USING OTOLITHS TO DETERMINE DAILY GROWTH RATE AND SIZE-SELECTIVE MORTALITY OF JUVENILE SALMON IN NANAIMO, BRITISH COLUMBIA

by

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ABSTRACT

Available evidence suggests that interannual variability in the recruitment of Pacific salmon is related to survival in the first few months juveniles spend at sea. Differential growth of smolts during this stage is often thought to result in interannual differences in marine survival, as those fish that grow faster may be less vulnerable to predators or physiological and environmental stressors associated with overwintering (i.e. the 'differential growth' hypothesis). Due to the limitations of traditional techniques, however, only rarely has salmon growth been reliably characterized during the early marine stage. Using juvenile chum salmon (*Oncorhynchus keta*) collected in the Nanaimo area (1999-2001), I demonstrate that otoliths provide a powerful means of examining the early life history of individual salmon in the field.

I used a fluorescent marker to validate the daily periodicity of otolith increment formation, and the formation of a marine entry check. I then back-calculated size-at-marine-entry for each chum smolt to provide individual estimates of early marine growth rate from the summers of 1999 and 2000. Mean daily growth rates were significantly higher, and size-at-entry significantly larger, in 1999 (0.084 cm day^{-1}, 4.48 cm) than in 2000 (0.076 cm day^{-1}, 3.97 cm). 1999 was also a year of significantly higher gut fullness and lower sea surface temperatures. By comparing growth rate frequencies across trips, I found evidence for size-selective mortality of slow growing fish in the midsummer of 2000. These patterns are consistent with the "differential growth hypothesis". In years of unfavourable ocean conditions, juvenile salmon may experience slower growth and higher rates of size-selective predation (possibly due to low food availability or quality). This, in turn, may lead to below average survival and recruitment in these years.

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For mom and dad

I feel a powerful lust for red salmon

- Dr. Gonzo

CHAPTER 1
Survival variability in the early marine life history stages of Pacific salmon

1.1 INTRODUCTION

The five species of Pacific salmon; pink (*Oncorhyncus gorbuscha*), sockeye (*O. nerka*), chum (*O. keta*), chinook (*O. tshawytcha*), and coho (*O. kisutch*), are of great cultural and economic importance in countries of the North Pacific Rim. First nations groups throughout the region have been catching salmon for thousands of years. For these peoples, salmon is more than just a staple foodstuff – it is a cultural symbol (Roche and McHutchison 1998). For the past century, Pacific salmon stocks have supported large commercial and sports fisheries. In British Columbia alone, commercial salmon catches are valued annually in tens to hundreds of millions of dollars. The associated recreational and tourist industries can be even more lucrative. It follows that variations in the abundance of salmon have important cultural and economic consequences.

Salmon are a relatively short-lived species with few year classes, and can have considerable interannual variations in stock size and biomass. Two to twenty-fold variations in abundance of recruits are quite common (Peterman 1987). Reliable catch data for B.C. salmon stocks exist for only the past century, and show considerable fluctuations (figure 1.1). As exploitation rates have been high throughout this period (65-85% in the coastal fisheries where a large percentage of these fish are caught), catch trends are believed to reflect abundance trends (Beamish and Bouillon 1993). Evidence from stable isotopes in sediment cores suggests that such variations in the abundance of Pacific salmon have occurred since at least the early 1500s (Finney 1998). The past 30 years have seen an overall decline in Canadian catches (figure 1.2). Since the late 1980s/ early 1990s, catches, and thus presumably abundances, have declined by as much as 60% (McFarlane et al 2000).

Understanding interannual variation in recruitment is one of the most important problems in fisheries science (Sissenwine 1984, Houde 1997). Despite considerable research over the last few decades, causal mechanisms of recruitment variability in marine fish remain unclear (Houde 1987, Anderson 1988). However, the catch declines noted above have reinforced the widespread recognition that the factors regulating
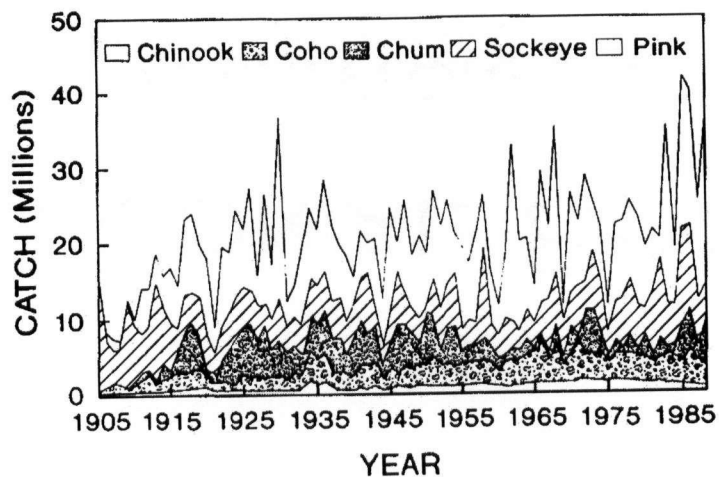
Figure 1.1 Fluctuations in Canadian catch for the last century (from Healey 1993).
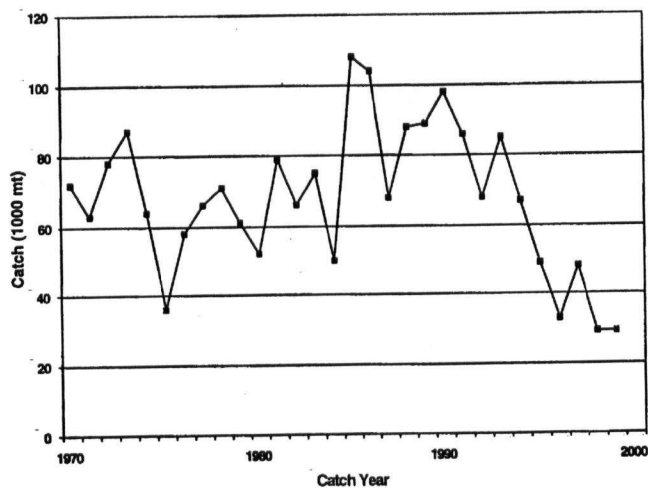
Figure 1.2 Canadian salmon catch over the last 30 years. Note the downward trend in the last decade (from McFarlane et al 2000).

abundance of Pacific salmon must be better understood. This understanding could help in better forecasting population size, as well as influencing the approaches used to manage populations. Salmon recruitment variability is thought to have three components: variability in egg-recruit survival, somatic growth rate, and age at maturity schedule (Peterman et al 1998). The first is the most variable, and, consequently, the factors affecting survival are most often investigated as a source of recruitment variability.

The unique life history of Pacific salmon, which includes anadromy and migrations of thousands of kilometers, makes them vulnerable to a wide variety of environmental variables. Most early research on variability in survival focused on the early freshwater life history stage of salmon, and sought to link variations in stock size to variations in the number of spawners and conditions in spawning and rearing habitats. The marine environment was usually ignored – when marine carrying capacity was considered at all, it was assumed to be so large as to be relatively unimportant (Pearcy 1992). Part of the bias in research was due to logistical problems. It was (and continues to be) much easier to study salmon in lakes and streams, where populations were isolated, and abundance easily estimated. Previously, sufficient resources and technology were not available to study salmon at the broad scale necessary to understand their marine ecology. However, the last 25 years have brought a growing awareness of the importance of the marine environment in determining production (Pearcy 1984, Neilson et al 1985). Recent interest has focused on factors that may influence survival during the marine life history stage of salmon, including marine density dependence and changing oceanographic conditions. I will review proposed freshwater and marine sources of stock size fluctuations, though the former only briefly, as they have been covered extensively elsewhere (Ebel 1985, Groot and Margolis 1991, Bardonnet and Baglinière 1999).

1.1.1 *Variability in freshwater survival*

The major freshwater sources of survival variability have been well documented since the 1950s and 60s. These include both density dependent (e.g. competition and predation) and density independent (e.g. temperature and water flow) mechanisms. The effect of parental body size on reproductive success and fecundity has also been studied, as has the relationship between variable egg size, competition for redd sites, and depth of

redds on brood size (reviewed by Peterman 1987). The two major freshwater concerns in both the scientific literature and the media have been stock-recruit relationships and the quantity and quality of freshwater habitat.

Until recently, many fisheries scientists accepted that for exploited populations variability in fishing pressure was the primary determinant of population size. Common dogma viewed changes in abundance as related to spawning stock size. Modeling efforts focused on taking advantage of the natural 'resilience' of fish populations to harvesting; relatively simple models were (indeed still are!) used to determine the 'holy grail' of fisheries management – the maximum sustainable yield (Pitcher and Hart 1982). Management efforts involved trying to set escapement from the fishery to optimize recruitment and thus maximize productivity (Ricker 1954). However, as with many other marine species (Myers 1997), salmon stock:recruit relationships are notoriously poor; they explain little of the variation seen in survival rates (Peterman 1987). Additionally, there are many biases inherent in the curve-fitting procedure (Peterman 1987). The poor fits and the biases involved therefore result in stock:recruit relationships that are of only limited use to managers and researchers.

Variation in the quantity and quality of freshwater spawning and rearing habitat is also commonly put forward as a major source of interannual variability in survival; publications on this subject number in the hundreds (reviewed by Ebel 1985, Lawson 1993, Bardonnet and Baglière 1999). Mortality rates during the early freshwater life history stage are extremely high (Beamish and Mahnken 1998), and changes in habitat quality are widely held to affect these rates considerably. However, solid empirical evidence for this claim remains elusive. Although human activities (i.e. logging, forestry, mining) can clearly have large impacts on habitat per se, it is not yet clear how (or whether) these impacts affect fish survival (Holtby and Scrivener 1989, Bradford and Irvine 2000). Beamish and Bouillon (1993) have pointed out that although available habitat in the Pacific Rim has certainly been reduced through industrialization over the past century, and despite high exploitation rates, total all nations catches of salmon actually began to increase in the 1970s. This trend runs opposite to that predicted by the habitat quality hypothesis. In the Strait of Georgia (SoG), Walters (1993) has argued that even if freshwater habitat destruction negatively impacts stocks, it is unlikely that the

present rate of habitat loss could wholly explain the large declines in chinook and coho stock size seen in this area.

1.1.2 *Variability in marine survival*

In recent years, the widespread lack of solid relationships between freshwater variables (such as spawning stock size and habitat quality) and abundance of recruits has led salmon researchers to investigate other life-history stages. One way of looking at this problem is to examine survival rates throughout the different life history phases of salmon. Total mortality of Pacific salmon can exceed 95% from egg to spawner (Groot and Margolis 1991). Two questions are generally considered when trying to pinpoint the key source of abundance fluctuations – at what life history stage does most of this mortality take place, and at what stage does mortality vary most?

Bradford's (1995) review of the subject concludes that both freshwater and marine habitats contribute substantially to total egg-adult mortality. Furthermore, he suggests that both habitat types contribute roughly equally to interannual variation in mortality. Even pink and chum, which spend very little time in freshwater, can experience considerable freshwater mortality and with a variance equal to that experienced in the ocean (Bradford 1995). Similarly, the available evidence suggests that both freshwater and marine factors are important in determining survival, and thus recruitment variability, of Atlantic salmon (reviewed by Friedland et al 1993). Comparable patterns in returns and ocean growth from widely disparate stocks indicate the importance of the marine environment in determining fish survival at a broad scale (Friedland et al 1993, Friedland et al 1996).

Bradford's (1995) conclusion that both freshwater and marine factors influence recruitment is consistent with Walters' (1988) observation that the lognormal distribution of salmon recruitment rates with many average or below average years punctuated by occasional strong year classes indicates that recruitment is the product of survival rates over both freshwater and marine life-history stages – all of which must be high to produce a strong year-class. Peterman et al (1998) examined 29 sockeye stocks in B.C. and Alaska for covariation in survival rates. The observed covariation between the two regions was due to variation in both freshwater and marine survival, whereas among

Fraser River stocks, marine survival rates were most important. Obviously, there is still a lot to be learned about the mechanisms underlying the various scales of variability in salmon recruitment. Both freshwater and marine mortality rates are high enough to be significant, and can have similar variances. What is clear, however, is that contrary to what traditional fisheries theory dictated, marine survival can be important in determining overall stock size.

Some of the strongest evidence for the importance of the marine environment comes from the SoG chinook and coho fisheries. Catches in both fisheries began to decline in the late 1970s, and low numbers continued until the mid-90s (Beamish et al 1995). Synchronous with catch declines were declines in the marine survival rate (MSR) of hatchery chinook and coho (from coded wire tag data (Beamish et al 2000) – indicating some change in the ocean ecology of the fish. There is also a growing body of evidence that since the decline began, the number of chinook and coho smolts entering the ocean remained constant or increased due to hatchery input (Beamish et al 1995), but the numbers returning fluctuated erratically (coho) or declined (chinook) (Beamish et al 1997). Similarly, Walters (1994) argues that the number of smolts entering the SoG must be approximately the same today as it was in the 1970s, as wild catch plus escapement would have declined by 50% if both smolt numbers entering the Strait and marine survival rates had declined. If the same number of smolts are still entering the Strait today, then it would appear that declining catches are the result of events taking place in the marine, rather than the freshwater, environment.

1.1.3 *Regime shifts and survival variability*

As to the actual source of variability in marine survival, a greater understanding may be obtained by examining the oceanic phenomenon known as 'regime shifts'. The idea of regime shifts first appeared in the oceanographic literature about 20 years ago, gaining momentum in the mid 1990s (Bakun 1999). The hypothesis is that in addition to variation on a daily, seasonal, or yearly scale, there are longer period variations in atmospheric and oceanic dynamics. The ocean environment is thought to undergo decadal scale changes that affect physical variables such as sea surface temperature (Mantua et al 1997), sea surface pressure (Trenburth and Hurrell 1995), and even length of day

(McCarthy and Babcock 1986). In the North Pacific, these shifts are thought to operate by affecting the intensity of the Aleutian Low, a low pressure atmospheric system that forms over this area in the fall of every year (Beamish and Bouillon 1993). Regimes with strong Aleutian Lows are characterized by intense cyclonic flow around the Alaskan Gyre, strong eastward transport of surface water, resultant downwelling along the coast from B.C. to California, causing upwelling of cool, nutrient rich water in the central North Pacific (Beamish 1993). Many fisheries scientists now believe that decadal-scale trends in fish abundance may be linked to these climate-ocean variations. A host of papers have been published showing correlations between a variety of different regime shift indices and salmon catches (Beamish et al 1995, Hare and Francis 1995, Beamish and Bouillon 1995, Beamish et al 1996, Mantua et al 1997, Hare et al 1997), survival rates (Peterman et al 1998, Beamish et al 2000), phytoplankton and zooplankton production (Sugimoto and Tadokoro 1997, Brodeur and Ware 1992), and the abundance of many other fish, bird and mammal species in the North Pacific (Beamish and Bouillon 1995, Benson and Trites 2001). The synchrony of population shifts by many different marine species is seen as evidence that large scale oceanic phenomena may be responsible. Furthermore, though small-scale impacts have been observed (King et al 1999), there is no evidence of synchronous large-scale climatic impacts in freshwater (Bradford 1999). What this implies is that instead of remaining constant, the carrying capacity of the ocean may fluctuate over time. This idea marks a drastic change in thinking about the ecology of salmon, and marine fauna in general. Large scale hatchery rearing of salmon in the Pacific Rim is premised on the belief that this practice circumvents freshwater limits on production. Evidence from the regime shift literature strongly challenges this ideology, indicating that hatchery additions may have no positive effect on adult abundance (and may in fact provoke density dependent interactions in the ocean) if ocean conditions are unfavourable.

1.1.4 *The importance of the early marine stage*

When juvenile salmon reach the coastal ocean, they enter a critical life-history stage. They feed intensively and grow much more quickly than in freshwater (98% of an individual's final weight is gained in salt water (Pearcy 1984)). Mortality rates of salmon

during their first few months at sea are much higher than later in marine existence (Parker 1965, Ricker 1976, Bax 1983, Furnell and Brett 1986). Much of this mortality may be due to predation (Cooney et al 1978). For example, birds and salmonids can remove up to 85% of smolts as they leave fresh water (Parker 1968). Empirical and modeling studies have demonstrated that marine mortality is highest immediately after ocean entry, with rates declining as fish grow larger (reviewed by Pearcy 1992). Most variability in marine survival occurs at this time as well (Peterman 1981, Bradford 1995). However, the causes of this mortality are poorly understood. Predation, starvation, and advective losses have all been hypothesized.

1.1.5 *Mechanisms of survival variability*

As the early marine phase represents a critical life history stage, factors affecting interannual variations in survival probably have their largest influence during the first year of coastal life (Peterman 1987, Francis and Hare 1994). However, hypothetical mechanisms whereby ocean conditions can influence survival during this stage are rare in the regime literature. The two most common mechanisms proposed are related to 1) differential predation (independent of size or growth) and 2) differential growth (via food limitation).

The differential predation hypothesis

The first mechanism posits a direct physical phenomenon (such as upwelling intensity) and/or variability in predator production as the causal forces behind changes in the distribution or availability of smolts to predators (Pearcy 1992). Hare and Francis (1995) argue that in Alaska, regimes with a warmer sea surface temperature (SST) lead to altered migration patterns, making salmon less vulnerable to predators. In British Columbian waters, Hinch et al (1995) hypothesized that SST can be used as a surrogate for predation pressure, for in warm years, non-resident predators move north while resident predators increase their foraging to meet higher metabolic needs -- both of which increase smolt mortality. Evidence to either support or refute these hypotheses, however, is not easily obtained. Determining the identity and relative importance of various predators on juvenile salmon actually is quite difficult. Chinook salmon, for which

predation on juveniles is best understood, are thought to have 2 principal predators – spiny dogfish and lamprey (Beamish et al 1992, Beamish and Neville 1995). Together, these species can cause considerable smolt mortality. However, neither of these predators have juvenile salmon as their principal prey – as might be expected from the seasonality of smolt availability. The few studies that have attempted to examine predation on smolts empirically (from gut contents of potential predators) have found either a diverse array of predators, or none at all (Healey and Jordan 1982, Pearcy 1992, Mortensen et al 2000, Orsi et al 2000) making it very difficult to properly test the hypothesis. Although Pearcy has deemed differential predation the most likely hypothesis for a climate-juvenile survival linkage, McFarlane et al (2000) believe it is unlikely that such a large scale response in population size could be due to predation pressure. They argue that synchronous basin-wide heavy feeding on salmon is unlikely.

The differential growth hypothesis

Shifts in indices of salmon production (catch and marine survival rates – see above) often mirror shifts in the timing or composition of phytoplankton and zooplankton communities (i.e. food for smolts). The differential growth hypothesis proposes a climate-induced, bottom up forcing of the ocean's capacity to support fish populations over time. This results in differential smolt growth in the early marine stage depending on ocean conditions. What this means for juvenile salmon is that the environment encountered upon marine entry today may be very different from the environment that existed even a year ago.

As for the mechanisms linking ocean conditions to survival, one possibility that has received considerable attention is the potential for environmental variability to result in changes in the prey field encountered by young salmon. Walters et al (1978) and Cooney (1993) modeled the relationship between salmon feeding and zooplankton production in the early marine stage. Both concluded that juvenile salmon feeding pressure has a minimal impact on zooplankton abundance (i.e. that prey abundance was likely not limiting salmon production). However, empirical evidence from otolith analysis (Neilson et al 1985) and field studies (Bailey et al 1975) suggests that food can indeed limit the estuarine growth (and therefore production) of juvenile salmon in the

field. Furthermore, foraging success appears to determine residence time in the estuarine environment (Healey 1980a, Simenstad and Salo 1980). Beamish and Bouillon (1993) propose that in regimes characterized by strong Aleutian lows (such as the current regime), upwelling intensifies in the central North East Pacific gyre, leading to high nutrient concentrations and copepod concentrations at Station P. The Subarctic Current may then transport the copepods and nutrients to the coast. Hare and Francis (1995) propose a similar scenario, with years characterized by a strong Aleutian Low and better feeding conditions in the central Alaskan gyre benefiting coastal juveniles as zooplankton-rich water is advected onto the shelf. Most convincingly, Gargett (1997) hypothesizes a link between the intensity of the Aleutian Low and coastal water column stability along the west coast of North America. She proposes that in British Columbia, reduced water column stability in years of strong Aleutian Lows is associated with coastal upwelling, high nutrient levels, higher levels of primary production, and ultimately higher production of zooplankton and fish. Differential timing of ocean entry could also affect growth in a match-mismatch scenario (*sensu* Cushing 1990). Anderson and Hinrichsen (1996) propose that smolt survival is determined by the degree of overlap between the timing of estuarine entrance and the date of the spring transition.

An interannual change in prey timing or composition could lead to differential survival of juvenile salmon in two ways – either predator-mediated or predator-independent. In British Columbia, years of weak Aleutian lows and warmer SST are associated with weak upwelling and poor production. Since lower food concentrations or food quality can reduce growth rates (Neilson et al 1985), predation rates could increase because smaller fish might be more vulnerable to predation (Hargreaves and LeBrasseur 1986, Miller et al 1988). However, to date, little has been done to explore interannual differences in early marine growth rates. Fisher and Pearcy (1988) found that growth rates of juvenile coho in Washington and Oregon were as high in low upwelling years as in high years. Condition factors, as well as stomach contents, were also the same under both conditions. Recently, Mortensen et al (2000) found interannual differences in the growth of tagged pink salmon smolts in Alaska.

