Fine-scale structure in the ecology of juvenile Chinook Salmon at sea

by

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Abstract

Fisheries oceanography often aims to link large scale atmospheric and oceanic processes to variability and trends in the productivity of economically and ecologically valuable fish species. Declines in productivity of multiple species of Pacific Salmon (genus *Oncorhynchus*) in recent decades have spurred the search for a 'smoking gun;' an explanation that could explain trends in productivity across populations, regions and species. Despite extensive investment of research effort and funding, such an explanation remains elusive. The lack of a unifying explanation for declining productivity of Pacific Salmon may be due to the spatial and temporal complexity of their interactions with the marine environment. This complexity has historically been understudied, in part due to logistical limitations of research on Pacific Salmon at sea. This dissertation reports the results of a detailed study of how juvenile Chinook Salmon *O. tshawytscha* interact with marine habitats during their first summer and fall at sea. I first developed and validated a novel, hook and line-based method of sampling juvenile Chinook Salmon (microtrolling). I then reviewed and empirically compared methods (insulin like growth factor-1 concentration, RNA to DNA ratio, and scale circulus spacing) for indexing growth rate of juvenile salmon sampled in the ocean, a variable which is hypothesized to be related to subsequent survival. I integrated microtrolling with small vessel oceanography to relate distribution, diet, size and growth of juvenile Chinook Salmon to local scale variation in water column properties (stratification) and zooplankton community composition and abundance for five sites in the Southern Gulf Islands of the Salish Sea during a single summer (2015). While both stratification and zooplankton abundance and composition varied between sites, I failed to find support for the hypothesis that juvenile salmon distribution and growth was positively related to water column stratification at fine spatial scales. Juvenile Chinook Salmon were larger and faster growing where juvenile Pacific Herring *Clupea pallasii* were important in their diets, suggesting that Pacific Herring may play an important role in structuring the ecology of juvenile Chinook Salmon at sea. I built on 2015 results to conduct a detailed case study of juvenile Chinook Salmon ecology at two sites in the Southern Gulf Islands: Sansum Narrows and Maple Bay. Juvenile Chinook Salmon were consistently larger, more piscivorous, and faster growing at Sansum Narrows than Maple Bay across two years (2015 and 2016) despite lower zooplankton

abundance at Sansum Narrows. Hydroacoustic surveys in September 2017 confirmed prior qualitative observations of elevated occurrence of forage fish schools (likely age-0 Pacific Herring) at Sansum Narrows, and a novel, mobile acoustic tag tracking survey suggested that fish tagged at Sansum Narrows may co-locate with juvenile Pacific Herring over the tidal cycle. By relating a scale circulus spacing-based growth index to reconstructed size intervals I found that juvenile Chinook Salmon at Sansum Narrows had been faster growing that those at Maple Bay before the transition to piscivory, and perhaps before migration to the ocean. These results suggest that intrinsic growth potential, or growth conditions during freshwater rearing or the transition to marine residence, interact with fine-scale structure in marine habitats to regulate growth potential of juvenile Chinook Salmon at sea. These factors also likely interact with the basin and interannual scale processes that have received extensive study as regulators of marine survival of juvenile Pacific salmon. These complex interactions should be taken into account when designing or interpreting studies to determine factors limiting productivity of Pacific Salmon populations.

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I dedicate this dissertation to my wife Faron, her patience and support during this process were, as always, above and beyond the call of duty.

