corresponding author.

\*E-mail address: wrightcy@pac.dfo-mpo.gc.ca (C.A. Wright).

#### 1. Introduction

Pelagic fish stocks, particularly clupeids such as sardines and herring, are known for their "boom and bust" population cycles. This can be due to variable recruitment success, over-harvesting, and natural fluctuations in mortality (Cury et al., 1995). Studies of present-day clupeid stocks show that fluctuations in populations are the result of local density-independent environmental factors including sea surface temperature (SST), upwelling, and localized wind effects (Tanasichuk, 1997; Ware and McFarlane, 1989; Williams and Quinn, 2000a,b). Shifts in the position and intensity of the Aleutian Low Pressure System exert a major control on fish recruitment off British Columbia, by influencing stratification and coastal upwelling that can alter SST and plankton abundance (Brodeur and Ware, 1992; Ware and Thomson, 2000).

Historical fisheries collapses along the west coast of North America are well-documented (Soutar and Isaacs, 1969; Francis and Hare, 1994; Hare and Francis, 1995; Chavez et al., 2003) and include the decline of the northern Pacific sardine fishery from the 1920s to the 1960s. This progressive north to south collapse was apparently associated with a significant change in the pelagic habitat of the California Current system, which was associated with large-scale climate change in the Pacific Ocean (Ware and Thomson, 1991; Francis and Hare, 1994). The gradual return of sardines to waters off Vancouver Island since 1990 coincides with the gradual recuperation of the populations off southern California (Baumgartner et al., 1992). A recent northward expansion of the sardine population probably began soon after the large-scale regime shift in the Pacific in 1977 (Robinson and Ware, 1994), which is evidence of the apparently close link between fish populations and oceanographic processes.

El Niño-Southern Oscillation (ENSO) events, and the degree of oceanic versus atmospheric propagation to mid-latitudes, is another major modulator of coastal oceanic regimes. During an ENSO event, upwelling along eastern boundary regions in the tropics weakens or ceases entirely, leading to anomalously warm, low-nutrient waters, and reduced phytoplankton and fish populations. In some years, warm El Niño surface waters reach as far north as California (Barber and Chavez, 1983; Chavez et al., 2003; Lange et al.,

2000; Wilkerson et al., 1987). During major El Niño events, that occur on average every 10–25 years, the effects are also propagated northward through the atmosphere as teleconnections or along the coastal ocean (as an oceanic waveguide) where they can impact mid-latitude oceanic regions, such as the British Columbia shelf.

The nature of long-term oceanic variability and the accompanying effect on fish stocks are poorly understood, and the link between oceanic regime shifts and fish populations is only now beginning to emerge (Chavez et al., 2003). It appears that many of the oceanic processes that affect fish population dynamics and productivity in the northeast Pacific have greater than decadal-scale return times (Field and Baumgartner, 2000; Ware and Thomson, 1991, 2000), making an accurate assessment of natural fish population fluctuations from the written historical fisheries records alone, quite difficult.

The use of fish remains (osteological/bone and squamatological/scale) preserved in sediments as proxies to estimate paleofish populations was pioneered in the 1960s (Soutar, 1967) to better understand clupeid population dynamics off the coast of southern California in pre-historic times. Studies on the fish remains preserved in laminated sediment records from Santa Barbara Basin, California (Soutar and Isaacs, 1969, 1974) show that in pre-historic times, populations of pelagic fish were susceptible to large fluctuations outside the influence of commercial fishing pressures.

Laminated (also called varved) sediments are laid down in seasonal succession. Light-coloured laminae represent spring/summer phytoplankton productivity (often silicious diatoms) and dark-coloured laminae represent fall/winter terrestrial runoff. This type of sedimentary deposition occurs in basins where the bottom waters and pore waters are anoxic, thereby discouraging the colonization of bioturbators that mix the sediment column and destroy the seasonal banding. These annual layers provide excellent geochronological control, and in the case of the Santa Barbara Basin study by Soutar and Isaacs (1969), allowed for the hindcasting paleofish populations and illustrated the utility of laminated sediments for paleo-reconstructive work. Subsequently, paleofish research has been expanded along the west coast of North America to Saanich Inlet, on the southwest coast of Vancouver Island (O'Connell and Tunnicliffe, 2001), where fish bones preserved in anoxic laminated sediments show cyclical fish populations dynamics throughout the Holocene. The analysis of a long record of fish abundance data and an accompanying sediment proxy record of ocean-climate "regime shifts" in coastal British Columbia, is therefore of interest scientifically and also of strategic value to the Canadian west coast fishing industry.

This paper extends previous studies in the NE Pacific, reporting on paleofish remains in the anoxic annually laminated sediments of Effingham Inlet, on the west coast of Vancouver Island, British Columbia and also discusses the technical and methodological considerations required for meaningful analysis.

#### 2. Methods and materials

## 2.1. Study site

Effingham Inlet is a 17 km long fjord situated at the northern side of Barkley Sound, on the west coast of Vancouver Island (Fig. 1). The study site is ideal for fish scale research because annually laminated sediments are deposited in the quiet anoxic bottom waters, producing a well-preserved record of osteological (bone) and squamatological (scale) fish remains and other biologic proxies such as diatoms, dinoflagellates and foraminifera (Hay et al., 2003; Holmgren, 2001; Kumar and Patterson, 2002; Patterson et al., 2000). These sediments give a high-resolution time series of climate-ocean conditions in the region. Using studies of the modern oceanography and the sedimentology of Late Holocene deposits in the inlet, we have identified proxy sediment indicators of climate and coastal ocean dynamics in the area (Dallimore, 2001; Dallimore et al., in press).

Sedimentary deposition in the deepest parts of the inlet, where piston coring was conducted, consists of olive-grey diatom-rich laminated sediments (~50% of sediments), ungraded massive mud units (~10 cm in length; ~25% of sediments) intercalated within the laminated sediments, and graded mud units (~10–60 cm long; ~25% of sediments). The massive mud units appear to be deposited during rare oxygenation events of the bottom waters of the inlet, while graded mud

units are presumably deposition from debris flows (Dallimore, 2001; Dallimore et al., in press).

Profiles of salinity, temperature, density, and dissolved oxygen show that water properties in the present-day inlet are characteristic of a weakly mixed estuary (Dallimore, 2001). Relatively warm, brackish surface water overlies relatively cool, saline bottom water. Tidal variation in Effingham Inlet is small (<2 m) and tidal currents are negligible, except in the southern portion of the inlet and in constricted narrows in the vicinity of the shallow sills. The water column is weakly stratified below sill depth (>40m) in the inner and outer basins with bottom waters having near-uniform temperature and salinity structure. This indicates that the bottom waters in the basins are highly stagnant and infrequently affected by intrusive renewal (oxygenation) events from the outer portion of the inlet. Oxygen profiles of the inner basins show a progressive decrease in oxygen with depth, creating a water column that is uniformly oxic (DO<sub>2</sub>>4 ml/l) to hypoxic to low oxic (DO<sub>2</sub> 0.5-4 ml/l), then to anoxic (no oxygen) with increasing depth (Thomson and Burd, in prep.).

Wind-induced upwelling off Vancouver Island occurs mainly from May to August. The upwelling extends seaward of the shelf break, with subsequent transport of deeper slope waters onto the outer shelf (Thomson et al., 1989). The nutrient-rich upwelled water can originate from either the Alaska Current System or the California Undercurrent regime (Freeland and Denman, 1982) and is responsible for the spring/summer upwelling-induced primary and secondary production, including the high yield fisheries off southern Vancouver Island.