One possible explanation for the lack of an interannual difference in growth rate in Fisher and Pearcy's (1988) study, is that some threshold rate may exist (the growth rate

necessary to achieve a minimum overwintering size, for example), beyond which additional growth confers few advantages. Instead, what may fluctuate (with changing juvenile density, predator abundance, or food supply) is the amount of time individuals must spend foraging to achieve this minimum growth rate (e.g. foraging arena theory; Walters and Juanes 1993). More time spent foraging leads to higher predation-based mortality in years of poor food availability or higher predator abundance.

Beamish and Mahnken (1998) have posited a predator independent mechanism relating food supply to survival. They believe that the freshwater stage is a 'safe refuge' for reproduction in that although egg-smolt mortality can exceed 99%, the numbers of smolts entering saltwater will always exceed the capacity of the marine environment to support them. As such, factors in the marine environment determine final abundance. They propose marine mortality can be broken into two stages – early summer predator-based mortality (as above), and late fall condition-based mortality. They believe that although early summer mortality can be extreme, adult abundance is ultimately determined by the number of juveniles that grow at a critical rate to reach a critical size by a critical period in late summer such that they can survive the winter. Thus, summer growth rate becomes the important factor, and is influenced by both competition and physical changes in the environment. Beamish and Mahnken (1998) hypothesize that for those juveniles which do not reach the critical size, causes of death are believed to be largely physiological. These fish are unable to maintain the minimum metabolic requirements and enter a growth trajectory that leads to death. Friedland et al (1993) supplied empirical evidence for this hypothesis. They found that return patterns for one stock were correlated with the intensity of the winter 'minimum' -- an index of overwinter stress. Further research by the same group has pointed at late summer growth as the determinant of overwinter survival (Friedland et al 1996a, Friedland et al 1996b).

1.1.6 *Long term variability in survival*

Hare and Francis (1995) have stressed the importance of determining causes of long-term survival variability, as opposed to 'normal' interannual variability. I have outlined the main hypothesized causes of such variability above, though it is probable that these causes contribute to short-term variability as well. Bradford's (1995) review of

all the available salmon survival data sets concluded that juvenile salmon experience roughly the same survival and variability in survival in freshwater and marine habitats. This conclusion may be biased by Bradford's use of data sets with limited temporal spans – a minimum of 2 years data was his criterion. This criterion may have resulted in 'within-regime' estimates of survival and associated variability. It is likely that the changes in survival that determine large shifts in abundance occur over the course of a couple of winters (regime shifts occur rapidly; Hare and Francis 1995), and are then followed by relatively steady survival for the course of the regime. Evidence from the regime shift literature reviewed above suggests that such survival changes are probably due to shifts in the marine environment, causing either differential predation or differential growth of the smolts. In this framework, freshwater survival rates remain centered about one mean and marine survival jumps between two or more means, depending on the regime. This pattern would not be detected in a study such as Bradford's (1995).

1.2 OTOLITHS IN FISHERIES SCIENCE

One obvious feature in the salmon literature is that the number of proposed mechanisms of differential survival are few, and the number of field studies are even fewer. Although researchers have investigated the early marine life of salmon since the 1960s, many key questions still remain unanswered. On the Pacific coast of North America, work has been done in Burke Channel (Lebrasseur and Parker 1964, Parker, 1965, Parker 1968), Nanaimo (Healey et al 1977a, Healey and Jordan 1982), Washington (Bax 1983), in the Oregon Production Area (Pearcy 1984, Nickelson 1986, Fisher and Pearcy 1988), and Alaska (Murphy et al 1987, Orsi et al 2000), among other places. However, many questions still remain about the growth and mortality in this critical period – how much does growth rate vary on seasonal, interannual, and decadal timescales? Do bigger fish always grow faster? How do the various methods of determining early marine growth compare? Are smaller (or bigger) fish preyed upon preferentially? The combined logistic problems associated with large population sizes and wide dispersal of populations have made these questions difficult to answer using traditional methodology (see Ch.2, 3).

New technology

Recent advances in otolith microstructural technology provide a promising new angle from which to tackle these and other questions. Teleost otoliths are the first calcified structures to appear during development (Campana and Neilson 1985), and appear long before hatch (Marshall and Parker 1982). The otolith core (also known as the primordia) is then successively surrounded by concentric layers of $CaCO_3$ and a proteinaceous matrix. Differential deposition of the two types of layers creates what are known as 'increments'. Panella (1971) was the first to demonstrate that increments are formed at a constant frequency of 1 per day. Although the otoliths of larval and juvenile fish are quite small (0.1 - 1.0 mm in diameter in salmon), careful preparation and light or scanning electron microscopy can reveal their microstructure patterns. Much as in tree rings, the age of young fish (in this case in days) can be determined by counting the number of increments present. When viewed under transmitted light the increments are seen as thin dark bands (the 'discontinuous' organic layer) alternating with wider light bands (the 'continuous' $CaCO_3$ layer) (Mugiya et al 1981). In older fish, daily increments become harder to distinguish; however age in years can still be determined by counting annual increments.

The width of each daily increment is often related to fish somatic growth (Campana and Neilson 1985, Paperno et al 1997), allowing for the reconstruction of daily growth rates in young fish (Ch. 2). Panella (1971) was also the first to realize that periods of physiological stress in a fish's life (hatching, first feeding, transition from fresh to salt water) cause 'checks', or discontinuities, in the daily increment sequence. These checks are regions of poor light transmission, and the opacity of the check is proportional to the degree of stress undergone (Panella 1980). Checks can aid in otolith interpretation by providing key landmarks in the fish's life history (date of hatch, date of marine entry) that are useful in measurement and interpretation (Campana 1983).

Unlike other structures that are used for aging fish (such as scales), otoliths have the advantage of being conservative (resorption of the $CaCO_3$ matrix does not usually occur (Jones 1992)). Although I will be using otoliths to back-calculate early marine growth rates, the potential uses of otoliths extend far beyond this application. Otoliths are essentially 'black boxes'; environmental recorders which can be used to extract a wide

range of environmental information. Fish which spend at least part of the year in different water masses incorporate specific trace elements into their otoliths, resulting in different elemental compositions, or 'fingerprints'. Otoliths can thus serve as environmental tags used to differentiate stocks in mixed populations (Campana et al 2000). Furthermore, otolith chemistry has been used in the determination of migratory pathways and the reconstruction of individual temperature and salinity histories (reviewed by Campana 1999). Microsampling of individual daily increments allows for a detailed chronology of the environment encountered by individual fish (Campana 1999).

1.3 OBJECTIVES

This study presents data collected during the first 3 years of a 4 year field investigation of juvenile salmon ecology in the Nanaimo area. In the chapters that follow, I will use a combination of smolt size data, and data from smolt otoliths to investigate growth and mortality in the early marine life history stage. As I shall show, such data are rare in the literature. This study marks one of the first uses of otoliths to investigate these processes in a field setting.

The choice of study area also makes this report unique. My data were collected at the site of a multi-year examination of coastal juvenile salmon ecology during the late 1970's (Healey et al 1977a, Healey 1982). In addition to providing a solid foundation on which to base our study, this choice of location allows for comparison of contemporary data with historical data from the 1970's. These are the first such comparisons that have been made at this temporal scale.

I chose to focus on chum salmon (*Onchorynchus keta*, hereafter chum), as they are the most common salmon in the Nanaimo River. Juvenile chum spend considerable time in the coastal environment after they enter the ocean and are second only to chinook salmon in their use of estuaries (Healey 1982, Simenstad and Wissmar 1984, Iwata and Komatsu 1984). The early marine mortality of chum is also highest among the 5 species of Pacific salmon (Bradford 1995), and as such they are ideal for examining processes which regulate variability in early marine growth and survival.

It is important to keep in mind that this study is just one component of a much larger study and will focus specifically on marine growth. Much of the other data

collected in the program (such as zooplankton data and smolt gut analyses) are therefore not presented herein. That information will be compiled and included in future publications.

1.4 CONCLUSIONS

In this chapter I have argued that salmon population fluctuations are related to ocean conditions encountered by the smolts in their critical early marine life history stage. Ocean conditions may cause survival variation via differential predation, differential growth, or both. Due to the limitations of traditional techniques, there have been few studies examining key issues related to early marine growth and mortality of salmon. In the chapters that follow, I will first provide empirical evidence that chum salmon otoliths can be used for such analyses. I will then use otoliths and other recently developed techniques to examine growth rate flexibility at seasonal, inter-annual and inter-decadal timescales. I will also address the questions of whether big fish grow faster, how traditional growth approximations compared to otolith-derived estimates, and whether size-selective mortality is important, all with respect to the first few months that smolts spend in the coastal environment. The results of these analyses are key to our understanding of this critical period.

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CHAPTER 2
Early marine growth of chum salmon in the Nanaimo area

2.1 INTRODUCTION

In the previous Chapter, I outlined two hypotheses – differential growth and differential predation – that have been proposed to explain variability in survival during the early marine life of salmon. I also stressed the fact that although both hypotheses make assumptions about early marine growth and mortality, few studies have directly examined either process in the field. In this Chapter, I will review the existing research on the early marine growth of salmon before presenting my field study of the subject.

Growth of salmon during the early marine period is often correlated with recruitment (Healey 1991), as larger fish often survive better than smaller fish (Bilton et al 1982, Healey 1982b). Indeed, there is ample evidence that growth during this stage may be key in determining adult population abundance (Friedland et al 1996, Mortensen et al 2000). However, very few *direct* estimates of early marine growth exist for salmon. Most studies have used apparent growth or mark-recapture techniques to estimate growth (LeBrasseur and Parker 1964, Ricker 1964, Table 2.5) – methods which are often quite inaccurate.

2.1.1 *Methods of early marine growth determination*

Traditionally, three methods have been used to determine Pacific salmon growth rate during the early marine stage (the first few months they spend in the ocean in spring and summer): 1) the apparent growth method, 2) the mark-recapture method, and 3) the 'hard parts' method.

The apparent growth method

The apparent growth method is the most common and the easiest, but also least accurate of the three methods. It involves sampling a given area multiple times (usually 3-4× a summer), and using changes in the mean lengths of captured fish to infer a mean fish growth rate for the population over the sampling period (LeBrasseur and Parker 1964). The underlying assumption is that the same population is being sampled over time

under a standard set of conditions. If different stocks with different growth characteristics are sampled, growth estimates will be inaccurate. Additionally, continual recruitment from freshwater to the population, and size-selective emigration of larger fish offshore can result in a sampling bias towards smaller fish, leading to growth rate underestimates. Nonetheless, as this method is simple (only size-at-time data are needed) it is still widely used. Locally, the method has been applied to juvenile salmon in Fitz Hugh Sound (LeBrasseur and Parker 1964), Nanaimo (Healey et al 1977b), the SoG (Phillips and Barraclough 1978), and Oregon (Pearcy 1984), among other areas.

The mark-recapture method

The mark-recapture method involves capturing and measuring juvenile fish just leaving freshwater (or very early in their ocean existence), tagging them (with coloured grit, coded wire tags, or fin clips), then recapturing and measuring them at a later date. As both the original and final lengths and time between captures are known, a growth rate can be calculated. This method is, however, very labour intensive. Given the size of some runs (tens of millions of fish), tens to hundreds of thousands of juveniles must be caught and marked, and the surrounding area must be intensively sampled to ensure sufficient recaptures. Mark-recapture has been used fairly often to estimate Pacific salmon early marine growth (LeBrasseur and Parker 1964, Healey et al 1977b, Pearcy 1984, Pearcy et al 1989, Mortensen et al 2000). One additional drawback of this method is that fish cannot be tracked individually. Growth rate is still calculated from a change in *mean* lengths over the time between captures. Individual fish growth rates are not calculated. In studies such as those of Healey et al (1977a), additional (and unquantified) error can also be introduced by the use of one mark to identify fish that have left the river over a period of several days. If, for example, a given tag is used to mark outmigrants on 3 or 4 consecutive days, then growth rates calculated upon recapture will incorporate 3-4 days of error. This results in the loss of considerable information about the way that individuals grow. Other concerns are tagging effects on growth, and size related mortality in the interim between mark and recapture. Thermal marking of the otoliths of different cohorts of hatchery fish is one promising alternative to marking the fish externally, and is

much more cost effective. Courtney et al (2000) have used this technique to estimate growth of juvenile chum in Alaska.

Methods using fish 'hard parts'

The 'hard parts' of fish (vertebrae, scales, otoliths) have been used in fisheries science for the aging of fish populations for more than 2 centuries (Henderstrom 1959 *in* Jones 1992). This is possible because these features grow incrementally, often adding increments (or layers) at an annual frequency (Beckman 1995). Additionally, the otoliths of many young fish produce increments on a daily frequency (Chapter 1). Cross sections of hard parts thus yield a time series of increments which can be counted to determine an age in days or years. More importantly, in scales and otoliths the width of each increment is often related to fish somatic growth rate (Campana and Neilson 1985). If the relationship between hard part size and fish size is determined, then fish size at the time of formation of a previous hard part increment can be back-calculated. Growth rate (in units of length day^{-1}) is described as:

$$G = (L_c - L_b)/ (T_c - T_b) \tag{2.1}$$

where T_c is the time (in days or years) of capture; T_b is the time (in days or years) at which a specified increment was laid down; L_c is the fish length at capture; and L_b is the back-calculated length of the fish at time T_b. The denominator in the expression is determined by counting increments from the specified increment to the outer edge of the otolith. One key advantage of the approach is that it doesn't require the assumption of linearity in fish growth. A number of points (one per increment) can be obtained for the same fish, allowing for the reconstruction of individual growth trajectories. Additionally, this technique leads to estimates of population growth based on *individual* fish growth rates, not sample means.

The scales of many young fish lay down increments (or circuli) every few days. Scale circuli have thus been used to infer early marine growth rates of salmon (Healey 1982, Friedland et al 1993, Mathews and Ishida 1989, Holtby et al 1990). The disadvantage of this technique is that when circuli are used in young fish the rates

obtained are only indices of growth. Like annuli (yearly scale increments), circuli in young fish are thought to be laid down at a fixed frequency. Unlike annuli, however, it is often difficult to assign individual circuli to a fixed date. Thus, growth indices calculated with the method are not easily converted to absolute growth rates (in units of length day^{-1}) and may not be comparable between populations. Age, genetic factors, feeding frequency, and photoperiod may also affect the production of scale structures (Blacker 1974, Bilton 1974). Furthermore, scales can easily be lost, and may be resorbed in times of stress, leading to biased growth values (Jones 1992).

Recently, otoliths have been used in much the same fashion as scales, but without some of the disadvantages of the latter method. As outlined in Chapter 1, otolith increments are generally formed every day. Growth rates based on fish-length: otolith-length regressions are not relative (as with scales), but absolute – an exact day can be assigned to each increment. In fact, growth rates can theoretically be determined for each day of a fish's life, based on the width of each corresponding increment. In practice, however, this level of detail is often impossible due to autocorrelation in widths between successive increments (Gallego et al 1996, Pepin et al, in press). Growth rates at a weekly frequency are more easily obtained, and not subject to this bias. As outlined in Chapter 1, otoliths also provide a more representative growth record than do scales; they are generally not resorbed under food deprivation or stress, and being internal structures they are not lost. Otoliths also offer greater resolution and precision than do scales, due to a greater frequency of formation. Furthermore, there is evidence that, for salmon, fish length : otolith size plots used in growth back-calculation give better fits than do fish length : scale radius plots (Jonsson and Stenseth 1977 *in* Neilson et al 1985).

2.1.3 *Differential growth and juvenile salmon survival*

In the previous Chapter, I outlined the differential growth and differential predation hypotheses that have been proposed to explain variability in survival during the early marine life of salmon. My study does not allow for an exploration of the latter hypothesis (since predators on juvenile salmon were not sampled). In this chapter, I will focus on several aspects of the differential growth hypothesis. A careful examination of this hypothesis yields several testable predictions.

If recruitment of Pacific salmon is related to early marine growth rate, then we would expect interannual differences in mean growth rates, with higher growth rates in high survival years and vice versa. In the lab, salmon otoliths have been used to show that higher food rations, or rations with higher quality food, can lead to higher fish growth rates (Volk et al 1984). However, with two exceptions (Fisher and Pearcy 1988, Mortensen et al 2000), field studies using apparent growth and mark-recapture techniques have failed to examine interannual growth differences. Fisher and Pearcy's (1988) findings that growth rates do not vary between years may lend support to the 'foraging arena' theory of Walters and Juanes (1994). Growth rates of juvenile salmon may be relatively inflexible; instead, individuals may moderate the amount of time they spend foraging such that they achieve a certain minimum growth rate (or size) required to overwinter. Individuals which do not meet this growth rate must take more risks while foraging, and are more likely to be eaten (and therefore less likely to be sampled). Alternatively, the lack of variability in growth rate may be due to the low statistical power typically involved in growth rate comparisons of this sort (see below). The question of whether growth rates can vary remains unresolved.

Differential timing of ocean entry may also lead to differential growth (and survival), as peak salmon outmigration can be 'matched' or 'mismatched' with peak abundance of their prey (in the manner of Cushing 1990). If differential timing of ocean entry between years is important in determining juvenile survival, then over the long term we might expect variability in average time of ocean entry, with years corresponding to a 'match' between peak outmigration and peak zooplankton abundance associated with higher survival. A number of studies have determined peak time of ocean entry (reviewed by Healey 1980b), but none have examined interannual variation in outmigration timing. Within years, we might also expect to see differences in early marine growth rates between late and early outmigrants, with fish 'matched' to zooplankton peaks growing faster than fish which aren't. Empirical evidence showing differences in growth between early and late outmigrants has been shown, though no consistent pattern has been recognized (Wilson 1990, Mortensen at al 1991, Volk et al 1995, Mortensen et al 2000).

Using otolith microstructure to study growth rates and early life history is a well established practice in the study of larval fish (e.g. Radke 1989), but few such studies

have examined early marine growth of salmon in the field. Nielson et al (1985) performed the first such study by using otoliths to examine the early marine stage of juvenile chinook salmon in the Sixes River Estuary, Oregon. By measuring individual increments over the estuarine residence of chinook, they found evidence that growth was food-limited in midsummer when juvenile abundance was high and benthic standing crop was low. Volk et al (1995) used otoliths from juvenile pink salmon in Alaska to show that earlier outmigrants grew more slowly, and formed increments with a lower periodicity than later outmigrants. To date, only one study has used otoliths to examine the early marine life history stage in chum salmon. Wilson (1990) showed that in Netarts Bay, Oregon, estuarine residence time was inversely related to the average back-calculated size at which juvenile chum entered saltwater. He also found that early outmigrants grew faster, possibly due to lower chum density and favourable water temperatures.

Clearly, salmon otoliths can be used to examine the early marine growth of salmon. However, the past 20 years have seen only 3 attempts to do so in the field. There remain many potential uses for otoliths in this area which have not been explored. In this Chapter, I will use otoliths to re-examine seasonal variability in growth and the relationship between growth, time of ocean entry, and size at ocean entry. I will also provide the first information on interannual variability in otolith-derived growth rates, and the relationship between apparent and otolith-based growth rates from salmon. My study includes a validation of the marine entry check in chum salmon. Additionally, the study also allows for a unique historical comparison between my data and historical data collected in the area in the mid 1970s (Healey et al 1977a, Healey 1982).

2.2 MATERIALS AND METHODS

2.2.1 *Study Area*

The Nanaimo River enters the Strait of Georgia on the east coast of Vancouver Island (49°8' N, 123°54' W, fig 2.1). The coastal Nanaimo area is dominated by the Nanaimo estuary, which is 9 km^2 in area (6 km^2 of which is intertidal mud flat). The mouth of the river lies at the south end of the estuary. Rain drives winter freshets; flows are lowest in the summer. Historically, four species of Pacific salmon have spawned in
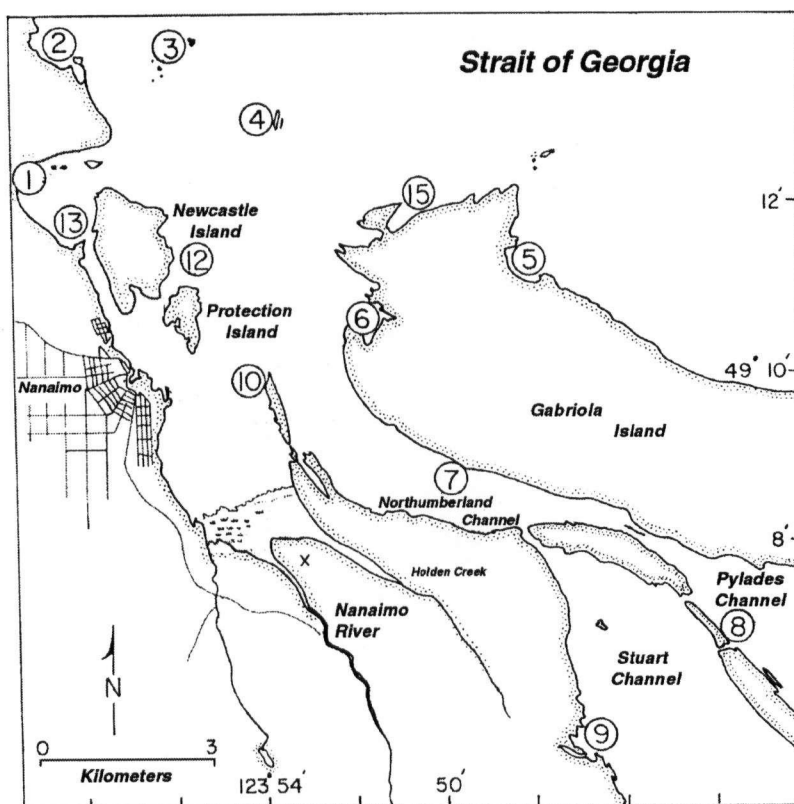
Figure 2.1 Study area for our juvenile salmonid sampling program, located on the central east coast of Vancouver Island. Numbers refer to sampling sites (see below). 'X' marks the site of my enclosure experiment. Map redrawn after Healey et al (1977a).