Chapter 1 - Introduction

The spatial and temporal scales at which organisms perceive their environment are both consequences and ongoing drivers of ecological and evolutionary processes; however, our understanding of how species experience environmental variability may be limited by the scales at which we are capable of studying an ecosystem (Levin 1992). This challenge is particularly apparent in the oceans, where our observational abilities are limited by our physiology. In pelagic habitats in particular, spatio-temporal patterns may be transient and direct detailed observation is generally not possible (Steele 1991). Nevertheless, it has long been recognized that pelagic habitats are strongly structured on multiple spatial and temporal scales (Stommel 1963), and that most pelagic organisms likely depend on a heterogeneous distribution of resources for effective foraging (Steele 1980). A variety of approaches have therefore been developed to investigate spatiotemporal structure in pelagic ecosystems, including satellite-based remote sensing (e.g. Haney 1989, Etnoyer et al. 2004, Bi et al. 2008), hydroacoustics (e.g. Simard et al. 2002), continuous plankton recording (e.g. Mackas et al. 1980, Richardson et al. 2006), and survey designs employing plankton nets (e.g. Shanks and Wright 1987, Dower and Mackas 1996) and fishing gears of various types (e.g. Orsi and Wertheimer 1995, De Robertis et al. 2005).

Overcoming the challenges of studying pelagic ecosystems is fundamental to fisheries oceanography, a discipline that can be defined as "the study of oceanic processes affecting the abundance and availability of commercial fishes" (Wooster 1961). From its genesis in the ideas of Hjort (1914), one of the key themes of fisheries oceanography has been how environmental processes mediate fishery recruitment (survival to harvestable size) through the availability of food to early life history stages of marine fish. The critical period hypothesis of Hjort (1914) and its derivatives - notably the aberrant drift hypothesis (Hjort 1926), match-mismatch hypothesis (Cushing 1974) and stable ocean hypothesis (Lasker 1978) - were concerned primarily with impacts of ocean conditions on starvation or survival of larval fish at the stage where they transition from endogenous reserves to exogenous feeding. Over the last century, awareness has grown that there is no single stage or process that controls recruitment, but rather that

environmental factors, predation, density dependence and their interactions, operating at multiple spatial scales throughout pre-recruit stages, all play a role (reviewed by Houde 2008).

Ontogenetic shifts in habitat and trophic position add spatio-temporal complexity to the already complex interactions regulating recruitment of marine fish. Pacific Salmon (genus *Oncorhynchus*) are a case in point, beginning their life in freshwater ecosystems before migrating to the ocean, where they exhibit species and population specific occupancy patterns in estuarine, nearshore epipelagic, and offshore habitats in the course of extensive migrations during growth and maturation (Quinn 2005). The spatio-temporal scales on which Pacific Salmon ecology has been studied vary by habitat and life history stage. In freshwater habitats, where direct observation is relatively easy, extensive work has investigated development (e.g., Dill and Northcote 1970), trophic ecology (e.g., Sagar and Glova 1988), and habitat use (e.g., Everest and Chapman 1972) of juvenile Pacific Salmon at scales of centimeters to meters and hours to days. Similarly, adult habitat use (e.g., Kondolf and Wolman 1993) and reproductive behavior (e.g., Hendry et al. 1994, Quinn 1999) in freshwater have been studied at very fine scales. In the course of their migration to the marine environment, juvenile Pacific Salmon may occupy estuarine habitats (Quinn 2005), where they are again accessible to fine-scale ecological work (e.g., Healey 1980, Levy and Northcote 1982, Semmens 2008). However, as juvenile salmon move offshore they become more challenging to study, particularly at fine spatio-temporal scales in very large open marine systems, due to the cost and logistical limitations of ship-based sampling gears.

A growing consensus that interannual variability and long-term trends in Pacific Salmon productivity may be related to a period of high mortality during early marine residence (Parker 1965, Furnell and Brett 1986, Neville et al. 2015) has led to growth in research focusing on this period. Much of this work is built around the hypothesis that juvenile survival is linked to size and therefore to growth. Support for this hypothesis includes greater reconstructed first ocean-summer sizes of adult survivors (based on scales and otoliths) compared to juveniles sampled in their first summer at sea (Moss et al. 2005, Zavolokin and Strezhneva 2013, Howard et al. 2016, but see Beacham et al. 2018 for a critique of this approach); and evidence that cohorts which exhibit elevated early marine growth (or achieve greater size) experience relatively greater