## 2.2. Coring and geochronology

Four Late Holocene sediment sites from the inner basin and one site from the outer basin of Effingham Inlet (Fig. 1) were cored from the *CCGS John P. Tully* in October, 1999. Each of the piston cores was 10 cm in diameter and approximately 11 m in length. Within 2 weeks of sampling, cores were split, photographed, and then stored at the Geological Survey of Canada-Pacific (Institute of Ocean Sciences) in a 4 °C cool-storage room. Each half was wrapped in cellophane and stored in sealed plastic tubes to maintain core moisture.

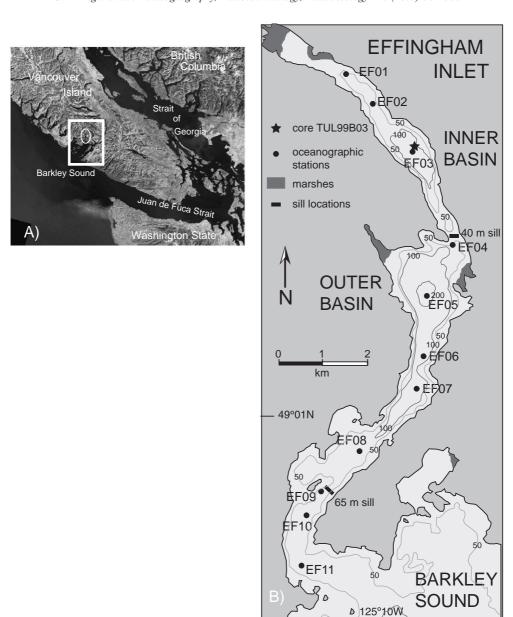


Fig. 1. Map A shows the relative location of Effingham Inlet on the West Coast of Vancouver Island. Map B shows the detailed bathymetry, locations of the oceanographic sampling stations and the core site TUL99B03 in the Inner Basin.

Twenty samples of wood and shell material were recovered from the piston cores for conventional and accelerator mass spectrometry (AMS) radiocarbon dating at the IsoTrace Radiocarbon Laboratory of the University of Toronto. Results are in radiocarbon years before present (y B.P.) and calendar years (cal y

B.P.), using the C<sup>14</sup>Cal program and the INTCAL98 database for terrestrial material and the MARINE98 database for marine material (Stuiver and Reimer, 1986, 1993; Stuiver et al., 1998a,b). Average basinwide sedimentation rates were established from all cores recovered (Dallimore et al., in press). The ra-

diocarbon dates for the core examined in this paper, TUL99B03, are reported in Table 1.

# 2.3. Sediment preparation for fish remains

Piston core TUL99B03 (11.3 m in length) from the inner basin (Fig. 1) was chosen for high-resolution micro-paleontological analysis because it recovered the highest percentage of undisturbed laminae of all the cores. Sediment samples for fish remains analysis were taken at 5 cm intervals along the core, with each interval representing an average of 23 years of sedimentation. For poorly laminated regions of the core, the sample interval was larger (~7–10 cm representing ~31–45 years of sedimentation). The average sediment volume for laminated sections of the core was 393 cm<sup>3</sup>. Massive and graded mud units were not sampled for fish remains, since any remains contained in these sediments may have been re-worked and/or re-deposited from elsewhere in the inlet.

Sediment samples were disaggregated and sieved through a 250  $\mu$ m mesh, and the residue was stored in 70% ethanol. Fish scales and bones were separated and identified using a dissecting microscope; other biogenic and fabric remains were also noted.

# 2.4. Identification of fish remains

Fish scale material in the sediments was identified to at least genera by referring to a British Columbia fish scale atlas (Patterson et al., 2001) and a preliminary reference collection provided by the Bone Laboratory, Department of Anthropology, University of Victoria, British Columbia. Identification to low taxonomic levels such as Order and Family are reasonably straightforward providing that there is an

adequate reference collection for comparison. Some scales can be brought to species level but higher level taxonomic assignments are not always possible.

Fig. 2 shows scale specimens of the major species identified in this study. Identifying scale characteristics include, overall scale shape, position and shape of focus; circuli appearance; the appearance of the lateral, anterior, and posterior fields (Casteel, 1976); and to some extent, thickness/robustness of the scale. Size is not always a distinguishing characteristic due to variations and overlap, not only between species and individuals, but also within a single specimen.

Scale counts are reported as number of scales/cm<sup>3</sup> of sediment. For a fish scale to be considered countable, the following criteria were applied:

- 1. The scale must be >50% intact and/or have the focus intact.
- Those scales with a focus but no defining edges were deemed "unidentifiable".
- 3. For fragmented herring and sardine scales, to be counted as a single scale, they had to have a minimum of 4 cross-circuli fractures (see Fig. 2).

For Pacific herring, scales were differentiated between juvenile and adult based on relative size with the use of the reference collection. Here, size is a workable tool as juvenile herring scales are noticeably smaller than adults. The identification of spiny dogfish (*Squalus acanthias*) from the elasmobranch material (e.g. sharks and rays) is not definitive due to the lack of reference material. The dermal denticles (Fig. 2) are not of one uniform type and it has not been recorded if the dermal denticles vary along the body as do cycloid/ctenoid scales in boney fish (Patterson et al., 2001).

Table 1 Radiocarbon dates obtained from core TUL099B03

Sample number	Isotrace lab number	Depth in core (cm)	Material dated	Radiocarbon year (y B.P.)	Calibrated year* (CAL y B.P.)	Calibrated calendar years
RC03S101	TO-8671	97	Wood	$160 \pm 40$	$195 \pm 150$	AD 1655–1955
RC03S201	TO-8672	169	Shell	$1170 \pm 60$	$970 \pm 135$	AD 595-1165
RC03S301	TO-8673	286	Twig	$2050 \pm 70$	$1858 \pm 62$	BC 80-AD 205
RC03S501	TO-8674	553	Twig	$2830 \pm 60$	$2980 \pm 150$	BC 1130-830
RC03S601	TO-8675	822	Shell	$3890 \pm 80$	$3435 \pm 185$	BC 1245-1620
RC03S701	TO-8676	937	Wood	$4190 \pm 80$	$4745 \pm 175$	BC 2920-2570

<sup>\*</sup>Calibrated results are reported at the 2-sigma range. Marine material is calibrated using Marine 98 database.

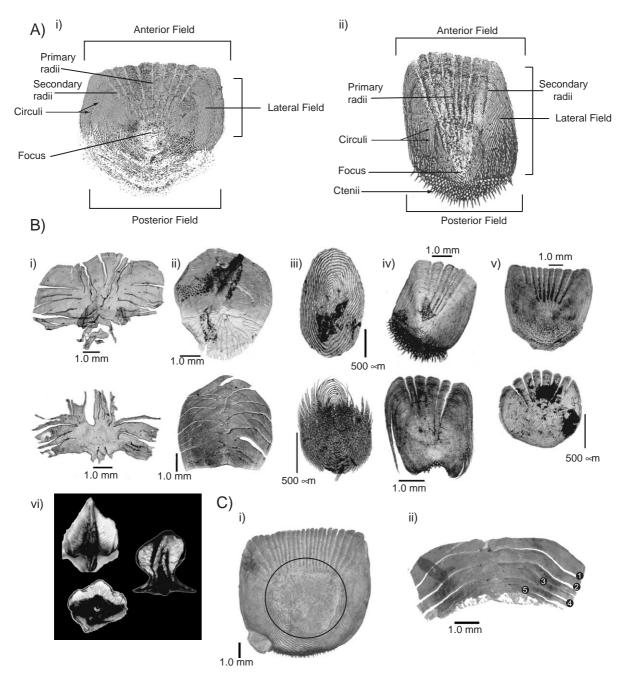


Fig. 2. A) Features of cycloid (i) and ctenoid (ii) scales used to identify fish scales (adapted from Casteel, 1976). B) Major types of scales found in Effingham Inlet. Top photograph is a modern example and the bottom photograph is an example from TUL99B03. i) Northern anchvoy, ii) Pacific herring, iii) Pacific hake, iv) rockfish species, v) surfperch species, vi) types of elasmobranch dermal denticles. C) Features of certain fish scales as discussed in text. i) A regenerated scale illustrating the distorted focal region; ii) a fragmented herring scale illustrating cross-scale fracture along circuli and that a minimum of four fragmented regions is required during the counting process.