Station Number	Station Name	Years Visited
1	Biological Station	1999, 2000, 2001
2	Hammond Bay	1999, 2000, 2001
3	Five Finger	2000
4	Snake Island	1999
5	Lock Bay	1999, 2000, 2001
6	Descanso Bay	1999, 2000, 2001
7	Northumberland Channel	1999
8	Pylades Channel	1999
9	Boat Harbour	1999
10	Jack Point	1999, 2000, 2001
12	East Newcastle Island	1999, 2000, 2001
13	Departure Bay	1999, 2000, 2001
15	Pilot Bay	1999, 2000, 2001

the river: chum, chinook, coho, and pink; though no pink remain today (Patti McKay, Nanaimo River Hatchery, pers. comm.). Chum are most abundant by an order of magnitude. Adult escapement for the period 1987-1997 averaged 52 400, 1100, and 2100 for chum, chinook, and coho respectively (DFO 2000).

Adult chum return to the area in October/ November and spawn in the lower 8 km of the Nanaimo river (Healey 1979). In March to May the chum fry emerge from the redds and go directly to sea. Initially, the tidal mud flats at the mouth of the river are an important nursery area. Here fry spend a few days to a few weeks feeding intensively in waters less than a meter deep, before moving to deeper waters in Mid-May and June (Healey et al 1977a). Most of the local chum population is thought to move offshore in late June and July, though some may remain until fall (Healey 1980b). Healey's (1979) production estimates for the river were 52 and 30 million fry for 1975 and 1976 respectively. The Nanaimo Salmonid Enhancement Project, a small community run hatchery, has been adding chum (on the order of 500 000 fry), as well as smaller numbers of chinook and coho every year since its inception in 1979 (Patti McKay, Nanaimo River hatchery, pers. comm.). It is unknown what effect hatchery additions have had on the wild population. Nearby streams which empty into the Nanaimo estuary (e.g. Holden Creek, Fig 2.1) are also known to support small spawning populations of chum.

The coastal area of Nanaimo is considerably disturbed by human influences. The estuary has been an important site for log storage and handling for over 50 years, although log storage was halved (from 400 ha to 200 ha) in the 1980s (Mike Davidson, Nanaimo Port Authority, pers. comm.). As log booms may have negative effects on chum fry (McGreer et al 1984), it is possible that the amount of available fry habitat has changed considerably since Healey's study. Other human influences include a number of mills in the area (6 sawmills and 1 pulp mill), storm water outflows from Nanaimo city, a nearby landfill, agricultural runoff, and frequent ferry and boat traffic. All of the above influences have intensified with Nanaimo's population growth in the last 25 years (Mike Davidson, Nanaimo Port Authority, pers. comm.). The Nanaimo estuary is a shellfish no-take zone due to consistent high coliform counts.

2.2.2 *Field work*

The juvenile chum salmon used in this study were collected in the coastal Nanaimo area with a 250 m purse seine (1/4" mesh size) on the Department of Fisheries and Oceans vessel *Walker Rock*, a 13 m long seiner. An effort was made to sample the same nearshore stations as Healey et al (1977a) to facilitate comparisons with historical data. Thirteen, nine, and eight of Healey et al's stations were sampled in 1999, 2000, and 2001 respectively (Appendix 1). In 2000 and 2001 we sampled a smaller area more consistently. Sites most distant from our base near station 1 were not visited. For ease of comparison, I conserved Healey et al's original station numbers (fig 2.1). Five sampling trips were conducted each year, ranging from 2 to 4 days (see tables 2.1-2.3 for specific dates).

Seine sets were made in waters between 13 - 30 m depth and thus sampled the nearshore as opposed to estuarine or offshore habitats. When catches were small, all fish were dip netted from the purse and placed in a large plastic tub filled with seawater on deck. All salmon were kept, and unwanted bycatch released. When catches were large, a sample of at least 30 - 50 fish was taken from the plastic tub, or scooped directly from the purse seine, before the remaining fish were released. We made an effort to avoid bias in our choice of fish from large sets by physically mixing the catch before scooping. Our primary goal was to examine patterns of early marine growth, and so only in 2001 was an effort made to estimate total number of smolts caught each set. Once onboard, smolts were immediately anaesthetized with carbonic acid (600 mg L^{-1}) and then fixed in 5% formalin in mason jars to ensure preservation of gut contents. We injected the guts of larger smolts with formalin before placing them in jars. Other studies have indicated that long term, the acidic nature of formalin degrades the $CaCO_3$ structure of otoliths (Butler 1992). To avoid this, smolts were rinsed and transferred to 95% ethanol for storage within 24-48 hours of capture.

After each successful set (i.e. each set in which salmon were captured), physical data and zooplankton data were collected on station. We obtained vertical profiles of conductivity, temperature, and depth from surface to bottom. A combination of internally recording Inter Ocean® S4 current meters (1999-2001) and a Seabird® SBE 19 CTD (2001) were used for the profiling and were lowered at 0.5 to 1 m/s.

2.2.3 *Lab work*

Smolt measurements

Smolts from 1999, 2000, and 2001 were identified to species in the lab following Phillips (1977) and Pollard et al (1997). As the preserved fish had often lost pigment and had brittle fins, it was often necessary to examine gill rakers to distinguish pink from chum. Pink have many long, narrow rakers, whereas chum gill rakers are fewer and stubbier (Phillips 1977). All collected fish were measured with a custom ruler (fork length, to nearest 1 mm) and weighed (after blotting excess moisture, to nearest 0.01g) within a year of capture. To evaluate the importance of shrinkage due to preservation, 30 fish were measured fresh, measured and weighed every day for a week following capture, then measured once a week for a month. Data indicated that shrinkage in length of preserved fish was most pronounced in the 2 days following capture, and did not exceed 1 % of initial length. As all fish were preserved using the same method, and all were measured a week after capture at the earliest, I have not corrected any lengths or weights in the analyses for shrinkage. Furthermore, I have chosen to follow LeBrasseur and Parker's (1964) assertion that lengths of formalin-preserved salmon approximate live lengths without correction. The length and weight measurements thus taken were used in the calculation of apparent growth (see below).

Otolith measurements

I re-measured and weighed 10 randomly chosen chum from each successful set in 1999 and 2000 for the otolith analyses. Owing to time constraints, fish from 2001 were not used in these analyses. Sagittal otoliths (the largest of the three pairs of otoliths in Pacific salmon) were removed. Otoliths were brushed clean, and stored dry in capped individual microtubules. I used only otoliths removed from the left ear for the analyses, as left and right salmon otoliths can differ in dimensions (Neilson and Geen 1982). When left otoliths were degraded, as was the case with many of the 1999 fish (2000 and 2001 otoliths were removed much closer to the date of capture, and thus spent less time in formalin), I chose more fish at random from the given set to yield approximately 10 fish from each set.

Otolith microstructure was examined following the basic methodology of Zhang and Beamish (2000). A maximum of one week prior to viewing, left otoliths were "cleared" by adding a drop of immersion oil or glycerin to reduce opacity (Secor et al 1992). I then affixed each otolith, sulcus (medial) side up, to a glass side with thermoplastic cement. Otoliths were ground by hand with 3M Imperial® lapping film: I used 30 μm grit film to grind to a plane where the primordia were clearly visible, before polishing with 3 μm grit film. Larger otoliths had a more opaque matrix and needed further processing. Slides were heated to melt the fixative, otoliths were turned over (sulcus side down), and once again ground to the primordial plane. To increase the refractive index, I placed a drop of immersion oil on each otolith (Secor et al 1992) and then viewed them at 40 to 1000× using a Leica® DM LS compound light microscope. Planachromat objective lenses ensured a flat field of vision. A Sony® CCD-IRIS high resolution video camera, a black and white Scioncorp frame grabber board, and Scion Image® (a PC image analysis package) were used to sharpen, enhance contrast, and to make all desired measurements. Electronic images of most otoliths were also archived.

Six different measurements were made on each otolith: 1) total otolith length from antirostrum to postrostrum (OL, fig 2.2a, 40×), 2) distance from longtitudinal axis of the primordia to dorsal edge (otolith radius, OR, fig 2.2b, 200×), 3) distance from the same axis to the marine entry check (marine entry radius, MR, 200×), 4) distance from the marine entry check to the dorsal edge (width of the marine zone, MW, fig 2.2c, 200×), and the width of the 5) first and 6) last 7 increments in the marine zone, when possible (fig 2.2d, 400×) (autocorrelation in increment widths is minimized in groups of 7 or more increments (Campana and Neilson 1985). Although the shortest of the radii, the dorsal radius was chosen as it generally has the clearest increments, and tended to preserve well even when the rest of the otolith was degraded. Salmon otoliths have multiple primordia and measuring the otolith radius from the axis of the primordia is standard procedure (Zhang and Beamish 2000). This axis was determined by eye. Repeated measurements of individual otoliths indicated that measurement error was negligible.

Increment counts were made from the marine entry check to the otolith edge. It was often necessary to make counts on several axes in order to avoid cracks and regions
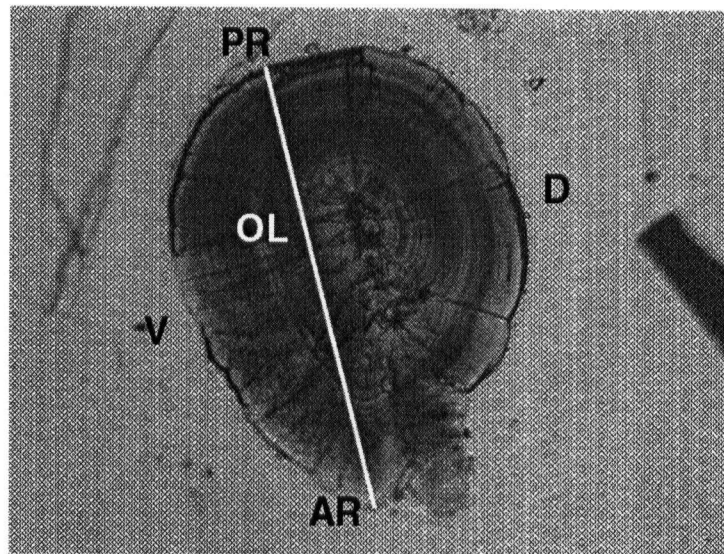
Figure 2.2a Left sagittal otolith of a chum smolt caught in Nanaimo, 1999
Total otolith length (OL) from antirostrum (AR) to postrostrum (PR).
Note characteristic dorsal (D) and ventral (V) morphology (40X mag.)
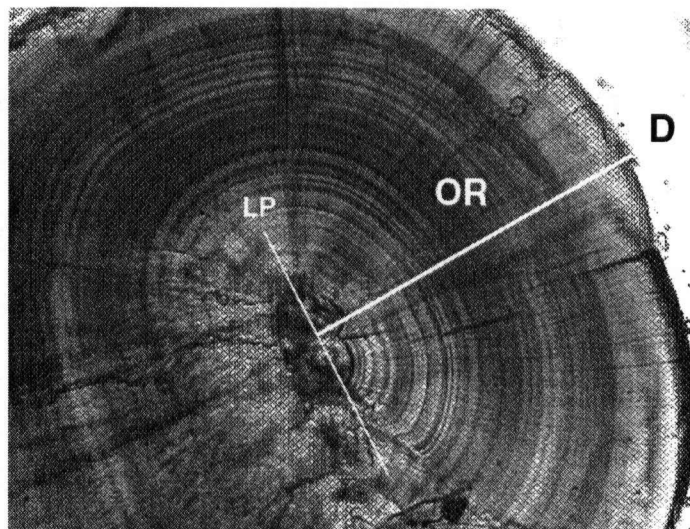
Figure 2.2b Otolith radius (OR) of the same otolith measured from the
longtitudinal axis of the primordia (LP) to the dorsal edge (D) (100X)
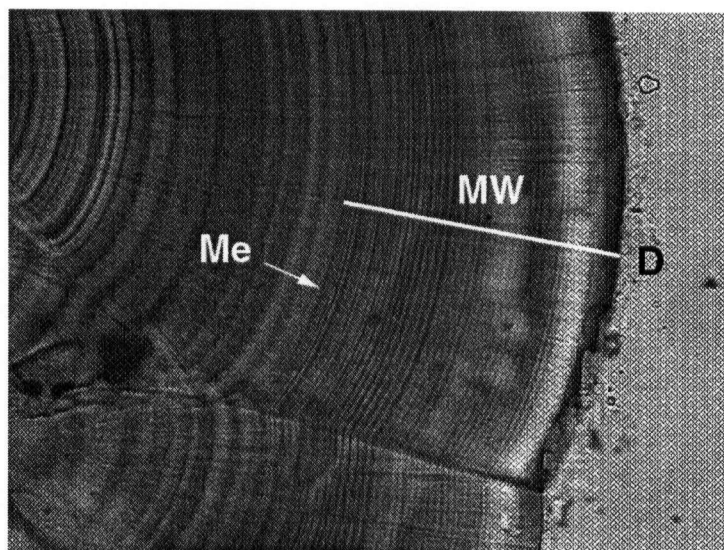
Figure 2.2c Marine zone width (MW) of the same otolith, measured from the marineentry check (Me) to the dorsal edge (D) (200X)
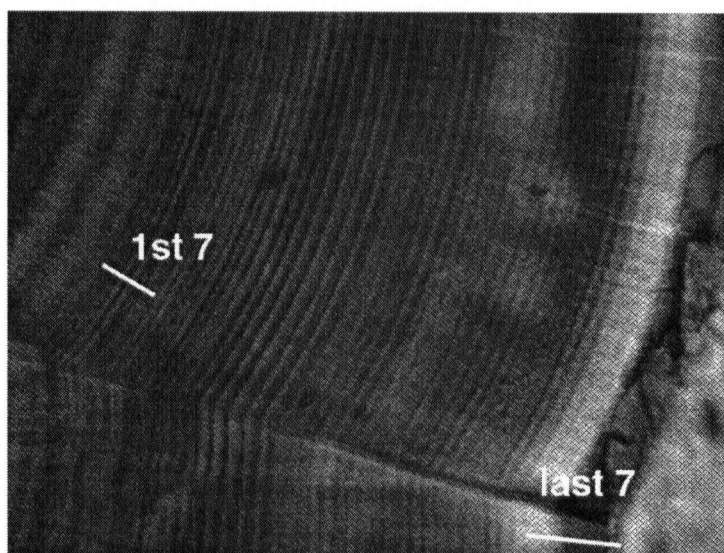
Figure 2.2d Width of first (1st 7) and last seven (last 7) marine increments on the same otolith (400X). This smolt has been in saltwater for 48 days (there are 48 increments in the marine zone.

of opacity. I found it useful to raise and lower the plane of focus to distinguish daily increments (which remain visible in all planes) from sub-daily increments (which disappear when the surface layer is slightly out of focus). The "edge effect", or propensity for light to refract at the edge of the otolith sometimes made counting increments at the edge difficult. Usually, a combination of the two above strategies – examining multiple axes and adjusting focal height – was effective in reducing the edge effect. In very old or very large otoliths (especially from 1999), where opacity was a problem, I interpolated increments if numbers of interpolated increments were small (less than 5). Otherwise the otolith was discarded. All otoliths were read a minimum of two times consecutively, or until I was satisfied that the counts were reproducible. To obtain an estimate of operator error, I had an inexperienced reader record the marine entry check, measurement of MR, and increment counts on 30 randomly chosen otoliths. I then measured these same 30 otoliths and compared our two sets of measurements.

2.2.4 Analyses

Length based growth

For most of the analyses that follow it was convenient to assume that all chum caught in the Nanaimo area were Nanaimo River fish, and formed an isolated Nanaimo area population. Strictly speaking, this was probably not the case. Sockeye and pink smolts, species which do not spawn in the Nanaimo River, have been caught in the area (Healey 1982, present study). This raises the possibility that non-local chum smolts were also caught in the study as well. Secondly, neighbouring creeks (such as Holden Creek, fig 2.1) with small spawning populations of chum empty into the Nanaimo estuary. Finally, our large early catches in Descanso Bay (which lies across the fast-flowing Northumberland Channel from the mouth of the Nanaimo River) indicate that chum from this area may be early outmigrants from a nearby system. Nevertheless, the majority of the fish we caught probably originated from the Nanaimo River, and it was therefore assumed that outside influences were negligible. For comparisons with historical data, we made the further assumption that we sampled the same stock as Healey did in the mid 1970s.

For each year, a linear regression was built between average fork length of chum caught on trips 1...n (L1...Ln; dependent variable) and sampling date (independent variable). The slope of this regression represented the change in mean fork length over time, and was taken as an estimate of the apparent growth rate of an average fish in the population (in cm/ day). Within years, the logarithm of fish weight was regressed against the logarithm of fork length to develop a linear weight-length relationship.

I followed Phillips and Barraclough (1978) in calculating instantaneous growth rate from:

$$G_w = (\ln W_n - \ln W_1)/ (T_n - T_1) \tag{2.2}$$

Where W_n = fish weight at the time of the final sampling date (T_n). This was calculated by converting the regression determined fork length at this time (as determined from the fork length : time regression) to fish weight using the weight-length regression

W_1 = fish weight at the time of first sampling (T_1), calculated in the same manner as above.

T_n = the date of the last sampling trip (Julian day)

T_1 = the date of the first sampling trip (Julian day)

To transform this to a growth rate in % body weight day^{-1}, instantaneous growth rates (G_w) were converted as:

$$\%W\ day^{-1} = (e^{G_w} - 1) * 100 \tag{2.3}$$

To facilitate comparison, growth rate data from older studies (Phillips and Barraclough 1978, Healey 1982) were re-plotted, and slopes compared to my data using analysis of covariance (ANCOVA, Zar 1984).

Otolith based growth

i) validation

In this study, 4 relationships needed validation before I could extract data from otoliths with confidence: 1) increment deposition rate, 2) the relationship of somatic to otolith growth, 3) environmental and physiological effects on deposition, and 4) formation of the marine entry check. Fortunately, much of the groundwork had been done. There is good evidence that otolith increments are laid down daily in Pacific salmon (Wilson and Larkin 1980, Marshall and Parker 1982, Neilson and Geen 1982). There have, however, been studies describing subdaily increment formation (Neilson and Geen 1982, Volk et al 1995). To validate the periodicity of increment formation in juvenile chum, I built an enclosure in a saltwater pool near the mouth of the Nanaimo River. Approximately 100 hatchery chum fry (obtained from Patti McKay, Nanaimo River Hatchery) were marked by immersion in alizarin complexone (2 hours at 150 mg L^{-1}), a fluorescent compound that adheres to fish otoliths (Blom et al 1994, Thomas et al 1995). Fish sacrificed immediately after immersion displayed a characteristic mark on the outer edge of their otoliths when viewed under fluorescent light. Fish sacrificed 6 days post immersion (n=30) displayed a bright otolith band close to, but not at the otolith edge, when viewed under the same conditions. Under transmitted light, the region of fluorescence corresponded to a darker 'check', followed by an average of approximately 5 more distal increments. This was taken as a validation of daily increment formation, for at least the first 6 days of oceanic life. I had planned a longer validation period, but unfortunately my enclosure was vandalized and all the fish swam away.

Good evidence exists that otolith growth is related to somatic growth (Volk et al 1984). In this study I have inferred the relationship between fish growth and otolith growth from the strong relationship between fish length and otolith length (see Results). Although Marshall and Parker (1982) documented temperature stress effects on deposition rate in the lab, I assumed that stress effects on deposition rate were negligible.

The marine entry check (ME)

Also necessary for this study was the ability to assign one increment as corresponding to the fish's first day in the ocean. All subsequent measurements and counts were performed in relation to this feature. A number of researchers have remarked on the coincidence of marine entrance with a dark check on the otolith (Volk et al 1984, Neilson et al 1985). Others have defined marine entry as the point after which increments get visibly wider (Neilson et al 1985) or clearer (Volk et al 1995), and have hypothesized that better growth in the ocean leads to these conditions. Figure 2.3a demonstrates the early, finely spaced freshwater increments deposited around the primordia in a chum smolt from 1999. Figure 2.3b shows a more distal view of the same otolith. The ME check is marked by the clear transition to more widely spaced increments representing marine growth. I have provided a solid validation of the ME in Pacific salmon by conducting the otolith marking experiment detailed above. The dark check coincident with the fluorescent alizarin mark was laid down on the day following transplant from the freshwater raceways of the hatchery to the saltwater enclosure.