survival (Holtby et al. 1990, Tovey 1999, Duffy and Beauchamp 2011, Tomaro et al. 2012, Graham et al. 2019). Beamish and Mahnken (2001) proposed a framework within which size is positively related to survival at two critical periods during the first year at sea. The first period occurs soon after ocean entry, when rates of size selective predation are hypothesized to be high (Parker 1971, Holtby et al. 1990). The second period occurs during the first marine winter, when fish which have not achieved adequate size (or in later formulations of the hypothesis, adequate lipid reserves, Beamish et al. 2008) experience mortality due to a nutrient deficit. This hypothesized link between growth and survival has led to a proliferation of studies focused on diet and growth during the first marine year (e.g. Duffy et al. 2010, Ferriss et al. 2014, Hertz et al. 2015, Journey et al. 2016, Chamberlin et al. 2017, Chittenden et al. 2017, Gamble et al. 2018, Davis et al. 2020).

Spatial analyses of the distribution, diet, or growth of juvenile Pacific Salmon in the pelagic environment are most often conducted at broad regional scales (e.g. Brodeur et al. 2007, Ferriss et al. 2014, Hertz et al. 2015). However, when similar analyses are conducted at sub-regional or sub-basin scales, spatial patterns which suggest finer scale variation in habitat quality are generally detected (e.g. Healey 1978, Perry et al. 1996, Peterson et al. 2010, Journey 2015). Understanding the mechanisms behind this spatial variability has proved challenging, as few studies have explicitly related catch per unit effort (CPUE) and biological characteristics of captured fish to local scale physical oceanographic features (but see St. John et al. 1992 and de Robertis et al. 2005). A number of studies have attempted to characterize marine habitat of juvenile salmon in the California Current system, but these have tended to be correlational at a relatively coarse scale. Catch per unit effort data over a trawl track of 3 km or more (Peterson et al. 2010), have been related to phytoplankton, zooplankton and/or physical data collected at a single station along that track (Bi et al. 2011, Pool et al. 2012, Burke et al. 2013) and/or remote sensing data collected at a relatively coarse scale (e.g. Bi et al. 2008). This work has increased understanding of what constitutes suitable juvenile salmon habitat at a broad scale. However, as patchiness in juvenile salmon abundance likely occurs at levels finer than a trawl track (Peterson et al. 2010), inferences about the fine scale interactions between salmon and their prey are not possible. Nevertheless, intriguing hints of fine-scale patterns exist. Orsi and Wertheimer (1995) found that juvenile Chinook Salmon in Southeast Alaska were concentrated just below

thermoclines and haloclines, and Journey (2015) suggested that regional patterns in growth rates of juvenile Salmon in the Strait of Georgia could be linked to regional differences in water column stratification. Peterson et al. (2010) suggested that patchiness of juvenile Chinook and Coho Salmon catches in the California Current could be related to fish targeting concentrations of euphausiids retained by canyon head circulation, and hydroacoustic work investigating herring and juvenile salmon distribution in Puget Sound detected concentrations of biomass associated with abrupt topographies (Kemp 2014). Recent work off California has found that stomach fullness of juvenile Chinook Salmon is higher adjacent to thermal fronts, oceanographic features which may concentrate prey (Sabal et al. 2020). Much work remains to be done to identify when, where, and how fine-scale processes are important to the trophic ecology of juvenile Pacific Salmon.

Linking environmental processes to survival is at the core of fisheries oceanography. Most studies investigating links between the environment and the diet, growth, size and survival of juvenile Pacific Salmon assume that variation in growth is a passive consequence of environmental conditions experienced by an individual (temperature, food quantity and food quality). The model of growth that is generally applied to fish is the von Bertalanffy growth curve which has its foundations in physical chemistry with growth conceived as the balance of processes which create (anabolism) and destroy (catabolism) tissue (von Bertalanffy 1938). As anabolism is a function of respiration, which is limited by two dimensional surfaces, while catabolism is a function of overall mass, growth rate under this model is proportional to the 2/3 power of mass, and reaches an asymptote at an organism's maximum size. The von Bertalanffy model is frequently an excellent fit to lifetime growth data (e.g. Chen et al. 1992). However, at the level of the individual and over shorter timescales fish growth does not follow a smooth convex trajectory. In temperate oceans, both food and temperature limitation induce seasonal variation in growth rate which can be described by a modified version of the von Bertalanffy model (Pauly et al. 1992, Ogle 2017). In addition to this seasonal variability, the realized growth rates of juvenile fish may also be a product of species, population, and individual level variability in behaviour and intrinsic growth rate.