Bone material with intact processes, or fragments sufficiently intact to determine bone type, were also picked and tallied to avoid potential bias from the presence of "dead fish." This bias can be introduced when a fish dies and is preserved intact on sediment bedding planes, rather than scales being deposited individually through deciduous shedding or other activities. A complete dead fish skeleton would artificially increase the number of scales in a sample, leading to erroneous conclusions about the population dynamics in that sample. In this study, when a relatively large number of scales coincided with a large number of bones, the sample was identified to the genus level by the University of Victoria's Bone Laboratory in Victoria, B.C. Bone identification has the benefit that it may also identify species that are not represented in the scale record, resulting in a more complete species listing.

# 2.5. Statistical analysis

The taxonomic assemblage and the relative percentage of groups have been determined from the total scale counts at each sampling interval. Abundance measurements of this nature do not lend themselves well to normal parametric analysis. Non-parametric unpaired Mann–Whitney and unpaired Kruskal–Wallis tests (Zar, 1984) were then performed both on the total scale abundance, and on Pacific herring and Northern anchovy scale data, to determine the statistical significance of down-core shifts in abundance and composition.

To determine the level of correlation between Pacific herring and Northern anchovy abundance down the core, Spearman rank-order correlations (Zar, 1984) were performed on all samples (after the massive intervals were removed) and also, within specific regions (see Table 3 for listing) of the core that showed nearly continuous laminations. For these regions, linear interpolation between adjacent samples was sometimes required. Additionally, for those regions of the core showing continuous laminations, cross-correlation and lag analyses were also performed (Emery and Thomson, 2001).

O'Connell and Tunnicliffe (2001), in their work on Saanich Inlet fish remains, suggested that outliers (those data points above and below two standard deviations) should be removed and replaced using next-to-neighbor linear calculations. However, we conclude that in our study these large values represent "real" biological events. As we show with the rockfish scales (see below), outliers are often attributed to one species in the assemblage, rather than the entire scale count. We have concluded, therefore, that it is preferable to consider data outliers on a case-by-case basis, and perform individual sample corrections to determine if the overall trend is altered.

#### 3. Results

## 3.1. Chronology

The chronology for the piston core studied here (TUL99B03) has been established from five piston cores and twenty-two radiocarbon dates (Table 1) indicating that the base of the core is at about 5000 y B.P., yielding an average sedimentation rate of 2.2 mm/year. Due to the unconsolidated nature of the sediments at the sediment–water interface, core TUL99B03 failed to recover the top 1.3 m of the sediment column. The paleofish record reported here therefore spans about 500–5000 y B.P (Dallimore, 2001; Dallimore et. al., in press).

## 3.2. Paleofish data

Ten fish taxa were identified from a total of 4236 scales in 95 sediment samples. Table 2 lists taxa and the relative percent composition. There is no significant down-core loss of fish remains in the Effingham sedimentary record. Linear regression of the down-core total scale abundance (Fig. 3) illustrates that the data are highly variable ( $R^2 \cong 0.015$ ). Plots of scale abundance for the two dominant taxa, Northern anchovy and Pacific herring (Fig. 4), indicate no obvious down-core trend in Pacific herring abundance (the series has a near zero slope) but there is a decrease in Northern anchovy. We do not believe the down-core decrease in anchovy is due to loss of remains though phosphatic dissolution for three reasons. 1) Anchovy scales are more heavily mineralized than herring scales, yet herring do not show any down-core loss; 2) there are a greater number of small juvenile herring scales down-core. If scale material was susceptible to dissolution, it would be

Table 2
Fish species from Effingham Inlet core TUL99B03 sediments as determined from scale and bone remains

Common name	Scientific name	Percent of assemblage	Life history note*
Pacific herring	Clupea pallasi	Total=32.75	Common in WCVI inlets: large spawning stock in
Juvenile		24.01	Barkley Sound shows typical boom and bust cyclicity
Adult		8.73	
Northern anchovy	Engraulis mordax	40.58	Common in WCVI inlets; residential population in
			Effingham; cyclicity is not well-studied
Rockfish	Sebastes spp.	13.36	Depending on species, is common in BC inlets,
			particularly inshore juveniles
Pacific hake	Merluccius productus	4.95	Offshore and onshore populations in BC; residential
			population in Effingham
Elasmobranch	Subclass: Elasmobranchii	3.06	Higher trophic level species common in BC waters but
			likely transient in inlets
Surfperch	Family: Embiotocidae	3.03	Depending on species, common in BC inlets,
			particularly amongst shallow vegetation
Pacific sardine	Sardinops sagax	0.41	Shows typical boom and bust cycle for pelagic forage
			species; tends to prefer broad continental shelf regions
Pacific cod	Gadus macrocephalus	0.35	Generally a "deeper" water demersal species (Hart, 1973)
Jack mackeral	Trachurus symmetricus	0.06	Generally an open water species but is recorded in
			Barkley Sound
Greenling	Family: Hexagrammidae	0.06	Depending on species, are common bottom fish in
			shallow waters (Hart, 1973)
Three-spined stickleback	Gasterosteus aculeatus	**	Common in shallow brackish water (Hart, 1973)
Ronquil	Family: Bathymasteridae	**	Usually found in brackish water (Hart, 1973)
Prickleback	Lumpenus spp.	**	Generally shallow subtidal; depending on species,
			many are found in and around brackish water (Hart, 1973)
Gunnel	Family: Pholidae	**	Most species are shallow rocky subtidal (Hart, 1973)
Poacher	Family: Agonidae	**	Most species are shallow to moderate rocky
			subtidal (Hart, 1973)

<sup>\*</sup>If citation is not listed in table, they can be found in the main text. \*\*Determined from bone remains only.

expected that the herring, especially fragile juvenile material, would also be affected; 3) the samples taken from the bottom of the core contained small and fragile post-larval anchovy bones with processes intact (B. Wiggins, pers. communication). If dissolution were an issue, these bones and their processes would unlikely have been retained. We conclude that the observed changes in anchovy down-core abundance are attributed to true changes in the anchovy population through time.

The most abundant species in the Effingham Inlet paleofish assemblage are Northern anchovy (41%), Pacific herring (32%), rockfish (13%) and Pacific hake (5%). Pacific sardine are scarce and appear sporadically only between ~1800 y B.P. (145 cm) and ~2500 y B.P. (512 cm). The lack of sardine material throughout the core is unlikely a function of poor preservation potential as these scales are quite heavily mineralized and are found well-preserved in sediments from the Santa Barbara Basin

(Soutar, 1967; Soutar and Isaacs, 1969, 1974; Baumgartner et al., 1992).

Paleofish work is predicated on the fact that many species of clupeids and small pelagic species exhibit scale shedding. However, there are other factors which affect the degree to which scale deposition in the sedimentary record is representative of fish populations. In addition to deciduous shedding, scales can enter the sediment from natural massive fish kills as well as from non-deciduous scale loss, including poor mastigation, defecation of prey fish and predator—prey interaction (O'Connell and Tunnicliffe, 2001). Fish can also simply loose scales randomly but those scales often grow back with the typical "regeneration" pattern where the focal area is distorted (Fig. 2). Rockfish, flatfish, and surf perches often show this feature.