Despite this, the ME was still sometimes difficult to identify. Otoliths from hatchery fish raised in freshwater, and wild fish trapped in freshwater near the mouth of the river (obtained from Marc Shepherd, PBS, Nanaimo), were used to visually characterize pre-marine entry fish. The marine entry check was observed directly in fish used in the enclosure experiment. A second opinion on some of the more difficult otoliths was made by Ziyang Zhang (PBS, Nanaimo). As all chum enter the marine environment soon after emergence, and at a similar size (Healey et al 1977a), the ME should appear at a similar distance from the primordial axis on all otoliths, with relatively small standard deviation. Additionally, as most growth occurs in the ocean as opposed to freshwater (Pearcy 1984), the width of the hypothesized marine zone should be positively correlated to fish size. Both predictions were tested in order to be confident in the ME.

ii) Growth

Two steps were taken in order to derive growth rates from otoliths. First, linear regression was used to establish a relationship between otolith radius and fish length.
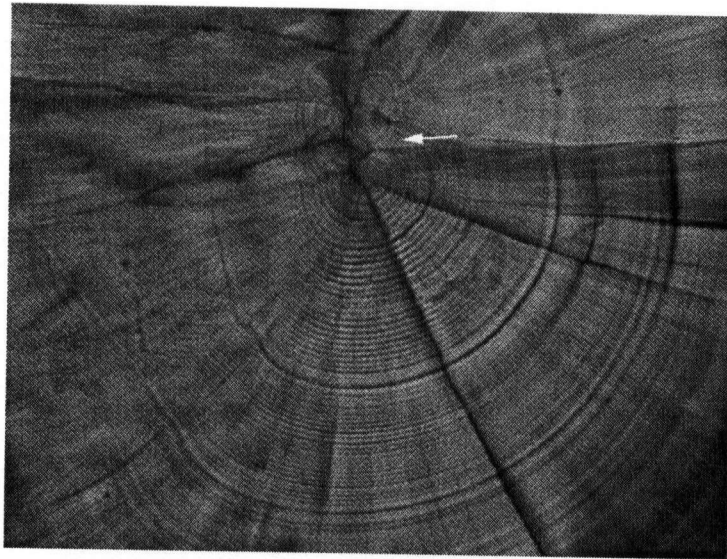
Figure 2.3a Otolith primordia (white arrow) surrounded by narrow freshwater increments
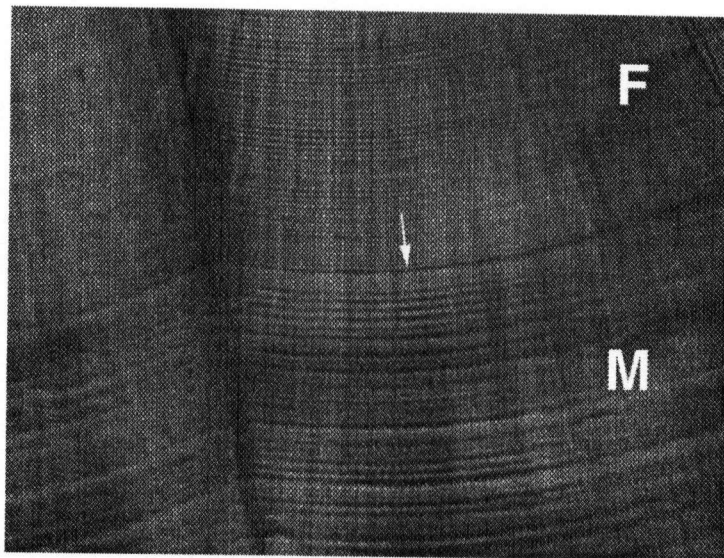
Figure 2.3b The freshwater(F)-marine transition(M). White arrow indicates marine entry check

Then, a back-calculation technique was used with the regression to estimate fish length at the time of ME check formation (i.e. the time of marine entry).

There are at least 9 back-calculation techniques that have been used in the literature (Francis 1995). Choice of technique is important, as each makes its own implicit assumptions about the growth of fish. Thus different techniques can give different back-calculated growth rates (reviewed by Francis 1990). Whitney and Carlander (1956) introduced what Francis (1990) called the "two competing hypotheses for back-calculation". The body proportional hypothesis (BPH) assumes a constant proportional deviation from mean body size throughout the life of the fish. Thus, "if a fish at time of capture were 10% smaller than the expected length for that size of scale (or otolith), the fish would be 10% smaller than the expected length for the size of that scale (or otolith) throughout life" (Whitney and Carlander 1956). The BPH back-calculates length at marine entry (L_m) as:

$$L_m = [(c + dO_m)/(c + dO_c)]L_c \qquad (2.4)$$

Where O_m = otolith radius at marine entry

O_c = otolith radius at time of capture

L_c = fork length at time of capture

c, d = y-intercept and slope, respectively, of fork length on otolith radius regression

Similarly, the scale (or otolith) proportional hypothesis (SPH) assumes a constant proportional deviation from mean size of the scale throughout life. The SPH back-calculates L_m as:

$$L_m = - (a/b) + (L_c + a/b)(O_m/O_c) \qquad (2.5)$$

Where a, b = y-intercept and slope, respectively, of otolith radius : fork length regression

Note that equation (2.4) uses a regression of fork length on otolith radius and equation (2.5) uses the opposite. Francis (1990) has recommended using a combination of body-

proportional (BPH) and scale-proportional (SPH) methods to back-calculate lengths at age.

The Fraser-Lee technique, most common of the back-calculation techniques (Francis 1995), has also had strong criticism leveled against it. Campana (1990) has noted its use of an incorrect regression intercept and Francis (1990) claims that the technique is based on a "misunderstanding of the role of regression". I have therefore chosen to follow Francis' suggestions (1990, 1995) and avoid these problems. The added benefit of using two back-calculation techniques is that the difference between these two estimates for each otolith represents a minimum measure of the imprecision of back-calculation (Francis 1990). This is an important term, rarely provided in studies of this type.

In a similar manner to equation (1), otolith-based growth rates were calculated as:

$$G_O = (L_c - L_m)/ (T_c - T_m) \tag{2.6}$$

Where $T_c - T_m =$ The day of capture minus the day of marine entry, or the number of increments (days) from the ME to the otolith edge.

Resultant growth rates were in cm day^{-1}. These rates were converted to instantaneous growth in weight and % body weight increase day^{-1} as per equations (2.2) and (2.3).

2.3 RESULTS

Chum smolts were caught from mid-April to late July in the summers of 1999-2000 (Appendix 1). Earliest catches were at Descanso Bay. Numbers of fish sampled at other stations tended to increase to a peak in mid-May, remained high until early June, after which they decreased. These catches are rough indicators of abundance, however, as no effort was made to record total catch in 1999 and 2000. Smolts were rare in the Nanaimo nearshore by early-July. No smolts were caught on the first trip of 1999, more likely due to our inexperience than an absence of fish.

Within years, data was averaged over stations to provide Nanaimo area population trends for each of the three years (Tables 2.1-2.3). Mean lengths and weights of captured chum smolts tended to increase over the sampling period, as did mean surface

temperature (0-10m). Within all three years there were significant differences in median fork lengths between trips (Kruskal-Wallis 1 Way ANOVA on Ranks, $p < 0.001$). In 1999 fork lengths from each trip differed significantly from every other (Dunn's Method of multiple comparison for unequal sample sizes, $p < 0.05$). In 2000, the last three trips did not differ from each other, and in 2001 trip 4 did not differ from trip 2, and trip 3 did not differ from trip 1 (Dunn's method, $p > 0.05$), but all other comparisons were significantly different (Dunn's method, $p < 0.05$). Success ratio (the number of sets in which chum smolts were caught relative to the total number of sets made) was used as a rough index of dispersal of the population. This ratio tended to increase to a maximum in mid-May to early June (tables 2.1-2.3), indicating that when abundance was high in the area, so was dispersion. Mean salinity followed no clear pattern, and was most likely related to tidal cycle, rather than time of year. Due to recurring technical problems with the CTD, our temperature (fig 2.4) and salinity data were rather patchy. More consistent CTD data for nearby Nanoose Bay were obtained for 1975, 1999 and 2000 (from Ron Perkin, IOS, Sidney), and showed similar patterns (fig 2.5). One-way ANOVA was used to compare the three years of Nanoose data. Average surface water temeratures were significantly warmer in April (Tukey test, $p = 0.013$) and June (Tukey test, $p < 0.05$) of 2000 than 1999. The summer of 1975 had by far the coolest surface waters of the three years (mean = 11.6 °C). Average summer surface water temperature was cooler in 1999 (mean = 12.4 °C) than in 2000 (mean = 12.9°C).

Slopes of weight-length relationships for each year differed significantly (table 2.4; ANCOVA, $p < 0.001$). Slopes from each year differed from every other year (Tukey test, $p < 0.001$). Such slopes are often taken as an indicator of fish condition. Years with a steeper weight : length relationship indicate years in which, on average, fish were heavier for a given length (possibly due to food supply). In the Nanaimo area, overall juvenile condition was highest in 2001, and lowest in 1999.

Notable in the fork-length frequency distributions of chum caught in all three years (figures 2.6-2.8) was the right skew from the early spring until mid-May/ early June. By July, fish were larger and distributions tended to be closer to normal or skewed to the left (Trip 1, 2001).

Table 2.1: Summary statistics for juvenile chum from Nanaimo caught in 1999. Success ratio, a rough index of dispersal, is the ratio of sets in which chum were caught : the total number of sets performed in a trip. Mean catch is the mean number of fish captured in a successful set. Mean L is the mean fork length (in cm) of all fish captured on a given trip. Mean W is the mean weight (in grams) of all fish captured on a given trip. Both Mean length and Mean weight are followed by their respective standard deviations, and ranges, in the same units. Mean temperature and mean salinity values were calculated by averaging surface values (upper 10m) obtained from CTD hauls across stations.

Trip	Dates	Total catch	Success Ratio	Mean catch	Mean L (cm)	SD	Range	Mean W (g)	SD	Range	Mean temp (°C)	Mean sal
1	April 26-29	0	0 of 8	0.0	-	-	-	-	-	-	10.6	27.5
2	May 17-19	1042	7 of 8	130.3	6.7	1.2	3.6 - 10.7	2.75	1.52	0.30 - 9.59	10.2	27.1
3	June 7-10	852	8 of 9	94.7	7.7	1.3	4.8 - 11.6	3.96	2.15	0.85 - 13.25	11.9	26.3
4	July 1-3	161	7 of 9	17.9	8.7	2.0	5.4 - 14.8	6.37	5.52	1.21 - 31.30	12.9	24.3
5	July 26-28	72	10 of 11	6.5	12.0	2.3	5.1 - 17.8	16.02	11.24	4.41 - 57.95	16.4	21.8

Table 2.2: Summary statistics for fish caught in 2000

Trip	Dates	Total catch	Success Ratio	Mean catch	Mean L (cm)	SD	Range	Mean W (g)	SD	Range	Mean temp (°C)	Mean sal
1	May 2-3	236	4 of 5	47.2	5.3	1.3	3.4 - 9.7	1.32	1.19	0.16 - 6.76	-	-
2	May 15-17	387	4 of 4 (4 acid)	96.8	5.6	0.9	3.6 - 9.6	1.50	0.98	0.34 - 7.45	12.3	24.9
3	June 2-3	172	9 of 9	19.1	7.5	1.3	4.4 - 11.2	3.46	2.04	0.56 - 10.8	-	-
4	July 1-2	53	5 of 6	8.8	7.6	1.3	5.8 - 11.2	3.28	1.82	1.29 - 8.4	16.9	24.4
5	July 10-12	31	1 of 9	3.4	9.0	1.4	6.8 - 11.9	6.66	3.39	2.3 - 13.6	16.3	24.7

Table 2.3: Summary statistics for fish caught in 2001

Trip	Dates	Total catch	Total sample	Success Ratio	Mean catch	Mean L (cm)	SD	Range	Mean W (g)	SD	Range	Mean temp (°C)	Mean sal
1	April 17-18	104	104	3 of 7	14.9	5.5	0.8	4.0 - 7.8	1.14	0.66	0.33 - 3.34	9.6	29.3
2	May 1-2	60	60	2 of 8	7.5	6.3	1.4	3.6 - 9.0	2.19	1.34	0.31 - 6.70	10.0	29.3
3	May 14-15	2397	484	7 of 7	399.5	5.9	1.3	3.8 - 10.2	1.99	1.68	0.41 - 11.03	-	-
4	June 4-5	419	418	8 of 8	52.4	6.6	1.0	4.9 - 11.9	2.24	1.38	0.59 - 12.54	-	-
5	July 4-5	34	120	6 of 8	4.9	10.1	1.4	7.0 - 13.2	10.17	4.29	2.64 - 22.04	17.7	22.6
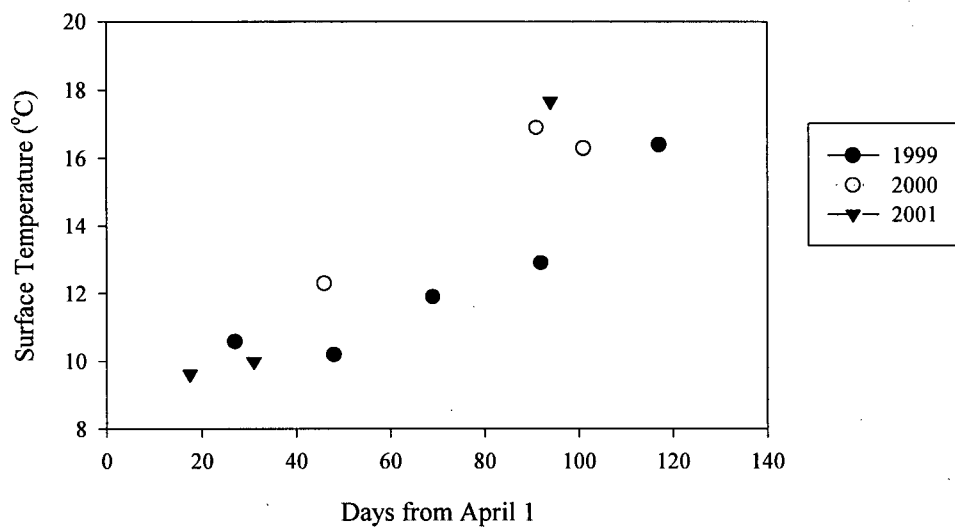
Figure 2.4 Mean surface temperature (upper 10m) of Nanaimo area waters, 1999-2001,
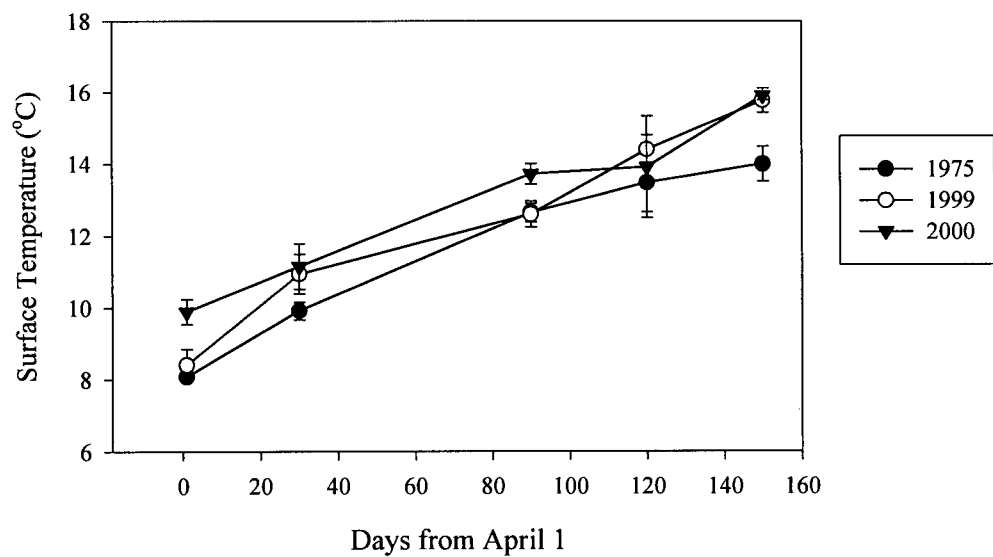
Fig 2.5 Mean surface temperature (upper 10m) of Nanoose Bay, near Nanaimo for 1975, 1999, and 2000. Error bars represent standard error.

Table 2.4 Summary of growth data for juvenile chum salmon in the Nanaimo area, 1999-2001

	1999	2000	2001
Apparent growth in length (cm day^{-1})	0.072	0.052	0.054
Apparent growth in weight (% body weight day^{-1})	2.48	2.40	2.61
Slope of log length- log weight rel. (condition)	2.92	3.09	3.31
Otolith based growth in length (cm day^{-1})	0.084	0.076	-
Otolith based growth in weight (% body weight day^{-1})	3.91	3.86	-
Average length at marine entry (cm)	4.48	3.97	-

Trip 2 May 17, 1999 (n = 1042)
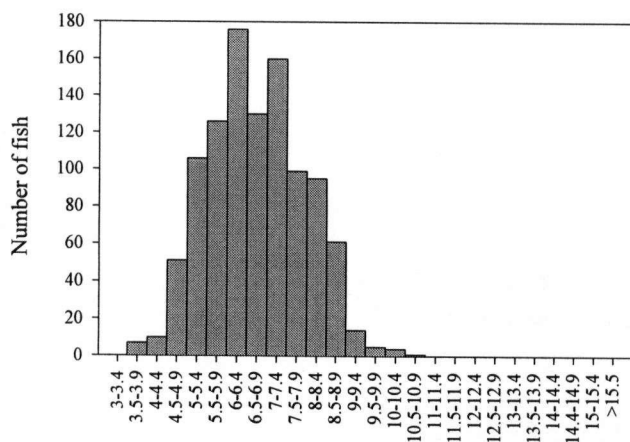
Trip 4 July 1, 1999 (n = 161)
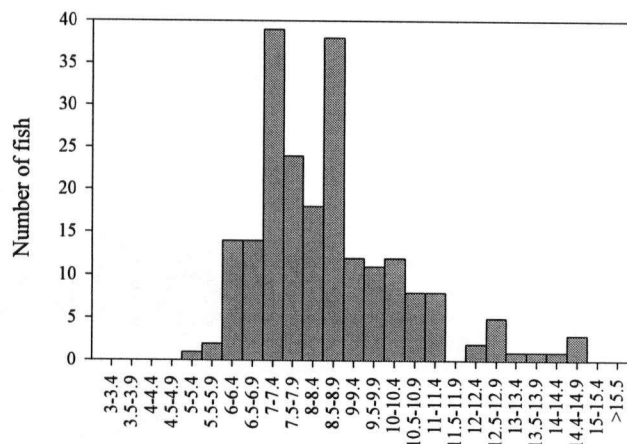
Trip 3 June 7, 1999 (n = 852)
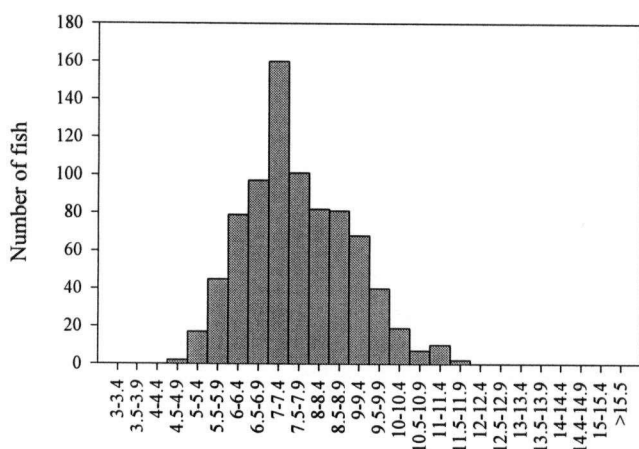
Trip 5 July 26, 1999 (n = 72)
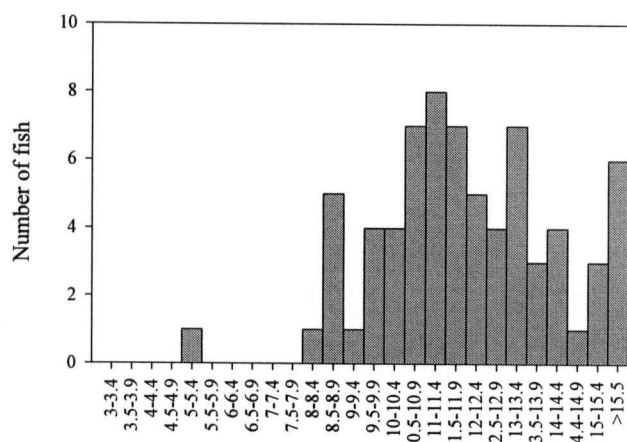
Fork Length (cm)

Fork Length (cm)

Figure 2.6 Length frequency histograms for Nanaimo area chum caught in 1999
Length classes of fork lengths on x-axis; number of fish on
y-axis. No chum were caught in Trip 1 (April 26-29) 1999.