Many organisms may experience growth-mortality trade-offs in which foraging behaviour that facilitates rapid growth also exposes individuals to greater mortality risk (see Werner and Anholt 1993 for a theoretical treatment and review of foundational literature). As conceptualized in foraging arena theory (Walters and Juanes 1993), such trade-offs can lead to strong selection on the amount of time that juvenile fish spend foraging and exposed to predation versus sheltering from predation. The adjacency of foraging arenas to sources of shelter from predation may limit the spatial volumes in which interactions occur between juvenile fish and their prey, leading to strongly density-dependent growth and survival even when prey is not limiting in the system (Walters and Juanes 1993, Aherns 2012). Vasbinder and Ainsworth (2020) invoked foraging area theory to explain divergent departures from the von Bertalanffy curve in the juvenile stages of pelagic and demersal fish. These authors suggest that growth is initially exponential in benthic fish due to increased time spent in the foraging arena as they outgrow predation risk. This contrasts with pelagic fish which have less access to refuge and exhibit an initially linear increase in size. In addition to such interspecific differences, intraspecific differences in the interactions between behaviour and growth have also been described (reviewed by Mittelbach et al. 2014). Domestic Rainbow Trout (*O. mykiss*) were more active in daylight and grew faster than wild-origin individuals in experimental lakes, but experienced higher mortality in the presence of predators (Biro et al. 2004). The fry of piscivorous *O. mykiss* from Kootenay Lake British Columbia were not only bolder than their insectivorous conspecifics in laboratory experiments, but also showed greater food intake, standard metabolic rate, and growth rate and efficiency (Monnet et al. 2020). Fry from the piscivorous stock also exhibited a greater investment in digestive organs and lower investment in heart and brain tissues than insectivores. As picivorous and insectivorous Rainbow Trout in Kootenay Lake also differ in life-history (piscivorous fish mature later and are longer lived), these results are consistent with the pace-of-life-syndrome hypothesis (Réale et al. 2010) which proposes that suites of behavioural, physiological and life-history traits may all covary at the individual, population or species level. There is ample additional evidence that growth rate in salmonids is under genetic (Hard et al. 2008, Debes et al. 2020) and behavioural (Metcalfe et al. 1988, Vøllestad and Quinn 2003), in addition to environmental, control. More work is required to integrate these concepts into our understanding of juvenile Pacific Salmon growth and survival at sea.

1.1 Dissertation Outline

This dissertation presents a multifaceted, fine-scale investigation of factors influencing juvenile Chinook Salmon growth potential during the summer and fall of their first year at sea. It includes the development of novel methods to support this investigation. This research formed part of the Salish Sea Marine Survival Project (marinesurvivalproject.org), a binational initiative to understand factors influencing marine survival of Chinook and Coho Salmon (*O. kisutch*) and Steelhead (*O. mykiss*) in the Salish Sea (collectively the inland waters of Southern British Columbia and Washington State: The Strait of Georgia, Puget Sound, and the Strait of Juan de Fuca).

Most sampling of juvenile Pacific Salmon at sea relies on large vessels (trawlers and seiners) that are expensive to operate and may not be able to sample fish at fine spatial resolution or in all nearshore pelagic habitats. These constraints present a challenge for attempts to investigate the marine ecology of juvenile salmon at fine spatial and temporal scales. Chapter 2 introduces a novel method of non-lethally sampling juvenile salmon at sea using systematic deployments of hook and line gear from a small vessel termed "microtrolling." I describe the approach and develop a generalized additive modelling-based analytical framework for investigating patterns of CPUE as a binomial response at the level of the individual hook. I also present data on a limited post-release holding study that assessed the short-term mortality associated with microtrolling capture, measurement, gastric lavage, and passive integrated transponder (PIT) tagging.