Catastrophic death of an entire school of fish can occur. Many small pelagic species school in coastal inlets during the winter, even those species that tend to be migratory. If resources are insufficient to

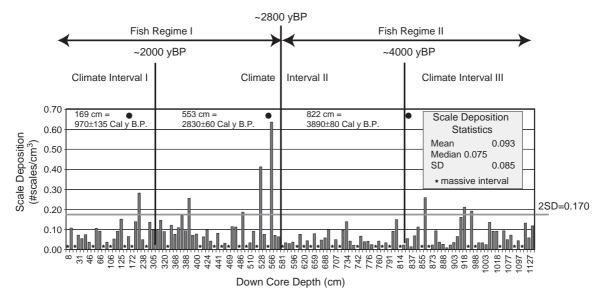


Fig. 3. Scale deposition as abundance versus down-core depth for core TUL99B03. Note that the *x*-axis is not a linear scale. Stars represent lithological intervals of massive deposition where fish remains were not analyzed. Solid circles are radiocarbon dates as given in Table 1. Climate regimes are approximated from Hebda (1995) and Dallimore (2001).

maintain the school or the fish are unduly stressed, they will often succumb to disease and the entire school can suddenly die. Although these remains are often consumed by other fish, sea birds and mammals, fish body parts, even entire intact bodies, also make it to the sediments. By extension, even incorporation of a single complete fish into the sediment can be problematic.

Of the 95 samples investigated, two were suspect as they were dominated by juvenile rockfish scales (samples 525–532 and 563–568 cm) and exceeded the 2STD of 0.17 scales/cm<sup>3</sup>. It should be noted, however, that correction by removal of the rockfish numbers only marginally changed the overall scale signal.

In the Effingham Inlet sediments, many intact fish skeletons were found within sediments of approximately 2000–4000 years in age in all piston cores of the inner basin (Dallimore, 2001). During the sampling process, they were visually apparent as intact skeletons lying between bedding layers. We conclude, therefore, that fish kills, and perhaps intrusions of dense bottom waters from the outer coast, were more common in the inlet between about 2000 and 4000 y BP (Dallimore et al., in press). Along-channel oceanography shows that at times, denser waters can

enter the inner basin forcing the deep anoxic and H<sub>2</sub>S laden water layer upwards. This could potentially initiate fish kills. Although skeletons from these fish may add a bias to the paleofish record, an inlet-wide fish kill gives valuable paleoenvironmental information, and illustrates the need for a close link between paleo-indicators in the sediment record, oceanographic data, and the paleofish record.

We tested that fish kills do not represent a serious bias in our record by comparing counts of fish scales with fish bones. A few samples exhibited a high number of scales corresponding with a high number of bones but there was no consistent pattern. A standard linear regression of scale abundance versus bone abundance showed a poor correlation ( $R^2 \cong 0.095$ ). We conclude that whole fish skeletons are not biasing the Effingham paleofish record. Analysis of the bone material indicated that of the five suspects, only one sample (1094-1099 cm) may have been biased. In this sample, there appear to be an almost complete herring skeleton and enough bones to estimate an individual hake specimen (Wiggins pers. commun., 2001). However, further investigation of this sample showed that there was not an unusual number of herring or hake scales, but only the number of bones.

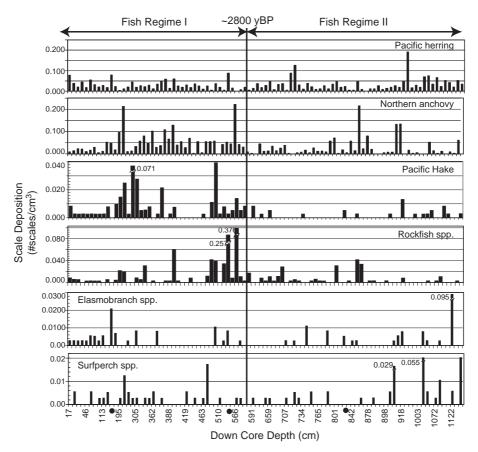


Fig. 4. Scale deposition of fish species that are greater than 3% of the total abundance. Demarcation of the fish regimes at 576 cm ( $\sim$ 2800 y B.P.) as determined in this study by unpaired Mann–Whitney analysis. Solid circles are the same radiocarbon dates as shown in Fig. 3. Note: massive intervals have been removed from the graph and the x-axis is not linear.

It is important to consider depositional factors on a "sample by sample" basis. We determined that there are two signals that a sample may have some bias: 1) the scales are dominated by one particular type of fish and/or 2) there is a large number of coincident bones with the scales. Many times, the result is that the counts for scale and/or bone abundance in that sample will exceed the 2STD for the entire dataset.

# 3.3. Statistical analysis

At approximately 576 cm down-core (~2800 y B.P.), there is a visual change in the pattern of deposition with a change to overall lower abundances with greater age (increasing depth down-core). Unpaired Mann–Whitney tests show there is a significant difference between these two regions of the core with a

Z value of 3.28 ( $Z_{\rm crit}$ =1.96; P1=0.0005, P2=0.001). To determine what may be the driving species for this shift in abundance, the two dominant taxa, Pacific herring and Northern anchovy were similarly examined. Pacific herring shows no significant difference between sections of core with a Z value of -0.06 ( $Z_{\rm crit}$ =1.96; P1=0.4761, P2=0.9522). However, Northern anchovy did show a Z value of 3.11 ( $Z_{\rm crit}$ =1.96; P1=0.0009, P2=0.0019) and is the primary species responsible for down-core decrease in deposition at ~2800 y B.P.

The West Coast of Vancouver Island experienced three main climate regimes in the Late Holocene (present–2000 y B.P., 2000–4000 y B.P., >4000 y B.P.) as determined from pollen studies by Hebda (1995) and supported by the lithology of the Effingham Inlet cores in companion studies (Dallimore,

2001; Dallimore et al., in press). Unpaired Krustal–Wallis tests were performed on scale abundance, grouping the data into the approximate dates of these regimes, to determine if these species were responding to climate periods. The results indicate that fish assemblages, as determined by scale deposition, were not responding to changes in the climate as neither the total scale abundance (H=1.87), Pacific herring scale abundance (H=0.86), nor Northern anchovy scale abundance (H=3.28) exceeded the chi-square critical value of 5.99.

Testing for species interactions, the results of the Spearman rank correlations on the entire core show that there is no significant correlation between Pacific herring and Northern anchovy ( $r_s$ =-0.196; t=-1.93;  $r_s^2$ =0.038). Seven specific regions of the core that showed continuous laminations (deposition was not disrupted by massive intervals) were similarly tested. The results are shown in Table 3 and also indicate a lack of correlation between these two species.

Further exploration using cross-correlation and lag analysis was performed on 719–767 and 824–1024 cm. These two sections exhibited laminated regions that were only interrupted once by a massive deposit, providing reasonably continuous time lines. The results were similar to the Spearman rank results. For section 719–767 the R-value at 0 lag was -0.62 with anchovy lagging herring by at most 1 unit (~21 years). The data from 824 to 1020 cm was more variable with no well-defined lag.

Table 3 Spearman rank order correlation analysis of individual core sections;  $r_{\rm crit}$  is from Zar (1984)

Down-core depth (cm)	N	$r_s$	$r_{\rm crit}$	$r_{\rm s}^2$
287–322	5	0.4000	1.00*	0.160
362-402	8	-0.1905	0.738	0.021
719–767	9	-0.6000	0.700	0.360
824-855	6	0.1420	0.886	0.020
878-920	11	0.0367	0.618	0.001
951-1020	9	-0.1695	0.700	0.287
824-1020**	27	-0.2853	0.382	0.080

<sup>\*</sup>Value from VassarStat web site (http://faculty.vassar.edu/lowry/corr\_rank.htm). \*\*Combined intervals using the average of the nearest top and bottom neighbors to extrapolate single massive intervals.