Trip 1 May 2, 2000 (n = 236)
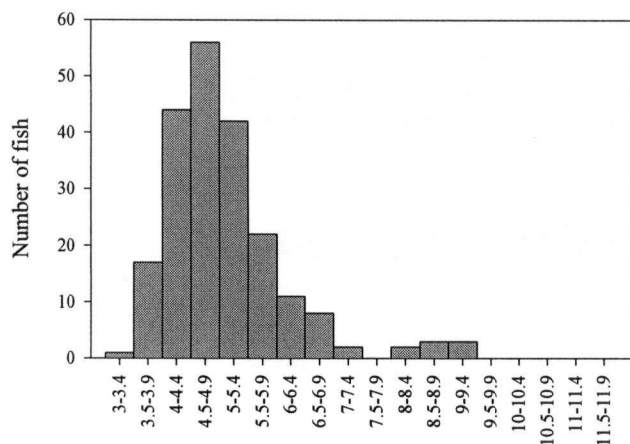
Trip 4 July 1, 2000 (n = 53)
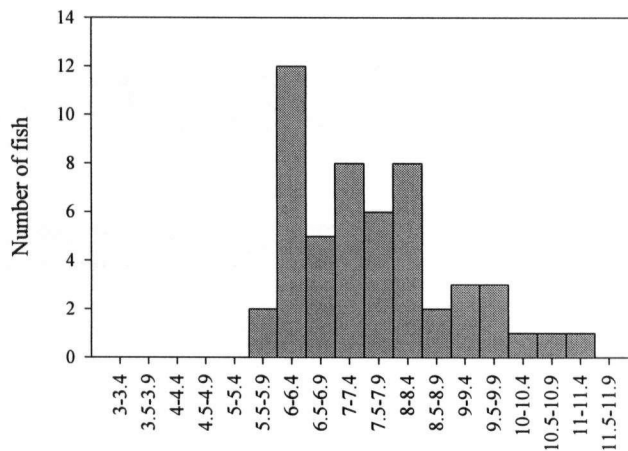
Trip 2 May 15, 2000 (n = 387)
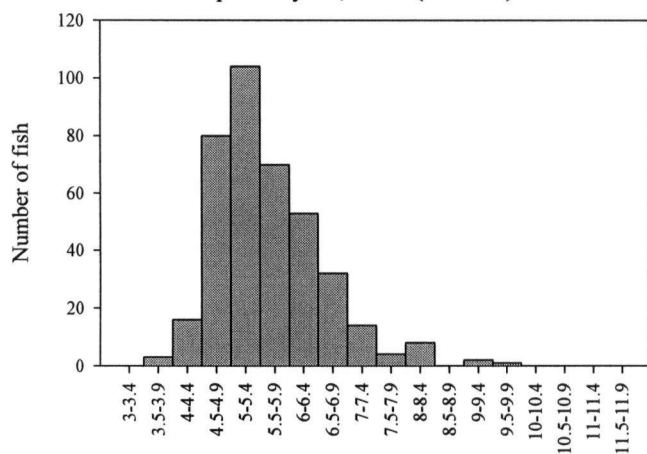
Trip 5 July 10, 2000 (n = 16)
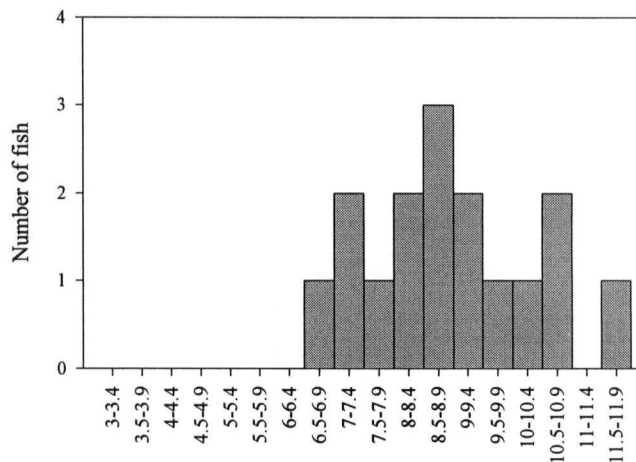
Fork Length (cm)

Trip 3 June 2, 2000 (n = 172)
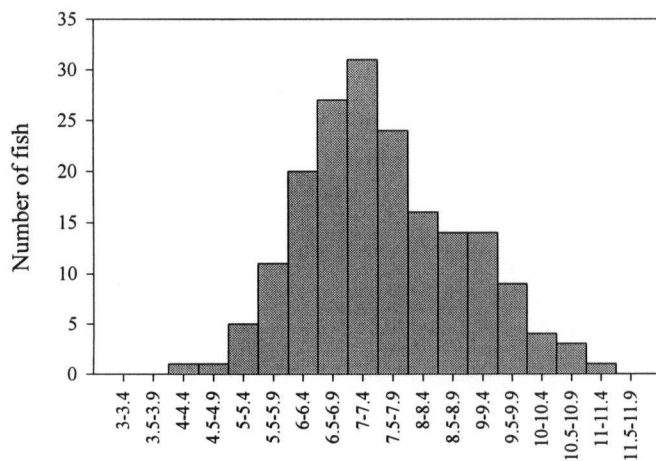
Figure 2.7 Length frequency histograms for
Nanaimo area chum caught in 2000.
Length classes of fork lengths
on x-axis; number of fish on y-axis.
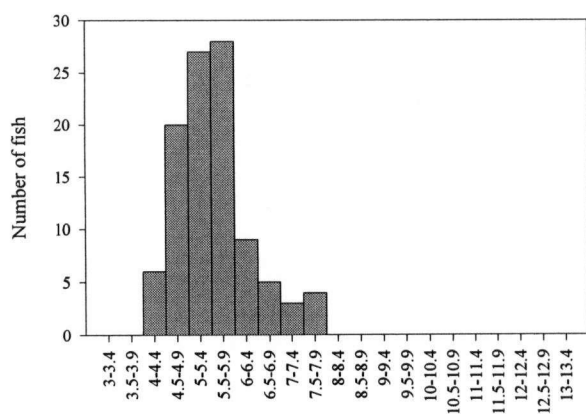
Fork Length (cm)

48
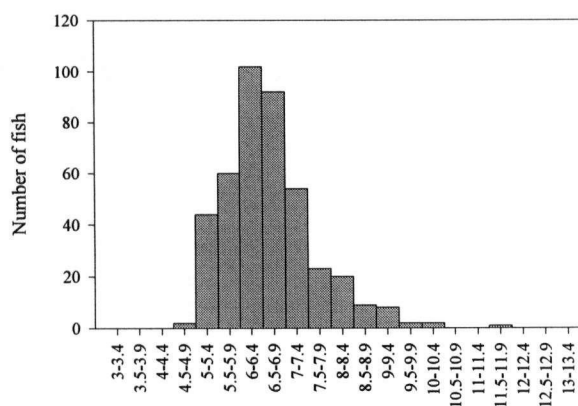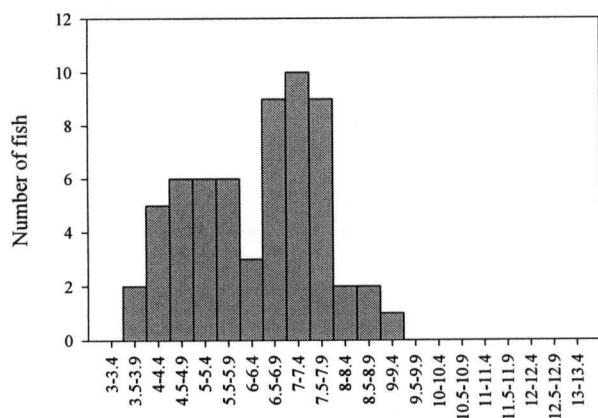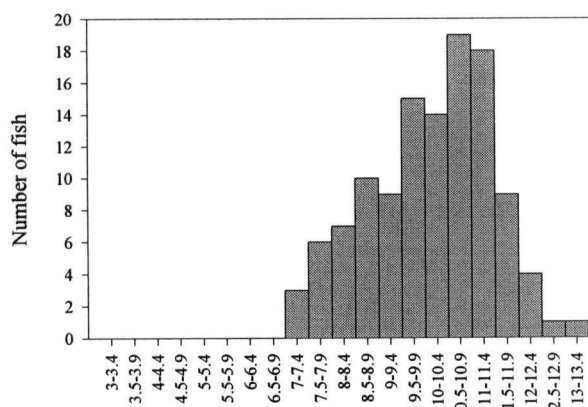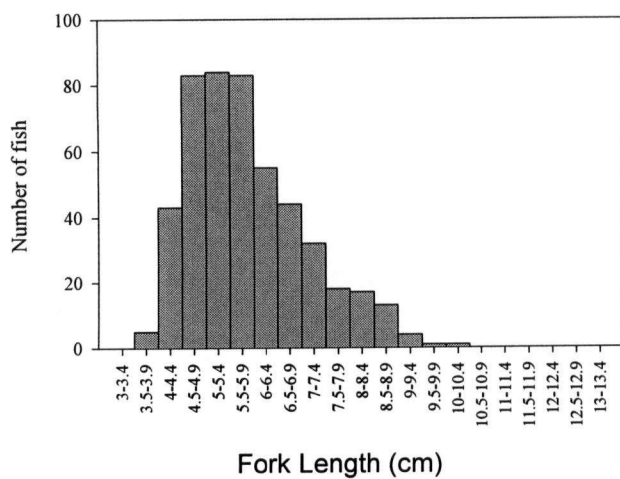
Figure 2.8 Length frequency histograms for
    Nanaimo area fish caught in 2001.
    Length classes of fork lengths
    on x-axis; number of fish on y-axis.

2.3.1 *Apparent Growth*

Mean fork lengths increased significantly with number of days from April 1 (fig 2.9a-c). This allowed for the estimation of apparent growth for the Nanaimo area population over the course of each summer. Although exponential curves fit the data slightly better in 1999 and 2001 (1999: $r^2 = 0.95$ vs $r^2 = 0.92$; 2001: $r^2 = 0.82$ vs $r^2 = 0.81$) and a logarithmic curve fit better in 2000 (r^2 0.90 vs r^2 0.89), the differences in explained variance were small. I therefore fitted the data from all three years with linear regressions to make comparisons between years easier. Apparent growth rates were 0.072, 0.052, and 0.054 cm/ day in 1999, 2000, and 2001 respectively (table 2.4). Neither the slopes (growth rates) nor the intercepts of these lines differed between years (ANCOVA, p > 0.5, p > 0.2 respectively).

I also made comparisons of apparent growth rates of juveniles for a number of other published data sets for the Strait of Georgia (table 2.5). Although growth rates varied between studies, no significant differences between growth rates or elevations was found between years (ANCOVA, p> 0.5, p> 0.5 respectively).

2.3.2 *Otolith Based Growth*

Due to edge degradation and crystallization (which renders otoliths unreadable) many otoliths were discarded after the grinding stage. In 1999, otoliths from 45 fish were discarded after preparation; 94 otoliths were successfully read. In 2000, 10 otoliths were unreadable, 82 otoliths were read.

Mean distance from the primordia to the ME did not differ between 1999 and 2000 (t-test, p = 0.21). The standard deviation of this distance was relatively low (20 μm), indicating that fish in both years entered the ocean at comparable sizes. Furthermore, fork length was positively correlated with both otolith marine zone width (fig. 2.10); and number of marine increments (fig 2.11), indicating that most fish growth occurs in saltwater, and that the magnitude of this growth is related to time spent in the ocean. These three relationships fulfill the requirements I laid out in the Methods section for a reliable ME check.

Slopes of otolith radius: fork length relationships did not differ significantly between years (t-test, p = 0.1). Data from an additional 20 otoliths from fish caught in

A 1999

$$y = 0.07x + 2.82$$
$$r^2 = 0.92, p = 0.04$$

B 2000

$$y = 0.05x + 3.45$$
$$r^2 = 0.89, p = 0.02$$

C 2001

$$y = 0.05x + 4.11$$
$$r^2 = 0.81, p = 0.04$$

Days from April 1
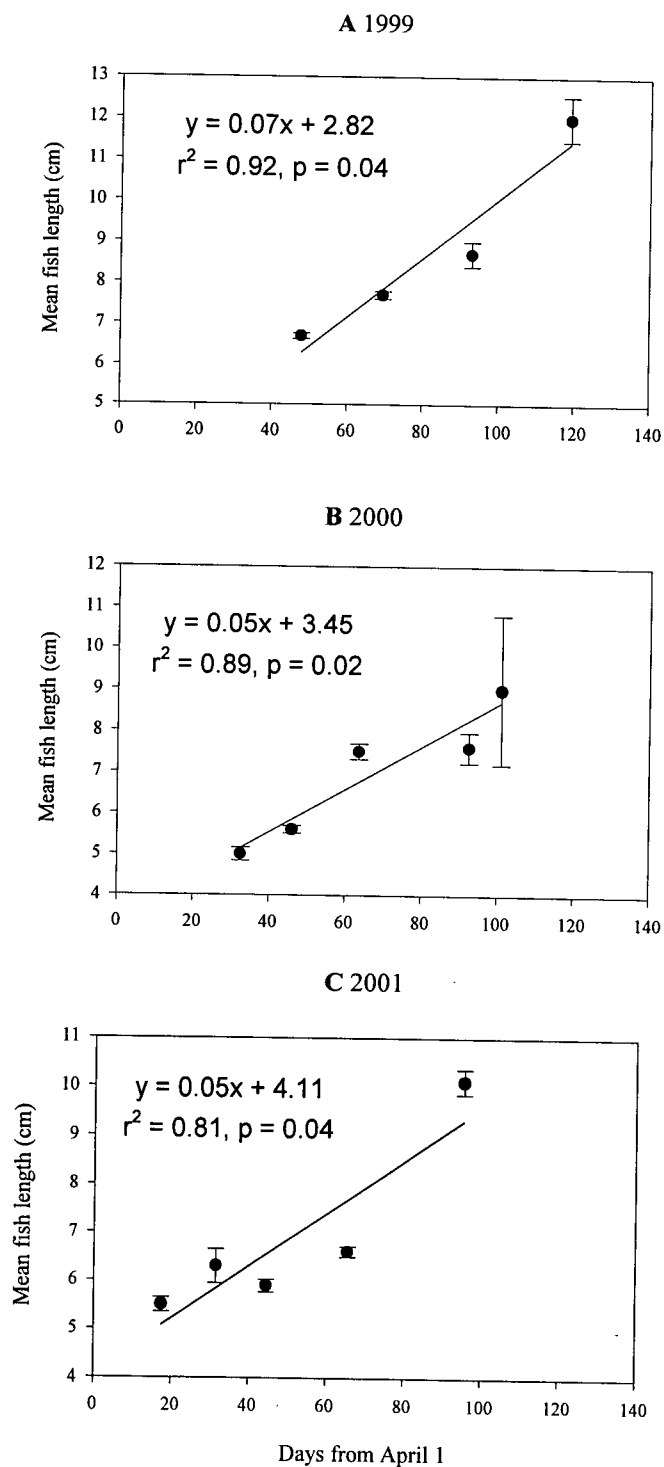
Figure 2.9, a-c. Linear regressions of chum fork length (averaged across stations) against time for 1999 - 2001. Slopes are apparent growth rates in cm/ day. Error bars are 95% confidence intervals.

Table 2.5 Apparent growth rates of chum caught in the Strait of Georgia. 1966 – 1969: Southern SoG, two-boat surface trawl in offshore waters (from Phillips and Barraclough 1978). 1974: Big Qualicum chum from the Northern Strait (Allen (1976) *in* Phillips and Barraclough 1978). 1975: Nanaimo area, purse-seined in nearshore (Healey (1976) *in* Phillips and Barraclough 1978). 1976: chum caught in Gulf Islands Region (Healey 1980b). 1999-2001: present study. Gw is instantaneous growth in weight; % bd wt day⁻¹ is the % increase in body weight per day

	1966	1967	1968	1969	1974	1975	1976	1999	2000	2001
daily growth (cm day^{-1})	0.094	0.095	0.097	0.073	0.077	0.082	0.072	0.072	0.052	0.054
Gw	0.0485	0.0487	0.0499	0.0374	0.0393	0.0410	0.0209	0.0245	0.0238	0.0257
% bd wt day^{-1}	4.96	4.99	5.11	3.81	4.00	4.18	2.11	2.48	2.40	2.61

Table 2.6 Growth in % increase body weight per day for chum salmon of various Pacific coast locations. "Mark-recapture" signifies mark-recapture studies; "apparent" signifies apparent growth studies.

Location	Study	% Bd wt/ day	Growth method
Nanaimo Estuary	Healey 1979, 1982a	6	mark-recapture
"	present study	2.5	apparent
"	present study	3.9	otolith based
Hood Canal	Bax and Whitmus 1981	8.6	mark-recapture
Fraser R. and Gulf Islands	Phillips and Barraclough 1978, Healey 1982b	4.2	apparent
Steamer Bay, Alaska	Murphy et al 1988	.4 mm day^{-1}	unmarked
Lab	Volk et al 1984	6-10	lab
Netarts Bay, Oregon	Pearcy et al 1989	1.6 – 2.3	mark-recapture
"	Wilson 1990	0.55-0.68 mm day^{-1}	otolith based
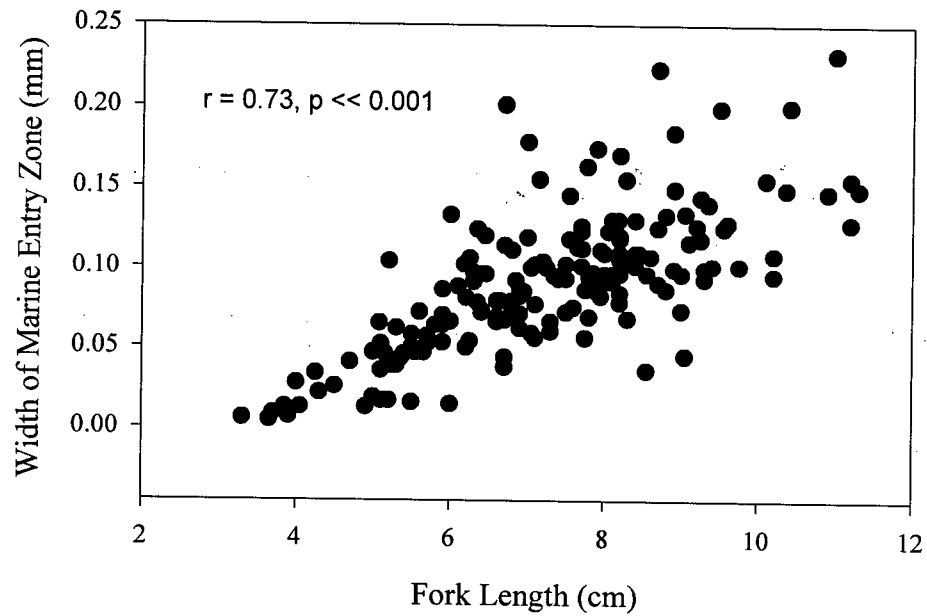
Figure 2.10 Correlation (Pearson product moment) between fork length
and width of the marine zone, 1999 and 2000
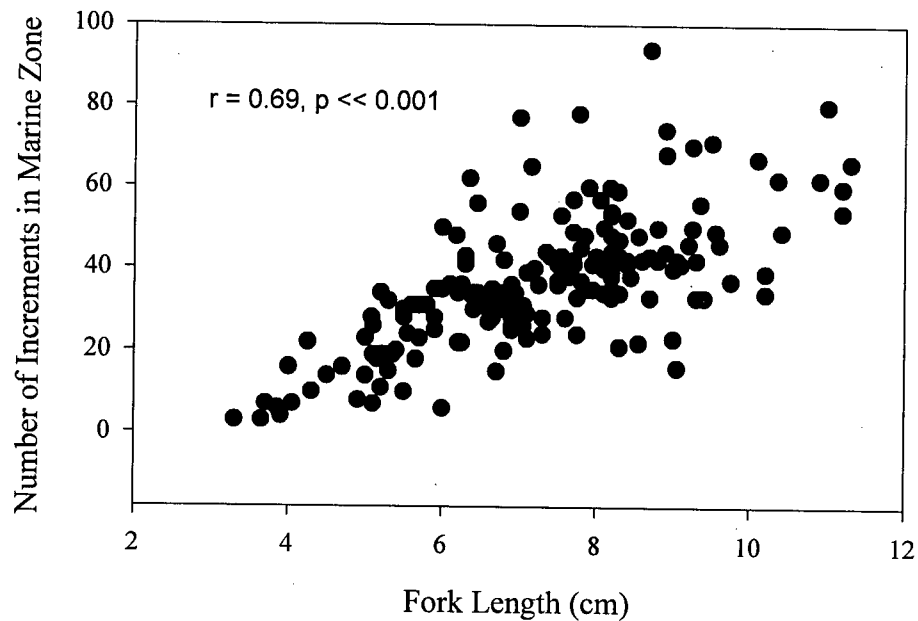
Figure 2.11 Correlation (Pearson product moment) between fork length
and number of increments in the marine zone

freshwater near the mouth of the Nanaimo River in 2001 (NR fish) were added to the relationship to fill out the bottom end of the plot. For BPH growth back-calculations the 2000 otolith radius: fork length relationship (with the NR fish) was used for the 2000 data (fig 2.13) as it was much tighter than the relationship for both years combined ($r^2 = 0.81$ vs $r^2 = 0.73$). The combined 1999-2000 relationship (with the NR fish) was used for the 1999 data (fig 2.12) as it was much tighter than the 1999 relationship alone ($r^2 = 0.73$ vs $r^2 = 0.63$). The higher unexplained variance in the 1999 relationship was probably due to the degraded nature of some of the otoliths. Fish captured in 1999 spent more time in formalin before being transferred to ethanol, and were preserved in ethanol for longer than in 2000. Residual error in both years may also have been due to the presence of multiple primordia in the otoliths. Neilson et al (1985) showed how this may add error to the otolith radius : fork length relationship.