One prerequisite for understanding factors regulating growth of fish in the wild is development of techniques for assessing recent growth history. Chapter 3 describes a laboratory study to validate and compare three indices of recent growth in juvenile salmon captured in the wild: insulin-like growth factor-1 (IGF-1), RNA to DNA ratio, and spacing of circuli near the margin of the scale. These three indices are compared both for their ability to index recent growth of post-smolt Chinook Salmon reared at ecologically plausible growth rates and for the speed at which they reflect a change in feeding conditions. I present a synthetic comparison of the growth rate indices available for ocean ecology research on Pacific Salmon, including theoretical and logistical considerations.

No previous work on juvenile Pacific Salmon during their first year at sea has linked within sub-basin variation in distribution, diet and growth to variation in physical and biological oceanography at fine spatial and temporal scales. Chapter 4 describes a study that related CPUE and biological characteristics of juvenile ocean-type Chinook Salmon at five sites in the Southern Gulf Islands of the Salish Sea to water column stratification and zooplankton community composition and abundance data collected concurrently with fish sampling between July and October of 2015. This work tested the hypothesis that juvenile Chinook Salmon would select more stratified local habitats where they would experience accelerated growth. One of the five surveyed sites was a tidal jet, and I also sought to assess whether this site represented a foraging hot spot for juvenile Chinook Salmon. In the course of this study it became evident that juvenile Pacific Herring (*Clupea pallasi*) might play a key role in structuring the marine ecology of juvenile Chinook Salmon in the study region. I therefore also tested whether size, growth rate, and stomach fullness of juvenile Chinook Salmon which had consumed Pacific Herring differed from those that had not.

The growth potential and survival of juvenile Pacific Salmon in the wild may be consequences not only of large scale spatial and temporal variation in environmental conditions, but also of local scale environmental variation, behaviour and intrinsic growth potential of individual fish, and the interaction of these factors and scales. The results presented in Chapter 4 suggested intriguing differences in the diet, size and growth of individual fish between two adjacent (4 km apart) sites within the Southern Gulf Islands of the Salish Sea (Sansum Narrows and Maple Bay). In Chapter 5 I developed these sites as a case study of how fine scale environmental variation and characteristics of individual fish may interact to mediate growth and survival. I combined CPUE and biological data collected in 2015 with second year of juvenile Chinook Salmon sampling in 2016 to determine if differences between Chinook Salmon at the two sites were consistent across years. Reconstruction not only of recent growth rates, but also of growth rates earlier in life, including at, or prior to, ocean entry, allowed me to assess whether growth and marine habitat use of juvenile Chinook Salmon was related to prior growth experience. I also attempted to characterize how and why juvenile Chinook Salmon prey availability differed between Sansum Narrows and Maple Bay using a combination of depth stratified zooplankton sampling and active acoustic surveys with an acoustic zooplankton fish

profiler (AZFP) in September of 2017. This approach allowed me to test the hypothesis that the tidal jet at Sansum Narrows provided feeding opportunities for forage fish prey of juvenile Chinook Salmon by providing a subsidy of zooplankton advected from depth, as has been described for other tidal narrows (Zamon, 2002, 2003). To assess the behavioural differences between fish captured at these case study sites, I also compared the distribution and tidal movements of juvenile Chinook Salmon captured and acoustic tagged at each site in the fall of 2017. This integration of biological sampling of juvenile salmon (diet and size), growth rate reconstruction, biological oceanography (zooplankton tows), hydroacoustic surveys, and acoustic telemetry, all focused on such a fine spatial scale, is unprecedented in juvenile Pacific Salmon marine ecology research. I trust that the work described in this dissertation will advance understanding of factors regulating growth and survival of juvenile Pacific Salmon in the ocean and will inform design of future studies to investigate factors limiting recruitment of these ecologically, economically and culturally important species.