#### 4. Discussion

## 4.1. The paleofish assemblage of Effingham Inlet

The paleoassemblage of fish species represented in the scale and bone remains is typical of present-day inlets and estuaries along the southern B.C. coast. The list of species presented here likely underestimates the number of species that inhabited Effingham Inlet during the Late Holocene, more likely the result of preservation potential of skeletal material rather than an absence of species. For example, although Barkley Sound and Effingham Inlet have salmon runs, salmon remains are absent in the core sample. This is due to the "soft" nature of salmon bones and scales which are not heavily mineralized and can breakdown rapidly after being deposited.

The assemblage in Effingham Inlet is quite similar to that identified further to the south in Saanich Inlet using bone remains alone (Tunnicliffe et al., 2001). Assemblage differences in the two inlets are primarily in percent composition, which is likely due to oceanographic factors related to geographic differences in the two sites. Effingham Inlet is open to the Pacific Ocean via Barkley Sound whereas Saanich Inlet is protected from the open ocean by the Strait of Georgia and Juan de Fuca Strait (Fig. 1), and is strongly influenced by both the Cowichan and Fraser rivers. This is also the likely reason for limited anchovy material in Saanich Inlet.

The high percentage of Northern anchovy (~41%) in Effingham Inlet is not unusual as this species is common in present-day British Columbia waters and deciduously sheds scales. In the NE Pacific, three anchovy populations, with independent spawning conditions are recognized: Northern (Oregon/Washington/B.C.), Central (California/Mexico), and Southern (Mexico). These stocks differ in their physical meristics (McHugh, 1951) and also in their reproductive timing (Richardson, 1981; Vrooman et al., 1981). Density-independent factors such as SST and upwelling affect the stocks in different ways. In British Columbia, the normally migratory Northern anchovy is a warm-water species at the northern end of its range and is likely susceptible to changes in SST, with populations expanding during warm water periods and contracting during cool. The population of Northern anchovy presently residing in Barkley

Sound is likely a satellite population that requires persistent influx from source populations off the Oregon/Washington coast. A shift to warm SST, especially during spawning season, either via El Niño, a Pacific regime shift, or a reduction in upwelling, may facilitate this Central stock expansion into B.C. coastal waters (Fiedler et al., 1986).

Northern anchovy show an increase in scale deposition at ~2800 y B.P. This enhanced deposition continues until approximately 1600 y B.P. when deposition drops off (mean=0.220 scales/cm³ at 2800–1600 y B.P. versus 0.030 scales/cm³ at 500–1600 y B.P.). Higher scale deposition reflects an increase in anchovy production either through localized increases or increased northward expansion from Washington/Oregon waters. It is also possible that at ~2800 y B.P., anchovy became more persistent in the Barkley Sound system, which could also indicate a more anchovy-favourable SST that lasted until approximately 1600 y B.P.

The high total percentage (32%) of Pacific herring, and the large percentage of the scales that are from juveniles (73% of total herring scales), in the assemblage is not surprising since present-day Barkley Sound is an important spawning habitat for West Coast Vancouver Island (WCVI) stocks. Herring spawn predominantly on the northwest side of Barkley Sound and the larvae then migrate to the southeast side and to nearby inlets including Effingham, where they spend the remainder of the spring and summer season (Hourston, 1959). Inlets provide larval and juvenile herring with a stable water column, increased shelter, and protection from currents and winds that could carry them offshore.

Although Pacific herring have a wide latitudinal distribution, in British Columbia they prefer cooler SSTs (Ware, 1991; Hollowed and Wooster, 1995; Ware and McFarlane, 1995). Thus, the presence or absence of these stocks can be an indicator of SST. Herring mortality appears to be high during years of high SST (Robinson and Ware, 1994) and the recruitment index for WCVI appears to be inversely related to SST (Schweigert, 1995), positively correlated with the Southern Oscillation Index, and negatively correlated with upwelling intensity (Williams and Quinn, 2000b).

Except for two instances were there was a "0" herring scale count (566 cm-~2750 y B.P. and 873

cm-~4210 y B.P.), herring were present throughout the Late Holocene in Effingham Inlet. Since British Columbia stocks of herring have limited migration, an increase in herring scale deposition would likely reflect an increase in the productivity of the WCVI herring population. There is a general appearance of cycling in the deposition of fish scales (Fig. 4), but the sampling resolution was too coarse in comparison to the recruitment which varies annually and exhibits strong year classes every 3-10 years (Williams and Quinn, 2000b). Herring population dynamics also exhibited cyclical behaviour in the Saanich Inlet paleofish record (Tunnicliffe et al., 2001; O'Connell and Tunnicliffe, 2001). The longer term population fluctuations for this species is, however, unknown (Williams and Quinn, 2000b) and the persistent presence of herring populations in pre-historic Effingham Inlet indicates that cyclical SST and offshore winds similar to today's were occurring throughout the Late Holocene in this region.

Although herring scale numbers are somewhat lower than anchovy numbers, this may be explained the differences in habitat use by adults and juveniles where the primary age class of herring in Effingham Inlet are juveniles spawned in that year from adults that stay on the shelf and in the Barkley Sound region. Northern anchovy in Effingham Inlet, from the scale record, appear to be primarily adults.

Although in British Columbia, herring prefer cooler SSTs and anchovy prefer warmer SSTs, correlation lag tests performed on scale counts of both species show that there is no significant relationship between Pacific herring and Northern anchovy scale abundance time series. This may indicate that although SST may be important, it may not be the most critical factor for some pelagic stocks.

There are two behavioural forms of hake in British Columbia: the offshore migratory stock and the inshore residential populations (Smith et al., 1990). Studies on the variations in the abundance of hake in the La Pérouse region of British Columbia show there is a positive relationship between SST and offshore hake biomass as determined using hydroacoustic methods (Robinson and Ware, 1999). In addition to interannual variations, offshore hake respond to ENSO events as a proportional increase in the fraction of stock that migrates into Canadian waters, and also by increasing their northward range

(Dorn et al., 1999). Strong upwelling conditions have also been linked to increased hake production as the enhanced upwelling supports increased euphasiid production.

In sediments older than ~2800 y B.P. (576 cm), hake scale deposition is quite variable, but in younger sediments, although "0" scale counts occur, the abundance is more consistent. This suggests that the species responded to conditions that support a more persistent population and perhaps an expansion of the inshore residential component. Since this is a response similar to anchovy, and both species, in British Columbia. waters, respond positively to warmer SST, it may be postulated that the coastal waters of the northeastern Pacific experienced a warming after 2800 y B.P.

Nearshore species of rockfish include copper, quillback, and brown. Many of these stocks, including offshore species, have shallow water juvenile stages (Boehlert, 1977; Love et al., 1991). As well, larval and juvenile rockfish of many species use inlets as nursery systems. It was noted by Hourston (1958) that upon the release of tagged herring in the Barkley Sound study region, small rockfish would come up to the surface and feed on the herring almost immediately after release. Rockfish scales comprise 13% of the total assemblage and most are identified as juvenile scales. The unknown environmental preferences for this species in the modern ocean makes it difficult to speculate about the proxy past conditions. The results from this analysis show that in the Late Holocene, Effingham Inlet was used as a nursery area for coastal rockfish species. The effects of changes in oceanic regimes or shifts in climate on rockfish populations has not been well-studied, but it does appear that ENSO and Pacific Decadal Oscillation events affect rockfish abundances (Moser and Charter, 2001) and possibly the range of individual species (Karpov et al., 1995).

Elasmobranch material comprises slightly more than 3% of the paleoassemblage, but abundances are highly variable with core depth. The major species is likely to be *Squalus acanthias*, the dogfish shark, which is common in British Columbia waters and an integral part of the food chain as it a major predator on hake. However, most elasmobranches, including dogfish sharks are unlikely to be residential or even seasonal visitors to inlets as studies indicate that this

species is transient in inlet systems (McMillan and Morse, 1999).