The SPH back-calculations used in the determination of the growth back-calculation error term used the same relationships, but with otolith radius and fish length as the dependent and independent variables, respectively (linear regression, 1999: OR = 0.022(FL) + 0.17, $r^2 = 0.81$, $p < 0.001$; 2000: OR = 0.025(FL) + 0.15, $r^2 = 0.73$, $p < 0.001$). As slopes and elevations of fish weight- fork length regressions differed significantly between years (see above), length- weight conversions for growth rates were made within years.

In 1999, mean back-calculated fish growth rate was significantly higher (0.084 cm/ day) than in 2000 (0.076 cm/ day) (table 2.4; t-test, $p < 0.001$) and back-calculated size-at-entry was significantly larger (mean fork length = 4.48 cm) than in 2000 (mean fork length = 3.97 cm) (table 2.4; t-test, $p < 0.001$). Mean back-calculated growth rate in % body weight day^{-1} was also greater in 1999 (3.91% day^{-1}) than in 2000 (3.86% day^{-1}) (Mann-Whitney Rank Sum Test, $p = 0.017$).

Mean date of marine entry in 1999 (April 26) was not different than in 2000 (April 24) (t-test on mean date from April 1, $p = 0.44$). In 1999 and 2000, 33% and 36% of chum fry respectively, left the river in the 10 days between April 21st and 30th (fig 2.14, 2.15).

There was a tendency for early entrants (< April 20th) to grow faster than later entrants (> May 1st) in 1999, and vice versa in 2000, though within-year differences in
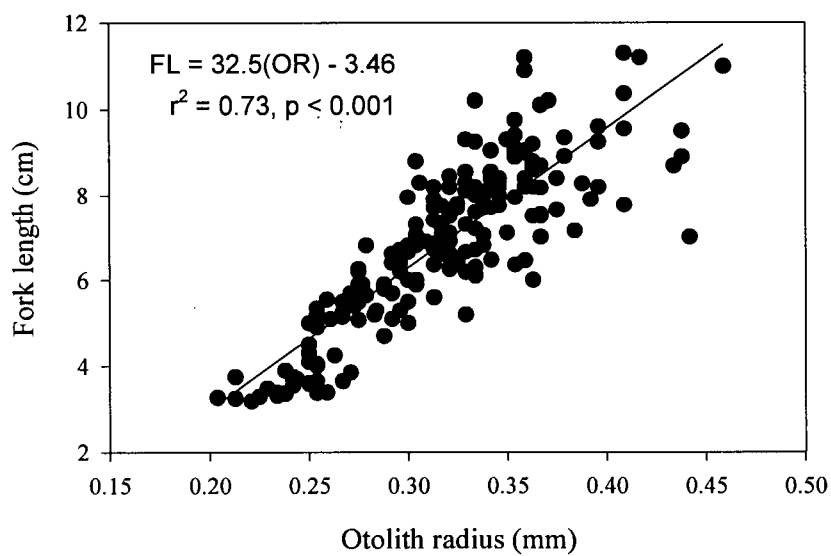
Figure 2.12 Otolith radius: fish length relationship (including NR fish), 1999 and 2000
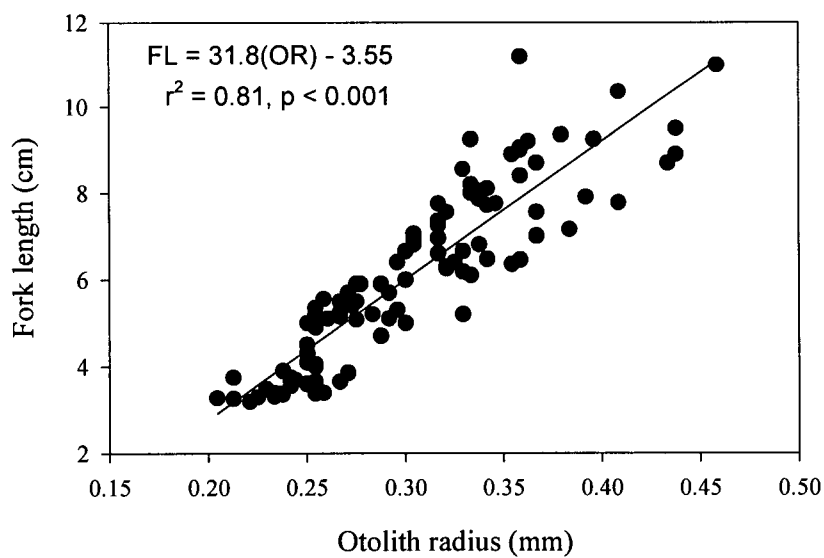
Figure 2.13 Otolith Radius: fork length relationship (including NR fish) 2000
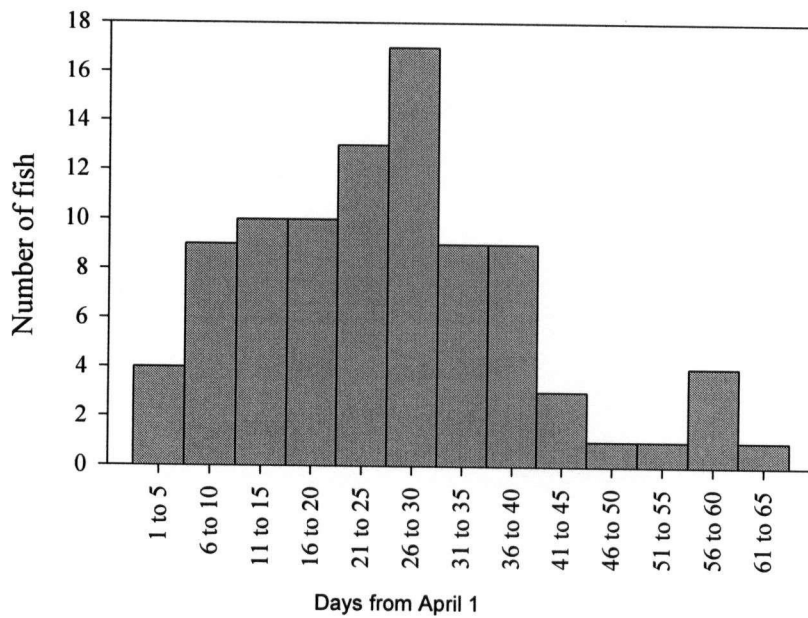
Figure 2.14 Date of marine entry back-calculated from otoliths, 1999. Days from April 1 on x-axis
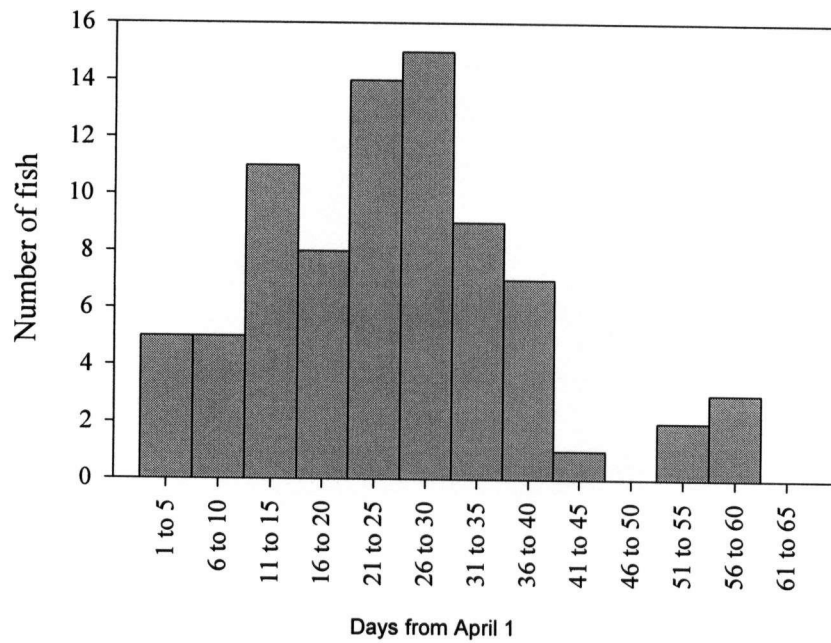
Figure 2.15 Date of marine entry back-calculated from otoliths, 2000. Days from April 1 on x-axis.

mean growth rates between early and late entrants were not significant (t-tests; 1999: p = 0.22; 2000: p = 0.12). There was no relationship between fish growth rate and time of marine entry in either year (linear regression; 1999: r^2 = 0.02, p = 0.21; 2000: r^2 = 0.02, p = 0.16). Nor was there a significant relationship between mean fish growth rate and size-at-entry within either year (linear regression; 1999: r^2 = 0.02, p = 0.19; 2000: r^2 = 0.01, p = 0.28).

Due to the poor quality of some otoliths, widths of the first and last 7 marine increments could not always be measured. Median total width of the first 7 increments in the marine zone did not differ between years (Mann Whitney Rank Sum Test, 1999: n = 76; 2000: n = 55; p = 0.87), nor did the mean total width of the last 7 increments (Mann Whitney Rank Sum test, 1999: n = 31; 2000: n = 44; p = 0.45). I pooled widths of 1st and last 7 increments across years, and found that last 7 increments were significantly wider (median 15.6 μm) than first 7 increments (median 14.5 μm) (Mann Whitney Rank Sum Test, p = 0.006).

Results of statistical tests were similar with both BPH and SPH back-calculation techniques. However, growth back-calculations made with the two techniques differed significantly within both years (Mann Whitney Rank Sum test; 1999: p < 0.001, 2000: p < 0.001). SPH-based rates were higher in both years (1999: 0.113 vs 0.084 cm day^{-1}; 2000: 0.092 vs 0.076 cm day^{-1}).

Error analysis

After the removal of one extreme outlier, the relationship between the marine entry radii measured by myself and the inexperienced reader had a slope approaching 1, and y intercept of approximately 0 (fig 2.16). The relatively consistent choice of marine entry check between readers lends confidence to the marine radius (MR) measurements made in this study. However, even with the removal of two extreme outliers (one of which was the outlier excluded in the above MR analysis), my counts were consistently lower than the reader's counts (fig 2.17).

My MR = 0.94(Reader's MR) - 0.01

$r^2 = 0.79, p < 0.001$

My MR (mm)

Observer's MR (mm)
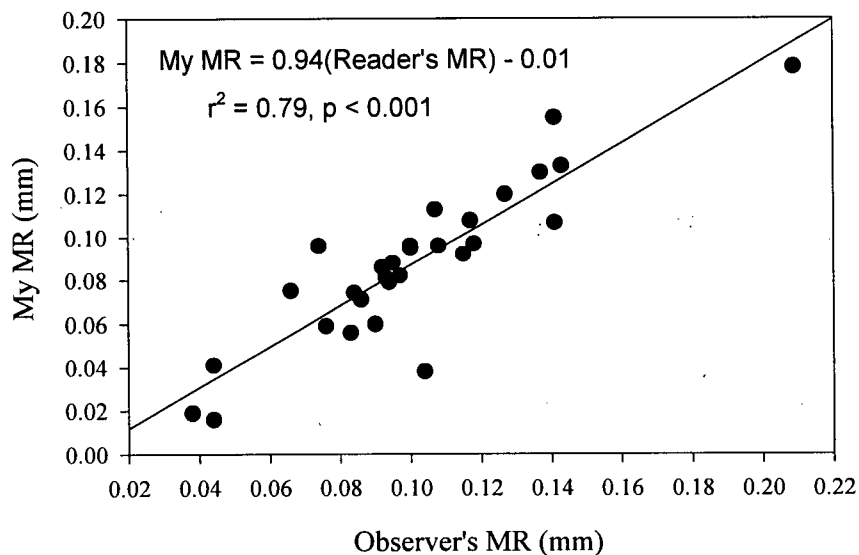
Figure 2.16 Agreement between my measurments and those of an inexperienced reader's of the marine entry radius (MR). n = 29

My counts = 0.90(Reader's counts) - 2.4

r2 = 0.90, p < 0.001

My counts
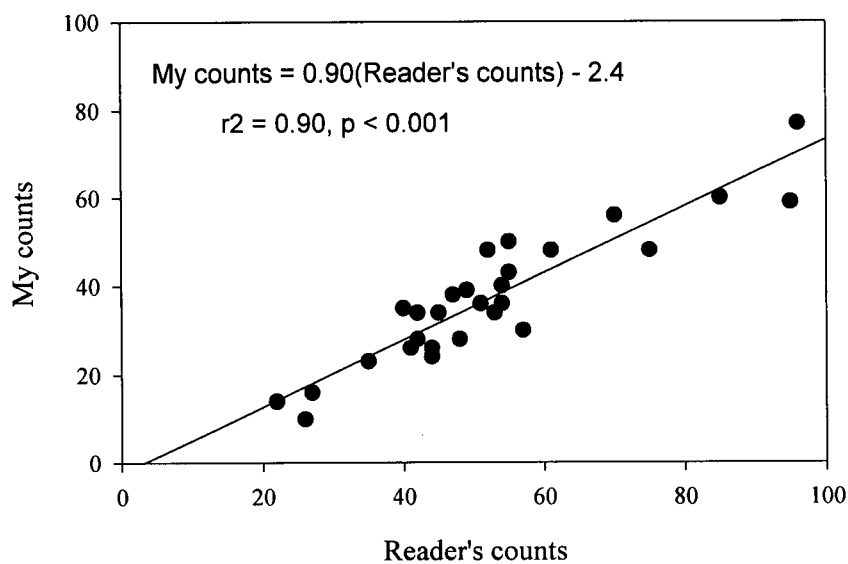
Reader's counts

Figure 2.17 Agreement between my marine increment counts and an inexperienced reader's; n = 28

2.4 DISCUSSION

In this chapter, I demonstrated that chum otoliths fulfill the necessary requirements to be used in otolith-based studies of early marine growth. They exhibit daily periodicity of increment formation, a clear relationship between fish growth and otolith growth, and the deposition of a marine entry check. Furthermore, I found that chum otoliths can be used in the field to answer questions about the early marine life history stage of Pacific salmon. These findings confirm Wilson's (1990) conclusions from a similar study on early marine growth of chum and should serve to encourage salmon researchers to follow the lead of larval fish ecologists in using otolith microstructural techniques to investigate fish early life histories.

Early life history of chum salmon in Nanaimo

The timing of outmigration from freshwater to the offshore, as inferred from otoliths, catches, and length distributions, was remarkably similar from 1999-2001. Although our sampling strategy was much less thorough than Healey's (1977a), who sampled continuously for an entire summer, our data led to similar conclusions for the same area (and presumably the same stock). Peaks in back-calculated time of marine entry were almost identical; chum left the Nanaimo River centered at April 25 in both studies. Healey et al (1977a) recorded a second peak in 1975 (on May 10), which we did not observe. Both our data and those of Healey show early high catches at Descanso Bay, with catches at other nearshore stations increasing in mid-May and early June. Prior to this, Healey found the juveniles were in the shallow waters of the Nanaimo estuary and surrounding nearshore. Presumably, fish followed the same patterns in 1999-2001. Our catches increased closer to mid-May than did Healey's, possibly due to our tendency to seine in slightly shallower waters (often < 20 m) than they did (>20 m). By July, chum smolts were more scarce in catches, indicating that by this time some smolts (possibly the largest ones (Pearcy et al 1989)) had already begun their offshore movement. If the historical patterns of behaviour still continue, these chum juveniles probably move out of the Strait of Georgia and into the North Pacific by November (Healey 1980b). However, Beamish and Folkes (1998) have reported longer residence times in the Strait in recent

years. Although they collected only one year of data, they claim to have shown that chum salmon shifted their behaviour as a result of physical changes associated with the 1977 regime shift.

Early summer length frequency distributions were skewed to the right in 1975 and 1999-2001, probably due to the continued movement of small chum from the shallows to the nearshore and possibly due to size-selective emigration of large chum from the nearshore to the offshore. Only by July did length distributions normalize, indicating recruitment to waters 15-30 m deep had ended. Fork lengths from Trip 5 in 2001 were skewed to the left, possibly suggesting size-selective mortality of smaller fish in late summer (Chapter 3).

Multi-modality in size-frequency distributions was a much more frequent occurrence in Healey's data than mine. I only saw evidence of this pattern in 2001 Trip 2. It could be that Healey's higher frequency of sampling (at least once a week at every station) and larger sample sizes (they kept all fish, whereas we released many) distinguished chum sub-populations that our study couldn't detect.

Growth rates of juvenile chum

This study showed that otolith-based early marine growth rates of chum salmon in Nanaimo waters varied significantly between 1999 and 2000. This interannual difference in growth rate may indicate a subsequent interannual difference in survival, as the two processes are thought to be correlated (Chapter 1). What are the sources of this variation in growth, and possibly survival? Although size at marine entry was not correlated with growth rate in either 1999 or 2000, size at marine entry was significantly larger in 1999, which was also the year of higher growth rates. It is possible that some difference in the early freshwater life of the chum, which led to longer sizes at entry in 1999, also led to higher marine growth rates *on average*, although within years, larger fish did not necessarily grow faster in the ocean.

There was also a tendency for early ocean entrants to grow faster than later ocean entrants in 1999 with the opposite trend observed in 2000. Smaller 2000 fish may not have been able to take advantage of some critical resource in the early marine environment, or may have been subject to higher size-selective predation pressure,

leading to slightly lower early marine growth rates, and lower mean growth rates for the summer. Future analysis of gut contents and marine zooplankton data from these same sampling trips will allow us to determine if some change in prey quality, quantity, or timing may have contributed to the observed differences in growth rates.

Previously, evidence for density-dependent early marine growth has been found for Pacific salmon (Peterman 1984). We have not estimated total Nanaimo-area smolt population size in our study, and thus cannot look for interannual patterns linking growth to abundance of conspecifics. However, we do know from our field study that pink and chum juveniles shared the Nanaimo nearshore in 2000, and not in 1999 (pink smolts are only present in large numbers in evenly numbered years in the Strait of Georgia). The early marine diets of these two species are known to overlap (Bailey et al 1975, Murphy et al 1987). It is possible that interspecific competition for food between pink and chum juveniles may have led to the lower early marine growth rates observed in 2000. However, our apparent growth rate data (which seems to be a good indicator of relative growth) indicates that growth in length was as low in 2001 (when there were no pinks) as in 2000 (when there were pinks). Furthermore, as pink smolts were far less numerous in our catches than were chum, I tentatively conclude that density-dependent interactions between chum and pink were not the source of lower 2000 growth rates.

The apparent growth method consistently estimated lower growth rates than did the otolith method (table 2.4). This is not surprising, given the assumptions of the former method. The systematic underestimation once again illustrates the influence of continual recruitment from the shallows and/ or size-selective emigration offshore. This should serve as a warning to other researchers who are still using the apparent growth method to estimate growth rates for populations that are not isolated. However, apparent growth may still be a good relative index of growth, as similar patterns were seen between years using both otolith and apparent growth methods.

Broad-scale spatial and temporal patterns

Early marine growth rates of juvenile salmon, in % increase in body weight per day have varied considerably for a number of different locales in the SoG (fig 2.5). Apparent growth rate estimates for juvenile chum caught in our study were the lowest of

such estimates made to date. However, although they seemed to demonstrate a general decline with time, I found no significant differences in apparent growth rates between the various SoG stocks over the last 40 years (table 2.5). Thus, it may be that early marine growth rates have remained relatively constant over the past 40 years. Alternatively, the reason for this lack of significance may be due to be the inherently low statistical power of such apparent growth comparisons. Unfortunately there is no standard method to determine statistical power in analysis of covariance (Zar 1984). However, a cursory examination reveals that each yearly rate is based on only a few (usually 3-5) data points representing mean size at time. Residual sums of squares for the regressions tend to be considerable, and lead to inflated values of the 'common regression sum of squares' (SS_c) term used in the calculation of the F statistic used in ANCOVA (Zar 1984, p.300). Inflated SSc values decrease the F value for a given ANCOVA, making it more difficult to detect significance. Given the biases associated with the apparent growth method, and the low power of the comparisons, it is difficult to conclude with certainty that there were no differences in growth between years. Clearly, this subject requires further study.

Otolith-derived mean growth rate in % body weight day^{-1} fell within the range of literature values reported for chum on the Pacific coast (table 2.6). The range of otolith growth rates displayed by the chum we caught (in cm day^{-1}) agreed well with growth rate estimates from the only other otolith-based examination of the early marine growth of chum (Wilson 1990; table 2.6). As otolith growth estimates have considerably less error associated with them than do other growth estimation techniques, this suggests that a growth rate of 0.05-0.07 cm day^{-1} may be the norm for juvenile chum in the early marine stage.

The differential growth hypothesis

In the Introduction to this chapter, I listed a number of predictions from the differential growth hypothesis regarding early marine growth and mortality patterns of chum smolts. If my predictions and observations agree, I can conclude that differential growth may be an important mechanism of survival variability. If none of the predictions were observed, I can conclude that in the years observed, differential growth was probably not an important mechanism.

The differential growth hypothesis predicts that in years of higher survival, growth rates of juvenile salmon in the early marine stage will be higher than average, and vice versa. As yet, there are no data on the oceanic survival rates of the chum brood years we sampled in 1999 and 2000. However, we know there were interannual differences in mean growth rate. That early marine growth rates of juveniles can vary is an important finding, and provides evidence that the differential growth hypothesis is in fact a possibility. If this hypothesis is correct, then we might expect oceanic survival of the 1999 year class to exceed that of the 2000 year clan.

Among other things, one possible reason for an interannual change in growth rates is a change in the quantity or quality of food available to the smolts. Both in the Strait of Georgia (Bornhold 1999) and the offshore NE Pacific (Mackas et al 1998) there has been evidence that the timing of peak abundance of at least one major copepod species (*Neocalanus plumchrus*) has shifted significantly in the last 20 years. If, as argued, these changes in *N. plumchrus* are due to changes in ocean conditions, then it is quite possible that the zooplankton prey field of juvenile chum can also vary with ocean conditions.