Sardine scales, although mineralized enough to withstand burial and diagenic processes, constitute a low percentage of the scale abundance, with only 9 scales between ~1800 y B.P. (145 cm) and ~2500 y BP (512 cm). In British Columbia waters, sardines seem to prefer broad shelf areas where productivity is high and where their major sources of food (euphausiids and other sardines) are more abundant (McFarlane and MacDougall, 2001). The low counts from the scale paleorecord suggests that, in the farther reaches of the inlet systems, sardines may only be transient visitors.

## 4.2. Paleoenvironmental interpretations

Unlike other micro-paleontological proxies such as foraminifera and diatoms, the number of fish scales and bones required for meaningful interpretation require large volumes of sediment. This study utilized a 10 cm piston core which required sampling for fish remains in both the working and archive sides of the core. Secondly, a decision was made to maximize volume by sampling on a 5 cm basis. However, this resolution is too coarse (~20 years) to investigate high-frequency cycles or to pinpoint causes of variability and trends because the resolution is lower than the cycle of the fish in question. The time series is therefore, highly aliased. For example, herring have a strong year-class every 3-7 years (Williams and Ouinn, 2000b) so we are unable to quantify this cycle with the sampling resolution used.

Cyclical 100-year population variations were found in the abundance of Northern anchovy in the fish scale record of Soutar and Isaacs (1969) off California. Baumgartner et al. (1992), using spectral analysis of scale deposition rates, found that anchovies cycled on a 60-year period and an additional 100-year period. This cycling between two dominant species off California (Northern anchovy and Pacific sardines) led Chavez et al. (2003) to establish regimes based on theses species and their responses to large scale shifts in atmospheric and oceanic forcing. In the NE Pacific, it is important to note that climate forcing that affects the California Current and the shift between cool (anchovy) regimes and warm (sardine) regimes has varying, and sometimes opposing

impacts, depending on latitude, especially between California and British Columbia. A study by Ware and Thomson (2000) showed that large-scale temperature extremes and phases of warm/cool air temperatures along the northern and southern portions of western North America are often coincident. On the other hand, an earlier study by Ware and Thomson (1991) also showed that more regional or basin factors such as wind forcing, upwelling intensity, and consequently primary production, along the northern and southern portions of the Coastal Upwelling Domian were often out of phase.

Fig. 5 illustrates the major paleofish shifts identified from four studies, including this one, along the west coast of the North and South America. Depending on the stock in question, it appears that between ~1600 and 2800 y B.P., sardines, saury and North American fish stocks of anchovy benefited from more favourable environmental conditions. When comparing the Effingham Inlet results against the Santa Barbara Basin studies it is important to note that for Northern anchovy, these are two different stocks with different ecological lifestyles and environmental preferences. The Santa Barabara anchovy population is a large, commercially valuable

migratory spawning population whereas the Effingham Inlet population is much smaller and less migratory. That being said, our results are somewhat complementary to those found by Soutar and Isaacs (1969). Both studies find that anchovy numbers were high from 2800 to 1800 y B.P. off California and to 1600 y B.P. off British Columbia.

The decline of anchovies off California after 1800 y B.P. has been attributed to a warming of the California Current and a shift to sardine dominance. Although there may be a coincident warming of SST in British Columbia, regional factors may play a more critical role in establishing the strength of a pelagic fish stock. It might be expected that warmer SST would benefit the expansion of anchovy in the northern Coastal Upwelling Domain. However, warmer SSTs are often linked with a decreased intensity of upwelling (even downwelling conditions) which would adversely impact primary production. The later is consistent with Ware and Thomson (1991) in their study of sardines in the northern Coastal Upwelling Domain, who find that cessation of northerly winds resulted in decreased upwelling intensity, with the coincident decrease in primary production linked to declining sardine biomass. Thus, with

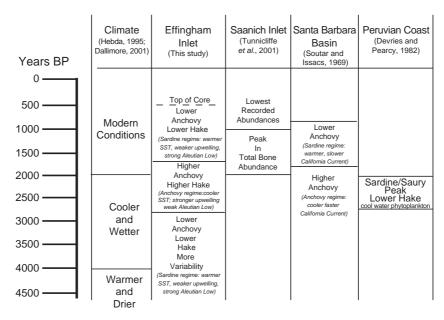


Fig. 5. Relative timing of paleoclimate changes and shift in fish stocks along the west coast of the Americas as based on fish scale deposition in anoxic basins (Hebda, 1995; Dallimore, 2001; Tunnicliffe et al., 2001; Soutar and Isaacs, 1969; DeVries and Pearcy, 1982). Fish regimes and oceanic conditions (in italics) from Chavez et al. (2003).

respect to anchovy, the positive effect of increased SST may have been more than compensated by the negative effect of decreased productivity.

Unlike Northern anchovy, Pacific herring do not show distinct changes in scale deposition, but the pattern does suggest some level of cyclicity. As mentioned, our data are aliased and we cannot resolve year-class strength. However, the scale deposition suggests that Effingham, for the period that this core represents, was an important nursery region of coastal Pacific stocks. The dominance of juvenile scale material suggests that adult herring were not prominent members of the fish community at the far reaches of the coastal inlets and were likely restricted to "near" Barkley Sound spawning areas.

Comparisons with previous studies of Pacific herring are difficult as they were not as dominant in the Santa Barbara studies and, although a large proportion of the bones analyzed by Tunnicliffe et al. (2001) were herring, the study addressed primarily total bone abundance. Tunnicliffe et al. (2001) do report that between 1000 and 2000 y B.P. there is a peak abundance of bone material followed by much lower abundances in the last 1,000 years and herring is likely driving this decrease. The importance of herring in Saanich Inlet differs from Effingham most likely due to the ecological use of the region. Effingham is primarily a nursery area for juveniles while Saanich Inlet is a region that attracts prespawning adult aggregates (cited in Tunnicliffe et al., 2001). Although in Effingham scale material we see a similarly timed peak in abundance and also a decline in scale abundance in the last 1000-500 years, this is driven not by Pacific herring but by Northern anchovy.

From the terrestrial pollen record, Hebda (1995) has identified three Late Holocene climatic regimes along the West Coast of Vancouver Island which indicate that from 2000 to 4000 y B.P., the climate was colder and wetter than today, whereas prior to 4000 y B.P. it was warmer and drier than today. Although these shifts in climate are also recorded in the sediments of Effingham Inlet (Dallimore et al., in press), they are not evident in the fish scale record. One possible explanation is that although fish populations respond to long-term changes in environmental conditions, there may be a lag between ocean-climate changes in an inlet system and

the resident/migratory fish assemblages. Studies by Cury and Roy (1989) and Ware and Thomson (1991) found that pelagic stocks respond to climate and oceanographic forcing in a non-linear fashion. Variations in upwelling may not have been captured by pollen-based studies. Although all pelagic stocks do not respond in exactly the same fashion to climate or oceanographic forcing mechanisms, they generally do reflect the general state of the ecosystems primary production and the state of upwelling intensity (Ware and Thomson, 1991).

#### 5. Conclusions

Considering the overall population ecology of the region, the remains found in sediments provide a general listing of the species that populated the region and evidence of simple food web structures such as a herring-hake-dogfish predation link. In Effingham Inlet, the dominant species are two common clupeids, Pacific herring and Northern anchovy. Their abundance is not surprising considering their proximity to the Coastal Upwelling Domain and also when considering the importance of Barkley Sound and the neighboring inlets as a nursery area for Pacific herring and other forage stocks. There is no apparent trend in the Pacific herring scale abundance data, possibly due to the course sampling resolution, although there appears to visually be some degree of cyclicity. For Northern anchovy there appears to be some changes in the structure of the population in Effingham Inlet that may be associated with large oceanographic factors such as SST but regional scale factors such as upwelling intensity and primary production may be more critical. However neither species appears to be affected by regional scale climate forcing as seen in the terrestrial pollen and marine lithological record.