One indicator of ocean condition is sea surface temperature. As such, changes in the prey community structure of juvenile salmon would probably be linked to ocean temperature. Data from Nanoose Bay showed surface temperatures in the area were significantly warmer in 2000 than in 1999. Temperature changes of a smaller magnitude may have been associated with lower zooplankton concentrations, and lower early marine growth of chum in other field studies (Orsi et al 2001). If the change in temperature in the Nanaimo area changed the amount or type of prey available to juvenile chum, we might expect a downward trend in gut fullness in 2000. Preliminary smolt gut analyses show just this – gut weight as a percent of body weight ('gut fullness') was significantly lower in 2000 in trips 2 (t-test, $p = 0.018$) and 3 (t-test, $p = 0.026$) than in 1999 (guts from other trips have not been fully analyzed yet).

Additionally, all else being equal, metabolic costs will be higher in warmer water, requiring more food in a warm year just to maintain the same growth rate as in a cold year. As noted above, we did not see the shift to higher gut fullness in 2000 that would have been required to maintain 1999 growth rates. This suggests that in 2000, fish may

have suffered from lower food availability or from higher metabolic demands associated with living in warmer water, either of which could have led to lower mean growth rates.

The results presented in this chapter provide evidence against the idea of a static growth threshold for juvenile salmon in their 1st summer at sea. Walters and Juanes' (1994) 'foraging arena' theory predicts that fish under intense predation pressure (such as juvenile chum) can modulate their foraging time (and thus their availability to predators) so as to take no more risks than are necessary to grow at the minimal level necessary for survival. There is some evidence that a growth threshold does exist for juvenile salmon; fish that do not meet a minimum size by late summer may not survive the first winter (Beamish and Mahnken 1998, Friedland et al 1993). However, there is no reason to believe that such a threshold (in size or in rate) will remain the same from year to year. Any such threshold would presumably vary with intensity of the winter, water temperature, predator density, and food concentration. If Walters and Juanes' (1994) theory holds, we would expect juveniles in late summer to have similar growth rates, this growth rate being the minimal growth rate needed to survive. However, I observed that individual growth rates varied widely even at the end of the summer.

If a match-mismatch scenario is important in determining growth rate (and thus survival), it appears that differential timing of peak prey abundance, and not peak outmigration timing, would be important. This study has shown that outmigration timing varies little interannually. We did see somewhat differential growth of early entrants vs late entrants, suggesting that food availability may vary over the course of the summer (possibly due to prey abundance). However, only future analyses of collected zooplankton data will allow a thorough investigation of this possibility.

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CHAPTER 3
Size selective mortality in the early marine life of chum salmon in the Nanaimo area

3.1 INTRODUCTION

Mortality in the early life history of marine fish is extremely high (Houde 1997) – numbers are typically reduced by 4-7 orders of magnitude between hatching and recruitment (Cushing 1974). Researchers have long recognized that the probability of survival of an individual fish changes with body size (Parker 1962, Ricker 1969). Body size (and the associated growth rate) during the early life history stages of fishes is now widely seen as a major determinant of ocean survival (McGurk 1986, Miller et al 1988, Anderson 1988).

Agents of mortality can sometimes act on individual variability in fish body size in a non-random fashion, resulting in selective mortality of the most vulnerable size classes. Evidence for such size-selective mortality has been found in numerous studies of larval (reviewed by Bailey and Houde 1989, Paradis et al 1999) and juvenile (reviewed by Sogard 1997) fishes. A number of mechanisms have been proposed to explain size-selective mortality, including gape limitation of predators, active behavioural selection by predators, size-bias in the escape ability of prey, and size-dependent susceptibility of prey to physiological stress (including overwintering) and disease. In any given case, the particular active agent of mortality determines which size classes will be most strongly selected against. For example, if a predator and prey species are of similar size, the predator's gape size (i.e. how wide its mouth opens) may only allow for the capture of the smallest size classes of the prey species. Alternatively, if small prey size classes are better able to hide or escape detection, larger size-classes might be selected against.

Although there are exceptions (Gleason and Bengtson 1996, Good et al 2001), the overwhelming majority of field and laboratory studies have shown that when it comes to questions of survival in fishes, "bigger is better" (reviewed by Miller et al 1988, Pepin 1991, Sogard 1997). Within a given fish species, the larger individuals are apparently less vulnerable to predators, more resistant to starvation, and more able to tolerate environmental variability. Empirical relationships have demonstrated that larval fish mortality decreases with increasing size or weight (McGurk 1986, Pepin 1991). Until the

mid 1970s, starvation was regarded as the most likely source of juvenile mortality in pre-recruit marine fishes (Hjort 1914, Bailey and Houde 1989). However, recently it has been shown that the magnitude of larval fish mortality is also consistent with the hypothesis that predation is the primary source of size-selectivity (Peterson and Wroblewski 1984, McGurk 1986). Miller et al (1988) have shown that across species, risk of predation decreases with increasing body size.

Studies of sources of size-selective mortality indicate that as for larval fish, predation is an important agent of mortality for juveniles (Sissenwine 1984). Sogard (1997) lists predation and overwintering stress (for temperate species) (Sogard 1997) as the primary causes of size-selective mortality in this age class of fish.

Fish size is strongly linked to growth rate, and several attempts have been made to establish the nature of the relationship between fast growth and size-selection (e.g. Lynch and Arnold 1988, Meekan and Fortier 1996). First, it may be that selection *is size-dependent*: larger size-at-age of fast growers may provide a survival advantage, in that those individuals with a larger size-at-age are generally susceptible to fewer predator fields than are smaller fish (the 'bigger is better' hypothesis (Miller et al 1988, Bailey and Houde 1989)). Alternatively, selection may be *growth-dependent*: fast growers may survive preferentially as they reduce the amount of time they spend in the vulnerable early life history stage or size class ('stage-duration hypothesis' (Houde 1987) and the growth-predation' hypothesis (Anderson 1988)).

3.1.1 Selective mortality in Pacific salmon

The ocean mortality of Pacific salmon appears to be greatest during the early marine period, declining steadily as fish grow larger (Ricker 1976). Early researchers noted that this mortality also appeared to be related to the size and the growth rate of individual fish (Parker 1962, Ricker 1962), and could be important in determining the number of returning adults in a given year (Parker 1962, 1968). There is considerable evidence for size-selective mortality during the oceanic life (from ocean entry until spawning) of coho (Hager and Noble 1976, Bilton et al 1982), chum and pink (Kobayashi 1980), and steelhead (Ward et al 1989). Less conclusive evidence of size-selective mortality has been found for sockeye during this life history stage (reviewed by

Henderson and Cass 1991). Most of the above workers have relied on broad scale sampling (Sogard 1997) – the comparison of smolt size measured at ocean entry with back-calculated smolt size (from otoliths or scales) of returning adults. Any shift between the initial and back-calculated size frequencies over this time can then be interpreted as evidence of size-selective mortality. However, this technique cannot distinguish between other agents of size-selective mortality, such as fishing pressure, that can often affect salmon during the course of their ocean existence.

Although the early juvenile period of fish plays an important role in population regulation and determination of year class strength (Sissenwine 1984, Bradford 1992), the potential importance of size-selective mortality in the early marine stage of salmon has been examined only infrequently. Experimental studies have suggested that coho salmon selectively feed on smaller size classes of pink (Parker 1971) and chum (Parker 1971, Hargreaves and LeBrasseur 1986). In the field, Healey (1982) used scale ciculi patterns to show size selective mortality in juvenile chum over the 45-55mm size class, the size at which chum move from the nearshore to the pelagic environment. The pattern of selectivity was consistent with the growth of juvenile chum through a size range available to one particular predator, possibly juvenile coho (Parker 1971, Hargreaves and LeBrasseur 1986). Also using scales, Fisher and Pearcy (1988) back-calculated size-at-entry and growth-at-entry, but found little evidence for size-selective mortality in Oregon and Washington coho.

Characteristics of survivors

Otoliths hold many advantages over scales (Chapters1-2), but both can be used to examine size-selective mortality using the robust "characteristics of survivors" method (Miller 1997). Using fish hard parts, previous fish size or growth rates can be back-calculated from surviving individuals, and then compared to the present frequency distribution. For example, if we were to sample a juvenile salmon population on two consecutive trips, a shift to the right in the frequency distribution between trip 1 and trip 2 in mean back-calculated size at entry would indicate that fish which were larger at marine entry made up a greater proportion of the total number of fish sampled later in the summer (fig 3.1a). If our assumptions regarding the unbiased sampling of an isolated

population hold, this also indicates the size-selective mortality of fish that were smaller at marine entry during the time between trips 1 and 4. Selection is not necessarily unidirectional. If both the largest and the smallest fish at ocean entry were preferentially preyed upon (perhaps by two different predators), then stabilizing selection would ensue – the resultant mean of the distribution wouldn't change, but the variance would decrease (fig 3.1b). Finally, if a certain predator can only access a certain size range in the middle of the juvenile size-distribution, or perhaps favours the most common size-class, then the the post-selection distribution would be bimodal (fig 3.1c). The particular type of selection that occurs can give insight as to what the important predators might be. For example, birds tend to select larger size classes of salmon smolts, whereas piscine predators generally select smaller classes (Pearcy 1992).

Although the 'characteristics of survivors' method has been used with otoliths to demonstrate size selective mortality in larval fish (e.g. Meekan and Fortier 1996), in Atlantic salmon fry (Good et al 2001), and for sockeye salmon at a broad scale (West and Larkin 1987), to date the technique has not been used to look for evidence of size-selective mortality in the critical first few months of Pacific salmon at sea. In this chapter, I use otoliths to look for evidence of size-selective and growth-selective mortality in the early marine life of chum salmon from the Nanaimo area. This information will help us determine why the few surviving members of a cohort are successful, and add new information to our scant knowledge of patterns of mortality in this life history phase. Additionally, these results will be coupled with my results from chapter 2 to provide a more thorough picture of growth and mortality in the early life of chum salmon.

3.2 METHODS

All field sampling and otolith analyses are as presented in the methods section of chapter 2. As in Chapter 2, I have made the assumption that the same population was repeatedly sampled in an unbiased (or at least consistent) fashion over the course of the summer. Also in Chapter 2, I outlined the reasons why, strictly speaking, this is not the case. In Chapter 2, this assumption probably had little effect on our results. However, in this chapter violations of the assumption are more serious. The BPH back-calculation
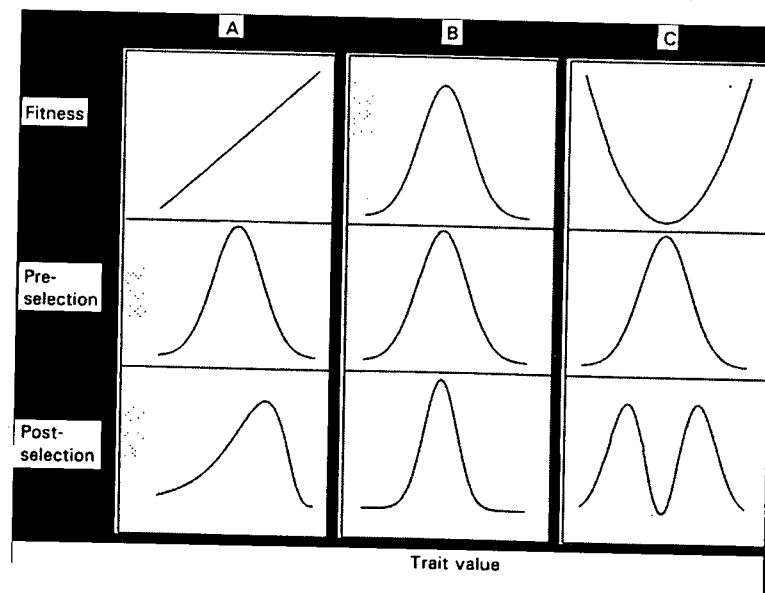
Figure 3.1 Three forms of size-selective mortality: (A) unidirectional, (B) stabilizing, and (C) disruptional selection. From Miller (1997)

technique for determining size at previous age was used primarily; the SPH technique was used only to verify results.

3.2.1 *Data analyses*

Size frequencies at marine entry were back-calculated for all chum salmon for which otolith analyses were made in chapter 2 (equation 2.4). Sample sizes were n = 95 in 1999 and n = 82 in 2000. Within each year, size frequencies were compared among trips to check for shifts in the mean and distribution over time that would indicate the size-selective mortality of fish which were smaller or larger than average at marine entry.

A growth rate frequency histogram was also constructed for each trip. These frequencies were compared between trips to determine if fish with higher or lower than average growth rates were found in greater proportions in later trips. Again, a shift in peak frequency to the right (or left) indicates that relatively slow (or fast) growing fish were subject to size-selective mortality. I have assumed that individual fish growth rates were consistent over the duration of the summer such that fast growers later in summer were fast growers early in the summer, and vice versa.

Kolmogorov-Smirnov 2-sample tests (Sokal and Rolf 1995, p.434) were used to detect between-trip differences in frequency distributions, and one way ANOVA was used to detect differences in mean back-calculated length at entry and growth rates.

3.3 RESULTS

No difference in median back-calculated length-at-entry were detected between successive trips for smolts caught in 1999 (Kruskal-Wallis 1-way ANOVA on ranks, p = 0.075), nor did frequency distributions differ significantly over time (figure 3.2; Kolmogorov-Smirnov two-sample test, $p > 0.05$). In contrast, mean back-calculated length at entry differed significantly between trips in 2000 (Kruskal-Wallis ANOVA, p = 0.001). Median back-calculated lengths of fish caught in trips 2 and 3 were longer than those of fish caught in trip 4 (Dunn's method of multiple comparisons, $p < 0.05$ for both). Similarly, frequency distributions of back-calculated lengths differed significantly between trips 2 and 4, and between trips 3 and 4 (figure 3.2; Kolmogorov-Smirnov two-

sample test, p < 0.05). Differences between trips 1 and 4 were marginally significant (p = 0.06).

Mean growth rates of fish caught in 1999 did not differ between trips (1-way ANOVA, p = 0.25), although length-frequency distributions did differ between trips 2 and 4 (figure 3.3; Kolmogorov-Smirnov two-sample test, p < 0.05). In 2000, median growth rate of fish caught in trip 3 was significantly greater than growth rates of fish caught in trips 1, 2, and 4 (Kruskal-Wallis ANOVA, p = 0.001; Dunn's method, p < 0.05 for all three comparisons). This pattern was echoed in the frequency distribution comparisons; the distribution of growth rates of fish caught in trip 3 was different from all 3 other such distributions (figure 3.3; Kolmogorov-Smirnov two-sample test, p < 0.05).

Although absolute growth rate and size-at-entry values for results were different using the SPH back-calculation, overall frequency distributions were similar. All statistical tests yielded the same results with SPH and BPH techniques.

3.4 DISCUSSION

According to my predictions, these data suggest that mortality selected *against* faster growing, larger individuals in the late summer. However, I will argue below that these shifts were probably effects of size-dependent migration of larger fish offshore in late summer. Instead, there is evidence that mortality selected against slower growing individuals between mid-May and early June.

Historical data (Healey 1977a, 1982) and the data presented in this study (chapter 2) indicate that most chum salmon leave the Nanaimo River in late April, spend early May rearing in the shallow nearshore, and move to the deeper nearshore by mid-May. By mid-June, juvenile chum become less frequent in nearshore catches and are thought to begin their offshore movement. This movement is hypothesized to be size-dependent, and to be related to foraging success (Healey 1980a,b). Larger fish leave the nearshore earlier, perhaps because they have achieved some minimum size necessary to overwinter or to migrate to the open ocean. This relationship between size and residence time has been observed in other studies as well (Simsenstad and Salo 1980, Wilson 1990, Mortensen et al 2000), and may be a general one for pink and chum.

Figure 3.2 Back-calculated length-at-marine entry for chum salmon caught in the Nanaimo area, 1999 and 2000

2000 01 (May 2-3)

1999 02 (May 17-19)

2000 02 (May 15-17)

1999 03 (June 7-10)

2000 03 (June 2-3)

1999 04 (July 1-3)

2000 04 (July 1-2)

Back-calculated fork length-at-entry (cm)

Back-calculated fork length-at-entry (cm)
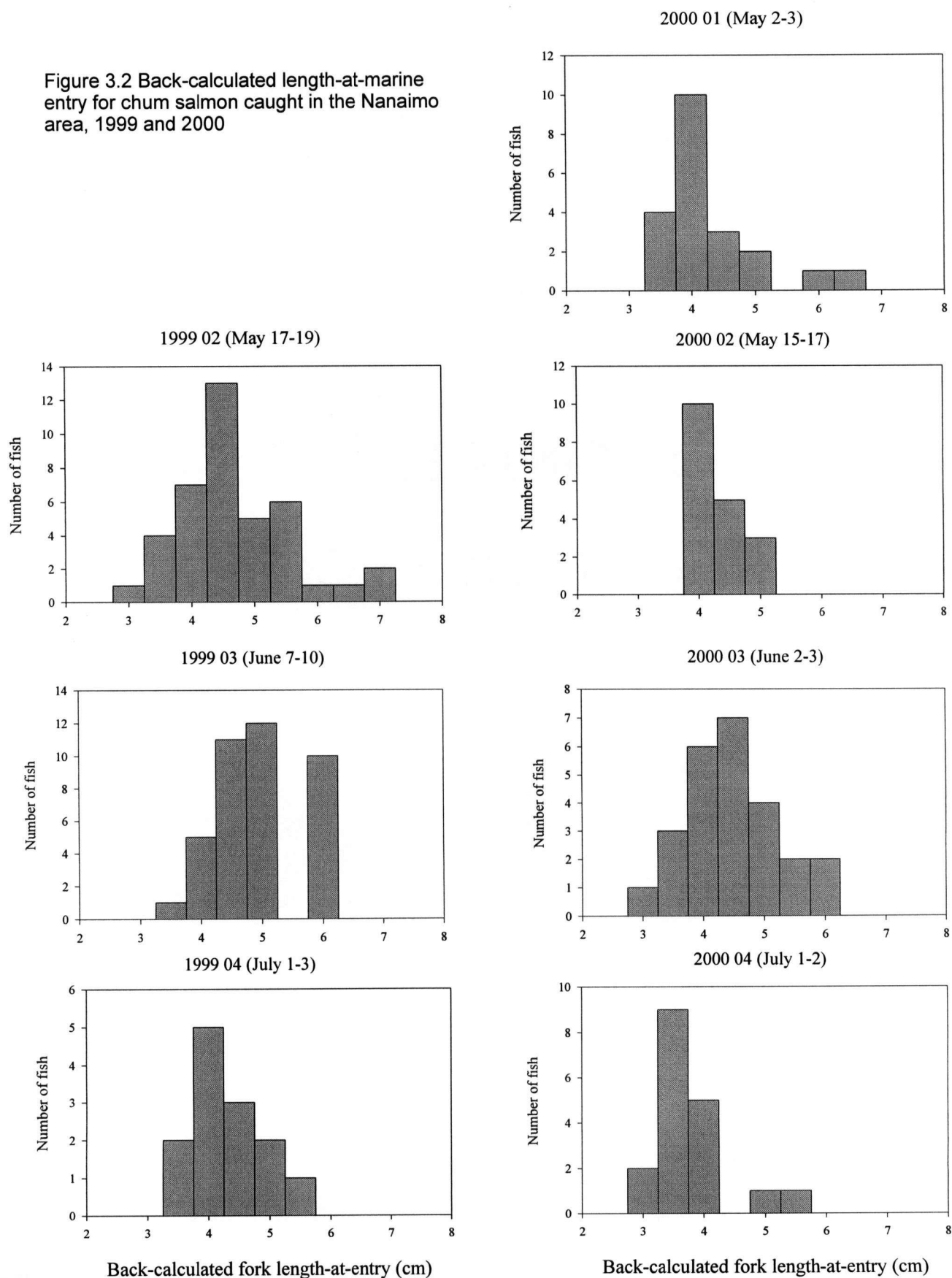
Figure 3.3 Mean summer growth rate for fish sampled on successive trips, 1999 and 2000