Overcoming the requirements for sediment volume should be considered prior to sampling. Most important is that the time resolution needs to be on a similar order of magnitude to the fish being investigated. The trade-off with having with a smaller diameter cores is that the frequency of sampling may need to be decreased. This is problematic when considering species that have their cyclicity on a shorter time scale. Ideally, the Inner Basin core should have been sampled at

a 2 cm interval rather than a 5 cm interval. It is unknown if this would have made abundance counts difficult to analyze but the shorter time frequency would have put our sampling at a similar resolution to the dominant clupeid found in the sediments.

Ideally, larger diameter cores will assist in achieving a reasonable sediment volume. Alternatively, sister or neighboring smaller diameter cores can be taken. The caveat with this approach is that diligence is required to ensure that intra-basin variability is small and that the cores are achieving similar penetrations depths to allow for stratigraphic correlation and that any variability in sediment deposition are accounted for. The other financial disadvantage to this approach would be the likely requirement for additional radiocarbon dates. In the case of Effingham Inlet, studies by Dallimore (2001) show that intrabasin variability is quite high and the stratigraphic correlation based only on sedimentology is tenuous.

Potential bias in the samples can come from many factors and needs to be considered on a sample-by-sample basis. Counts that are beyond 2 STD need to be looked at further for influences that might artificially inflate the count such as, for example, single-species dominance, or a whole dead fish, etc. It is best to use this knowledge to adjust the sample abundance rather than to discard the sample completely or to mathematically extrapolate a value.

# Acknowledgements

The authors would like to thank Rebecca Wiggins and the Bone Laboratory in the Department of Anthropology at the University of Victoria for their valuable assistance and insight. The authors would also like to thank the two anonymous reviewers for their constructive comments on this manuscript.

This work was partially supported by a NSERC strategic grant to R.T. Patterson with additional support from the Institute of Ocean Sciences, Fisheries and Oceans Canada.

# References

Barber, R.T., Chavez, F.P., 1983. Biological consequences of El Niño. Science 222, 1203–1210.

- Baumgartner, T.R., Soutar, A., Ferreira-Bartrina, V., 1992. Reconstruction of the History of Pacific Sardine and Northern Anchovy Populations over the Past Two Millennia from Sediments of the Santa Barbara Basin, California, vol. 33. California Department of Fish and Game.
- Boehlert, G.W., 1977. Timing of the surface-to-benthic migration in juvenile rockfish, Sebastes deploproa and a comparison with growth in the field. U.S. Fish. Bull. 79, 887–890.
- Brodeur, R.D., Ware, D.M., 1992. Long-term variability in zooplankton biomass in the subarctic Pacific Domain. Fish. Oceanogr. 1, 32–38.
- Casteel, R.W., 1976. Fish Remains in Archaeology and Paleo-Environmental Studies. Academic Press, London.
- Chavez, F.P., Ryan, J., Lluch-Cota, S.E., Niquen, C.M., 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science 299, 217–221.
- Cury, R., Roy, C., 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. Aquat. Sci. 46, 670–680.
- Cury, P., Roy, C., Mendelssohn, R., Bakun, A., Husby, D.M., Parrish, R.H., 1995. Moderate is better: exploring nonlinear climatic effects on the Californian northern anchovy (*Engraulis mordax*). In: Beamish, R.J. (Ed.), Climate Change and Northern Fish Populations. NRCan, Nanaimo, B.C., pp. 417–424.
- Dallimore, A., 2001. Late Holocene geologic, oceanographic, and climate history of an anoxic fjord: Effingham Inlet, West Coast, Vancouver Island. Ph.D. Thesis, Carleton University, Ottawa, Ontario, 464 pp.
- Dallimore, A., Thomson, R.E. and Bertram, M.A., in press. Modern to Late Holocene deposition in an anoxic fjord on the west coast of Canada: implications for regional oceanography, climate and paleoseismic history. Mar. Geol.
- DeVries, T.J., Pearcy, W.G., 1982. Fish debris in sediments of the upwelling zone of central Peru: a Late Quaternary record. Deep-Sea Res. 28 (1A), 87–109.
- Dorn, M.W., Saunders, M.W., Wilson, C.D., Guttormsen, M.A., Cooke, K., Kieser, R., Wilkins, M.E., 1999. Status of the coastal Pacific hake/whiting stock in U.S. and Canada in 1998. Canadian Stock Assessment Secretariate Research Document, 99/90 (101 pp.).
- Emery, W.J., Thomson, R.E., 2001. Data Analysis Methods in Physical Oceanography, Second and Revised Edition Elsevier, Amsterdam. 638 pp.
- Fiedler, P.C., Methot, R.D., Hewitt, R.P., 1986. Effects of California El Niño 1982–1984 on the northern anchovy. J. Mar. Res. 44, 317–338.
- Field, D.B., Baumgartner, T.R., 2000. A 900 year stable isotope record of interdecadal and centennial change from the California current. Paleoceanography 15 (6), 695–708.
- Francis, R.C., Hare, S.R., 1994. Decadal-scale regime shifts in the large marine ecosystem of the North-east pacific: a case for historical science. Fish. Oceanogr. 3, 279–291.
- Freeland, H.J., Denman, K.L., 1982. A topographically controlled upwelling center off southern Vancouver Island. J. Mar. Res. 40, 1069–1093.
- Hare, S.R., Francis, R.C., 1995. Climate change and salmon production in the Northeast Pacific Ocean. In: Beamish, R.J. (Ed.),

- Climate Change and Northern Fish Populations, Can. Spec. Publ. Fish. Aquat. Sci. NRC, pp. 357-372.
- Hart, J.L., 1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180, 740.
- Hay, M.B., Pienitz, R., Thomson, R.E., 2003. Distribution of diatom surface sediment assemblages within Effingham Inlet, a temperate fjord on the west coast of Vancouver Island (Canada). Mar. Micropaleontol. 48, 291–320.
- Hebda, R.J., 1995. British Columbia vegetation and climate histor with focus on 6 KA BP. Geogr. Phys. Quat. 49, 55-79.
- Hollowed, A.B., Wooster, W.S., 1995. Decadal-scale variation in the eastern subarctic Pacific: II. Response of Northeast Pacific fish stocks. In: Beamish, R.J. (Ed.), Climate Change and Northern Fish Populations, Can. Spec. Publ. Fish. Aquat. Sci. NRC, pp. 373–385.
- Holmgren, D., 2001. Decadal-Centennial Variability in Marine Ecosystems of the Northeast Pacific Ocean: The Use of Fish Scale Deposition in Sediments. University of Seattle, Seattle, Washington. 121 pp.
- Hourston, A.S., 1958. Population studies on juvenile herring in Barkley Sound, British Columbia. J. Fish. Res. Board Can. 15 (5), 909–960.
- Hourston, A.S., 1959. Effects of some aspects on environment on the distribution of juvenile herring in Barkley Sound. J. Fish. Res. Board Can. 16 (3), 283–308.
- Karpov, K.A., Albin, D.P., Van Buskirk, W.H., 1995. The marine recreational fishery in northern and central California. Fish Bull., 176.
- Kumar, A., Patterson, R.T., 2002. Dinoflagellate cyst assemblages from Effingham Inlet, Vancouver Island, British Columbia, Canada. Palaeogeogr. Palaeoclimatol. Palaeoecol. 180, 187–206.
- Lange, C.B., Weinheimer, A.L., Reid, F.M.H., Tappa, E., Thunell, R.C., 2000. Response of siliceous microplankton from the Santa Barbara Basin in the 1997–98 El Niño event. Calif. Coop. Ocean. Fish. Investig. V, 161–170.
- Love, M.S., Carr, M.H., Haldorson, L.J., 1991. The ecology of substrate-associated juveniles of the genus *Sebastes*. Environ. Biol. Fisches 30, 225–243.
- McFarlane, G.A., MacDougall, L.A., 2001. Biological information for Pacific sardine (*Sardinops sagax*) captured during research cruises 1992–2000. Can. Tech. Rep. Fish. Aquat. Sci 2372, 149.
- McHugh, J.L., 1951. Meristic variations and populations of northern anchovy, (*Engraulis mordax*). Scripps Inst. Oceanogr. Bull. 6, 123–160.
- McMillan, D.G., Morse, W.W., 1999. Essential Fish Habitat Source Document: Spiney Dogfish, *Squalus acanthias*, Life History and Habitat Characteristics. NMFS-NE-150, NOAA, Woods Hole, MA.
- Moser, G., Charter, S., 2001. Fisheries Resource Division Annual Report for FY 2001, Southwest Fisheries Science Center. National Marine Fisheries Service, La Jolla, California.
- O'Connell, J.M., Tunnicliffe, V., 2001. The use of sedimentary fish remains for interpretation of long-term fish population fluctuations. Mar. Geol. 174, 177-199.
- Patterson, R.T., Guilbault, J.-P., Thomson, R.E., 2000. Oxygen level control on foraminiferal distribution in Effingham Inlet, Van-

- couver Island, British Columbia. J. Foraminiferal. Res. 30, 321-335.
- Patterson, R.T., et al., 2001. Atlas of common squamatological (fish scale) material in coastal British Columbia and an assessment of the utility of various scale types in paleofisheries reconstruction. Palaeontol. Electronica 2 (2) (88 pp.).
- Richardson, S.L., 1981. Spawning and early life of northern anchovy, *Engraulis Mordax*, in the northern subpopulation off Oregon and Washington. Fish Bull. 78, 855–876.
- Robinson, C.L.K., Ware, D.M., 1994. Modelling pelagic fish and plankton trophodynamics off southwestern Vancouver Island, British Columbia. Can. J. Fish. Aquat. Sci. 51, 1737–1751.
- Robinson, C.L.K., Ware, D.M., 1999. Simulated and observed response of the southwest Vancouver Island pelagic ecosystem to oceanic conditions in the 1990s. Can. J. Fish. Aquat. Sci. 56, 2433—2443
- Schweigert, J.F., 1995. Environmental effects on long-term population dynamics and recruitment to Pacific herring (*Clupea pallasi*) populations of southern British Columbia. In: Beamish, R.J. (Ed.), Climate Change and Northern Fish Populations, Can. Spec. Publ. Fish. Aquat. Sci. Fisheries and Oceans Canada, pp. 569–583.
- Smith, B.D., McFarlane, G.A., Saunders, M.W., 1990. Variation in Pacific hake (*Merluccius productus*) summer length-at-age near southern Vancouver Island and its relationship to fishing and oceanography. Can. J. Fish. Aquat. Sci. 47 (11), 2195–2211.
- Soutar, A., 1967. The accumulation of fish debris in certain California coastal sediments. Calif. Coop. Ocean. Fish. Investig., Data Rep. 11, 136–139.
- Soutar, A., Isaacs, J.D., 1969. History of Fish Populations Inferred from Fish Scales in Anaerobic Sediments Off California, vol. XIII. California Department of Fish and Game. 1 July 1967 to 30 June 1968.
- Soutar, A., Isaacs, J.D., 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. Fish. Bull. 72, 257–273.
- Stuiver, M., Reimer, P.J., 1986. A computer program for radiocarbon age calibration. Radiocarbon 28, 1022–1030.
- Stuiver, M., Reimer, P.J., 1993. Extended <sup>14</sup>C database and revised CALIB radiocarbon calibration program. Radiocarbon 35, 215–230.
- Stuiver, M., Reimer, P.J., Bard, E., Beck, J.W., Burr, G.S., Hughen, K.A., Kromer, B., McCormac, F.G., Plicht, J., Spurk, M., 1998a. INTCAL 98 radiocarbon age calibration 24,000–0 cal BP. Radiocarbon 40, 1041–1083.
- Stuiver, M., Reimer, P.J., Braziunas, T.F., 1998b. High-precision radiocarbon age calibration for terrestrial and marine samples. Radiocarbon 40, 1127–1151.
- Tanasichuk, R.W., 1997. Influence of biomass and ocean climate on the growth of Pacific herring (*Clupea pallasi*) from the southwest coast of Vancouver Island. Can. J. Fish. Aquat. Sci. 54, 2782–2788.
- Thomson, R.E., Hickey, B.M., LeBlond, P.H., 1989. The Vancouver Island Coastal current: fisheries barrier and conduit. In: Beamish, R.J., McFarlane, G.A. (Eds.), Effects of Ocean Variability on Recruitment and an Evaluation of Parameters used in Stock Assessment Models. Fisheries and Oceans Canada, Inter-

- national North Pacific Fisheries Commission, Nanaimo, B.C., pp. 359-379.
- Tunnicliffe, V., O'Connell, J.M., McQuoid, M.R., 2001. A Holocene record of marine fish remains from the Northeastern Pacific. Mar. Geol. 174, 197–210.
- Vrooman, A.M., Paloma, P.A., Sweifel, J.R., 1981. Electrophoretic, morphometric, and meristic studies of subpopulations of northern anchovy, *Engraulis mordax*. Calif. Fish Game 67, 39–51.
- Ware, D.M., 1991. Climate, predators and prey: behaviour of a linked oscillating system. In: Kawasaki, T. (Ed.), Long-term Pelagic Fish Populations and their Environment. Pergamon Press, Tokyo, Japan, pp. 279–291.
- Ware, D.M., McFarlane, G.A., 1989. Fisheries production domains in the Northeast Pacific Ocean. In: Beamish, R.J., McFarlane, G.A. (Eds.), Variability on Recruitment and an Evaluation of Parameters Used in Stock Assessment Models. NRCan, Nanaimo, B.C., pp. 359–379.
- Ware, D.M., McFarlane, G.A., 1995. Climate-induced changes in Pacific hake (*Merluccius productus*) abunda nce and pelagic community interactions in the Vancouver Island upwelling system. In: Beamish, R.J. (Ed.), Climate Change and Northern Fish

- Populations, Can. Spec. Publ. Fish. Aquat. Sci. Fisheries and Oceans Canada, pp. 509-521.
- Ware, D.M., Thomson, R.E., 1991. Link between long-term variability in upwelling and fish production in Northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 48, 2296–2306.
- Ware, D.M., Thomson, R.E., 2000. Interannual to multidecadal timescale climate variations in the Northeast Pacific. J. Climate 13, 3209-3220.
- Wilkerson, F.P., Dugdale, R.C., Barber, R.T., 1987. Effects of El Niño on new, regenerated, and total production in eastern boundary upwelling systems. J. Geophys. Res. 92, 347–353.
- Williams, E.H., Quinn, T.J., 2000a. Pacific herring, Clupea pallasi, recruitment in the Bering Sea, and north-east Pacific Ocean: I. Relationships among different populations. Fisheries Oceanogr. 9 (4), 285–299.
- Williams, E.H., Quinn, T.J., 2000b. Pacific herring, Clupea pallasi, recruitment in the Bering Sea, and north-east Pacific Ocean: II. Relationships to environmental variables and implications for forecasting. Fisheries Oceanogr. 9 (4), 300–315.
- Zar, Z.H., 1984. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, New Jersey.