Mean summer growth rate (cm/ day)
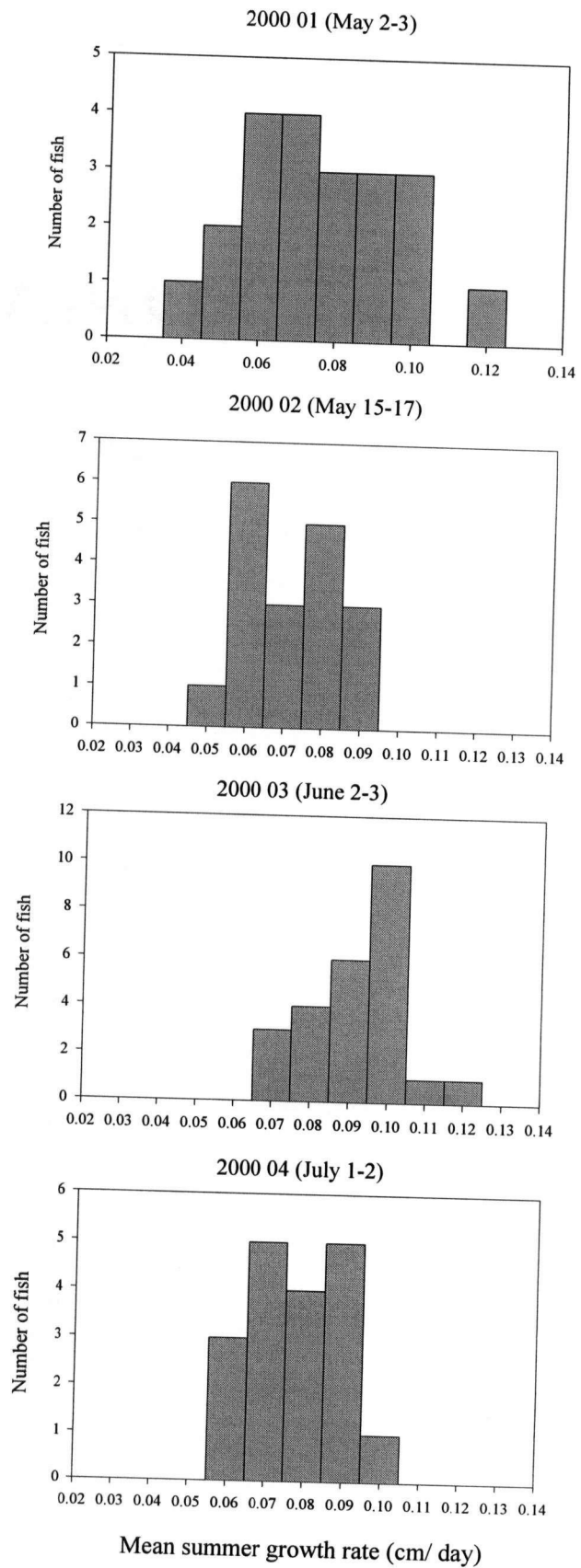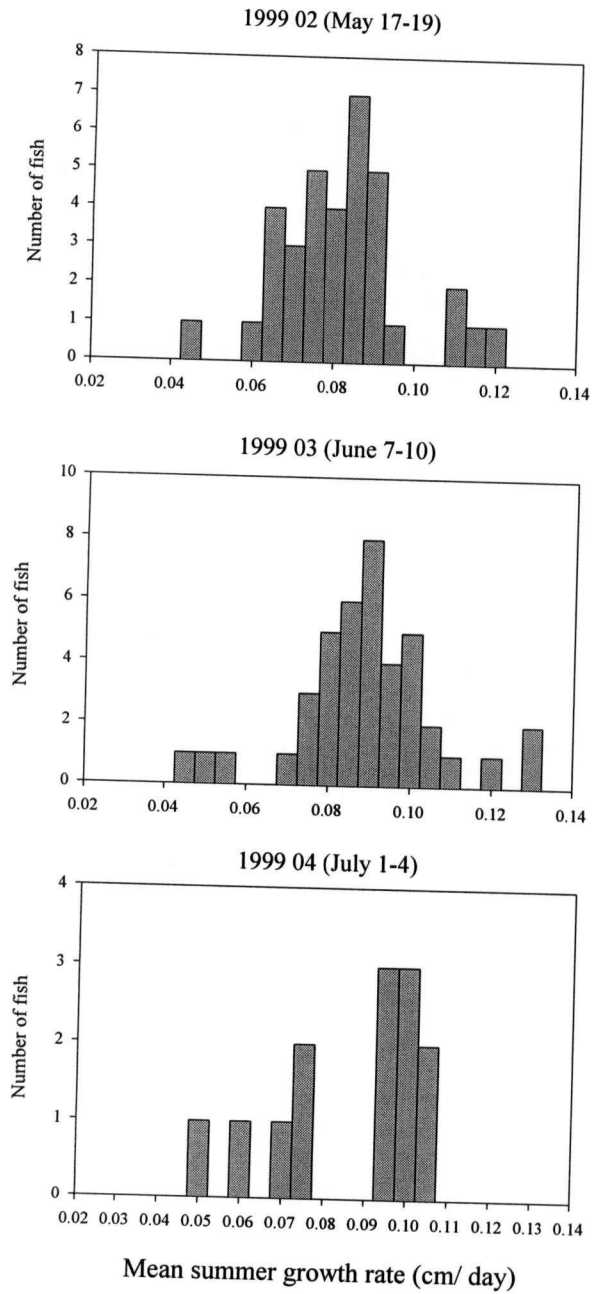
At first examination, my data would appear to indicate size selective mortality of fish that were larger at marine entry in 2000 – fish caught in trip 4 were significantly smaller at entry than those caught in trips 2 and 3. Furthermore, fish caught in trip 4 had significantly lower mean summer growth rates than those caught the month before, in trip 3. However, instead of representing selective mortality of larger, faster growing fish, these shifts are probably the signature of size-dependent emigration of the larger, faster growing fish in mid-June. By July, it is likely that only the fish which entered the ocean smallest, and grew the slowest, still remained in the nearshore Nanaimo area.

These data are not unequivocal, but instead suggest growth-selective mortality of slower growing juveniles in 2000. Chum present in the Nanaimo nearshore in early summer (trips 1 and 2) were largely fish which grew at between 0.07 cm day^{-1}. By early June, the mean had shifted to 0.09 cm day^{-1}. The same pattern of selection was seen in mean size at entry for 1999, but the shift was not significant. There are a number of possible explanations for the discrepancy between indices of selection. If selection is acting on size, size at ocean entry may not be a good indicator of size in the early marine stage. Instead, size during the early marine stage may be more strongly correlated with early marine growth rate. Alternatively, selection may act on growth rate itself. If a high growth rate is correlated with foraging success, then it may be that well fed, faster growing individuals are more likely to survive (more able to evade predators, more resistant to disease, etc). The selection for faster growers appeared to happen sometime in the period between mid to late May (between trip 2 and 3, 2000). This corresponded to the time at which mean fish lengths were 5.6 to 7.5 cm. This contrasts with Healey's (1982) results, in which he found size-selective mortality operating at lengths of 4.5-5.5 cm on juvenile chum in 1975. This discrepancy could indicate the importance of a different agent of mortality in the mid 1970s (such as a different predator field).

I found little evidence for size-selective mortality in 1999. Fish which entered the ocean at a relatively small size, and grew at a slow rate, were present in similar proportions to those which entered large and grew quickly, throughout the summer. Although there were slight indications of a positive shift in mean growth rate between trips 2 (0.081 cm day^{-1}) and 3 (0.088 cm day^{-1}), the trend was not significant.

As we saw in Chapter 2, juvenile fish grew faster in 1999 than in 2000. The "stage duration" hypothesis (Houde 1987) predicts that in years of poor growth, fish remain in vulnerable early life history stages for longer periods of time. Higher cumulative mortality rates in these years would thus presumably increase the intensity of size-selective mortality. Several other studies have shown that under food-limited conditions, average growth rates are low, and mortality is high and size-selective (Post and Prankevicius 1987, Holtby et al 1990, Blom et al 1994). It appears that the growth-selective mortality experienced by juvenile chum in Nanaimo in 2000 may have been a function of lower average growth rates in that year. In contrast, in 1999, when growth was higher, selective mortality was not as evident. I propose that growth-selective mortality occurs in both high and low growth years, but is only sufficiently intense to significantly alter distributions in years of low growth (and longer stage-duration)

In Chapter 2, I noted the possibility that higher sea-surface temperatures in Nanaimo in 2000 may have affected changes in the prey field available to juvenile chum, which led to lower mean growth rates for the summer (and may lead to lower returns for the brood year). Preliminary evidence from gut content analysis indicates that gut fullness was indeed lower for chum which resided in the Nanaimo area in 2000. I also suggested that these patterns were consistent with the differential growth hypothesis. In this Chapter, I presented evidence that the slower growing smolts were also subject to growth-selective mortality in 2000. This growth-selective mortality provides a clear mechanism whereby ocean conditions may influence juvenile salmon smolts through changes in food availability and differential susceptibility to predators.

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GENERAL CONCLUSIONS AND SYNTHESIS

In this study, I used my data, and evidence from the literature, to show that chum salmon otoliths fulfill the requirements to be useful in studying the early marine stage of salmon. Increments are formed daily, there is a strong relationship between otolith length and somatic growth, and a characteristic marine entry check is formed coincident with entry into the marine environment. Unlike many other studies, both the periodicity of increment formation and the formation of the marine entry check, were validated in the field. My enclosure experiment resulted in the first *real* validation of the deposition of the marine entry check in Pacific salmon to date.

Using otoliths collected from juvenile salmon in the Nanaimo area, I examined early marine growth rates and size-selective mortality in the early marine stage. I found evidence that while the mean growth of chum may differ significantly between years, and within a season, their timing of outmigration from freshwater is relatively inflexible. Possible causes of interannual differences in growth rate are variation in the size-at-marine-entry (which I found could also vary significantly between years), density-dependent interactions with conspecifics or pink salmon juveniles, or, most likely, variation in food availability resulting in higher predation rates on juveniles that suffer slow growth in years of poor prey supply. This last possibility is known as the 'differential growth hypothesis', and has been used to explain recruitment variability in Pacific salmon. To date, this hypothesis has received virtually no attention in the field.

Sources of error in this study were numerous, but such is the norm in studies of juvenile salmon ecology. For many of my analyses it was necessary to assume that all of the fish captured in the Nanaimo area formed a single, isolated population that we repeatedly sampled over time. Strictly speaking, this was not the case, but I have been careful to draw attention to this when this assumption could have influenced my results. Secondly, errors associated with the back-calculation technique used to derive growth rates from otoliths are potentially serious. In this study, significantly different growth rates were obtained by using two different back-calculation techniques. Nevertheless, back-calculation techniques are commonly used in the literature with much less attention to error than I have given herein. The science of otoliths is still relatively new, and with

time, a stronger understanding of the biases involved in back-calculation can be expected. The use of otolith-derived information, error included, remains the most powerful way (and sometimes the *only* way) of examining key issues in the early life history stages of fishes.

A look ahead

Early research on the high degree of interannual variability in recruitment of salmon populations focused almost entirely on examining possible freshwater limits to production. This focus on freshwater was probably not due to any deep-seeded belief on the part of early researchers that only the freshwater stage was important; more likely it was due to the considerable methodological, technological, and economic requirements of investigating the early marine stage. However, with time, it has become apparent that the marine life history stages play too important a role to be disregarded. Investigations of the importance of fishing pressure, the performance of hatcheries, and of natural variations in ocean environmental conditions have led many researchers to conclude that factors operating during the early marine stage of juvenile salmon may be key in determining year-class success. Unfortunately, this life history stage remains the most difficult to study effectively. Juvenile salmon enter the ocean from thousands of rivers, from large groups of mixed populations, they are preyed upon by a wide variety of predators, are subject to extremely high mortality rates, and in general, are only present in coastal waters for a few months before migrating offshore. Consequently, field studies of salmon early marine ecology have generally also been labour-intensive.

Using recently developed aging techniques, I have shown that otoliths from juvenile salmon captured in the field can be used to address similar questions, while providing higher resolution data and requiring less personnel hours. Most of the field sampling for this project was completed with just 3 people; the otolith analyses were completed by myself. Instead of estimating apparent growth (from the change in mean length of large numbers of fish over time, or from small numbers of mark-recaptured fish), otolith analyses can provide complete growth trajectories for each *individual* fish sampled. Similarly, otolith analysis offers an alternative to traditional methods of estimating peak date and size at outmigration (i.e. by capturing thousands of fish daily at

the river mouth); using otoliths, the date and size-at-entry can easily be back-calculated for each captured fish.

The robust 'characteristics of survivors' approach, which allows for the detection of selective mortality, is only possible with the knowledge of fish size or growth at an earlier date – a feature most reliably determined with otoliths. This ability to move from focusing at the level of the population to the level of the individual is one of the most important advantages of using otoliths, and mirrors a similar change in recent larval fish research. Scientists working with the early life history stages of fish are now realizing the power of individual-based models (IBM's) in modeling larval fish dynamics. Thus, the application of otolith techniques to studies of the early marine stage of salmon, though necessitated by the logistical difficulty of exploring the 'classical' issues of growth and mortality with 'classical' techniques, allows for an *individual*-based way of looking at juvenile salmon ecology. The results presented in this thesis merely point toward what is possible: I expect that within 5 years it will become common practice to use otoliths to determine the growth rate, temperature history, and origin of juvenile salmon with a daily resolution.

The ease with which individual growth histories can be determined with otoliths does not necessarily imply that sampling requirements will be any less intense. With early marine mortality rates as high as 90 %, juveniles must be sampled often enough to avoid the 'characteristics or survivors' bias. If we only examine the survivors, we cannot infer the characteristics of the initial population (which is composed of many fish that won't survive to the end of the summer). Thus, the ideal study examining the early life history stage of salmon would incorporate both the large scale of historical studies, and the use of otoliths.

Appendix 1A: 1999

St. 1 Biol Station (Dep't Bay West)

	N	mean l	Std	mean wt	SD	surf temp	surf sal	depth
9901								
9902								
9903	129	7.3	1.5	3.32	2.13	13.2	26.4	15
9904								
9905								

St. 2 Hammond Bay

	N	mean l	SD	mean wt	SD	surf temp	surf sal	depth
9901								
9902	171	5.6	0.9	1.51	0.68	10.2	27.4	23
9903	166	7.9	5.6	4.01	2.98	12.8	21.5	20
9904	0							
9905*	2	9.1	5.6	12.66	11.23	16.6	21.3	22

St. 4 Snake Island

	N	mean l	SD	mean wt	SD	surf temp	surf sal	depth
9901 x								
9902								
9903								
9904								
9905	6	12.4	0.9	18.51	6.69	16.36064	20.475	22

St. 5 Lock Bay

	N	mean l	SD	mean wt	SD	surf temp	surf sal	depth
9901								
9902	206	6.8	1.3	2.94	1.67	11.5	27.4	30
9903	115	7.9	1.5	4.21	2.11	12.6	26.4	25
9904	28	7.2	1.1	3.18	1.56	18.2	17.7	22
9905	6	14.3	2.6	28.11	16.63			25

St. 6 Descanso Bay

	N	mean l	SD	mean wt	SD	surf temp	surf sal	depth
9901	257	7.5	1.1	3.75	1.47	10.7	26.0	25
9902	55	8.0	1.5	4.63	2.33	11.2	27.3	15
9903	4	6.6	0.8	2.17	0.60	12.7	25.3	22
9904	2	12.6	0.8	14.68	6.68	15.4	23.0	25
9905								

St. 7 Northumberland Channel

	N	mean l	SD	mean wt	SD	surf temp	surf sal	depth
9901 x*2								
9902								
9903								
9904	23	10.9	2.5	13.74	9.46	13.5	20.8	22
9905	25	10.8	1.2	10.02	3.59	13.9	25.1	26

St. 8 Pylades Channel

	N	mean l	SD	mean wt	SD	surf temp	surf sal	depth
9901								
9902								
9903								
9904	53	8.09	1.34	4.59	2.89	12.5	23.7	15
9905	14	12.4	2.3	15.62	7.95	15.3	23.5	25

St. 9 Boat Harbour

	N	mean l	SD	mean wt	SD	surf temp	surf sal	depth
9901 x								
9902								
9903								
9904	42	9.6	1.2	7.07	2.56	12.5	25.2	15
9905	8	11.0	1.7	9.17	4.12	16.3	24.5	18

St. 10 Jack Point

	N	mean l	SD	mean wt	SD	surf temp	surf sal	depth
9901 x								
9902	108	6.8	1.0	2.80	1.07	9.8	27.6 ?	
9903*	116	7.2	0.8	2.91	0.86	11.2	26.8	23
9904								
9905	1	12.9	0.0	17.36	0.00	17.4	20.8	20

St. 12 Newcastle

	N	mean l	SD	mean wt	SD	surf temp	surf sal	depth
9901	24	7.9	1.6	4.19	1.64	10.0	27.6	19
9902	70	7.3	1.3	3.23	1.57	13.2	26.1	16
9903	0							
9904								
9905						17.4	20.8	25

St. 13 Departure Bay

	N	mean l	SD	mean wt	SD	surf temp	surf sal	depth
9901 x*3								
9902	112	6.1	1.1	2.01	1.06	10.6	27.5	
9903	94	7.9	1.7	4.42	2.34	10.0	27.4	25
9904	0					11.5	27.5	29
9905								

St. 15 Pilot Bay

	N	mean l	SD	mean wt	SD	surf temp	surf sal	depth
9901	164	6.5	1.1	2.48	1.24	10.5	26.8	25
9902	107	9.1	7.9	5.29	2.35	11.0	27.4	30
9903	8	8.3	2.2	5.85	5.09	13.4	24.6	22
9904	6	14.8	2.2	35.68	16.16	16.8	20.9	13
9905								

St. 24 Hudson Rocks

	N	mean L	Std	mean wt	SD	surf temp	surf sal	depth
9901	0							
9902	0							
9903	3	10.4	2.5	9.85	7.32			20
9904	2	13.6	0.1	22.53	3.06	16.4	21.5	16
9905								

Appendix 1B: 2000

St. 1 Biological Station

	N	Sub N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1	23		5.1	0.4	0.98	0.31			26
2	19		6.4	1.3	2.14	1.70			25
3	28		8.1	1.2	3.86	1.67	16.8	24.7	26
4	31	16	9.0	1.4	6.66	3.39	15.8	25.4	19
5									

St. 2 Hammond Bay

	N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1	51	6.0	1.0	1.87	1.30	12.3	24.9	30
2	20	8.7	1.2	5.22	2.40			20
3	0					17.0	22.8	18
4	0					16.2	25.0	15
5								

St. 3 Five Finger Island

	N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1								
2								24
3	33	7.1	1.1	2.83	1.47	16.3	24.6	
4								22
5	0							

St. 5 Lock Bay

	N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1	0							14
2 acid								
3	30	8.6	1.2	5.17	2.30			23
4	4	6.6	0.6	2.00	0.57	17.2	23.5	18
5	0							26

St. 6 Descanso

	N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1	126	5.5	1.2	1.52	1.21			17
2 acid								
3	11	8.0	1.0	3.79	1.43			26
4	5	7.1	1.8	3.06	2.99	15.6	25.7	25
5	0							24

St. 10 Jack Point

	N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1**	66	4.7	0.8	0.76	0.55			20
2 acid								
3	3	8.1	1.1	4.71	2.03			26
4						17.7	23.6	23
5	0							

St. 12 Newcastle

	N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1	5	4.0	0.6	0.42	0.23			16
2	106	5.8	1.0	1.95	1.05			31
3	36	7.3	0.8	2.90	1.13	16.8	25.6	23
4	1	8.9	0.0	5.29	0.00	16.9	23.8	23
5	0							18

St. 13 Departure Bay

	N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1	39	5.6	1.5	1.53	1.41			18
2**	207	5.4	0.8	1.24	0.75			25
3	19	6.5	1.1	2.09	1.13			21
4	15	7.1	1.2	2.60	1.55	14.6	26.2	25
5	0							17

St. 15 Pilot Bay

	N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1								
2 acid								
3	1	9.6	0	6.47	0.00			26
4								
5	0							26

Appendix 1C: 2001

St. 1 Biol Station

	N	Sub N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1	8	8	6.9	1.0	2.27	0.96			17.0
2	9	9	7.4	0.7	3.01	1.08			17.5
3	133	89	4.9	0.9	0.92	0.70			16.5
4	74	74	6.4	0.6	1.92	0.52			18.3
5	5	5	8.3	0.8	4.01	1.26			

St. 2 Hammond Bay

	N	Sub N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1	0	0							14.5
2	0	0							15.5
3	3	3	4.9	0.6	0.81	0.29			16.0
4	63	63	6.9	1.0	2.72	1.34			15.5
5	96	86	10.3	1.2	11.05	3.79			

St. 5 Lock Bay

	N	Sub N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1	7	7	4.9	0.3	0.69	0.10			15.0
2	0	0							17.0
3									
4	106	106	6.2	1.1	1.81	1.24			15.0
5	1	1							

St. 6 Descanso Bay

	N	Sub N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1	89	89	5.4	0.7	1.07	0.54			15.5
2	51	51	6.1	1.4	2.03	1.33			15.0
3	57	57	6.4	0.9	2.20	1.04			16.5
4	23	23	7.0	0.8	2.50	1.07			15.0
5	0	0							

St. 10 Jack Point

	N	Sub N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1	0	0							14.5
2	0	0							16.5
3	774	74	5.6	0.6	1.47	0.55			16.5
4	45	44	6.9	0.4	2.45	0.48			14.5
5	0	0							

St. 12 E. Newcastle Island

	N	Sub N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1	0	0							14.5
2	0	0							16.0
3	81	81	6.6	1.3	3.05	2.12			16.5
4	27	27	6.9	1.0	2.56	1.61			15.0
5	7	7	8.7	1.9	6.37	5.40			

St. 13 Departure Bay

	N	Sub N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1	0	0							15.0
2	0	0							17.0
3	366	116	5.1	0.8	1.15	0.70			17.0
4	67	67	6.3	0.7	1.84	0.57			15.0
5	19	19	10.1	1.3	9.11	3.40			

St. 15 Pilot Bay

	N	Sub N	mean L	SD	mean wt	SD	surf temp	surf sal	depth
1	0	0							15.5
2	0	0							17.5
3	1064	64	7.1	1.1	3.50	1.83			13.5
4	14	14	8.9	1.1	5.78	2.40			
5	2	2	11.5	2.4	14.51	10.66			