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Chapter 2 - Microtrolling: an economical method to non-lethally sample and tag juvenile Pacific salmon at sea

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2.1 Abstract

Mortality of juvenile Pacific salmon in their first marine year is hypothesized to be a primary driver of variable recruitment in a changing ocean. Much contemporary research focusses on diet, distribution, growth, and survival during this period; however, existing methods of capturing juvenile salmon at sea are expensive and may be limited by topography and tidal currents. We assessed the feasibility of using a small vessel and modified recreational fishing gear (microtrolling) to non-lethally capture, sample and tag juvenile Chinook Salmon *Oncorhynchus tshawytscha* during their first marine summer. Sampling was conducted in the Strait of Georgia from August to October 2014. We captured 168 Chinook, 13 Coho *O. kisutch*, and one Chum Salmon *O. keta* in 72 hours of active fishing; Chinook Salmon catch per unit effort was greatest between six and nineteen meters and increased late in the afternoon and on the flood tide. To assess short-term capture, passive integrated transponder (PIT) tagging, and sampling related mortality we maintained 66 microtroll-captured Chinook Salmon (41 of which were PIT tagged) overnight in a net pen; observing only one mortality and one incidence of tag loss. Microtrolling proved effective for systematically sampling juvenile Chinook Salmon across depths and habitats. Unlike alternative methods of sampling juvenile Pacific salmon (trawling and purse seining), the utility of microtrolling is likely limited to studies of Chinook and possibly Coho Salmon. The low cost of this method has potential to facilitate participation of frequently excluded stake holders, including First Nations and community groups, in marine research on juvenile Pacific salmon.

2.2 Introduction

Early marine residence is widely considered to be a period of high and variable mortality for juvenile Pacific salmon, with implications for both interannual variation and long-term trends in recruitment (Parker 1965; Beamish and Mahnken 2001; Wells et al. 2012; Wells et al. 2016). The mechanisms underlying this mortality are a major focus of contemporary research, much of which involves capture and sampling of juvenile salmon. Long-term monitoring studies annually measure abundance, distribution, diet, size, and condition of juvenile salmon at sea (Beamish et al. 2000; Brodeur et al. 2003); and in some cases these data contribute directly to forecasting of future returns (Karpenko et al. 1998; Wertheimer et al. 2013). Ocean sampling of juvenile

salmon also facilitates investigations of how size, condition, pathogen or parasite load, ontogenetic patterns in habitat use, and trophic position may relate to growth and survival (Duffy et al. 2010; Duffy and Beauchamp 2011; Miller et al. 2013; Kemp et al. 2014; Miller et al. 2014; Godwin et al. 2015; Hertz et al. 2015). Tagging studies seek to directly measure marine mortality (Furey et al. 2015) and in some cases to localize mortality in space and time (Melnychuk et al. 2013) or link it to a proximate cause (Berejikian et al. 2016).

Juvenile Pacific salmon in their first marine year are seldom encountered by commercial fisheries. Most research focussing on early marine residence and mortality of Pacific salmon therefore relies on fishery-independent sampling methods. Many gear types have been used to sample juvenile salmon in the marine environment. These include beach seines, purse seines, gill nets, dip nets, traps, surface trawls and midwater trawls of various types (reviewed in Beamish et al. 2003; Brodeur et al. 2003; Karpenko 2003). The primary contemporary methods used to capture juvenile Pacific salmon for research are rope trawling and purse seining. Rope trawling involves a large powerful vessel towing a net with a very large opening (often greater than 1000 m^2) at high speed (up to 9 km/h). This method can sample at all depths and in all weathers and is non-selective, capturing both juvenile and adult salmon of all species (Beamish et al. 2003). Rope trawling also allows large volumes of water to be sampled at a given depth stratum and large numbers of juvenile salmon to be obtained for sampling. Disadvantages of rope trawling are that the large vessels involved cannot operate close to shore or in narrow passages, nets cannot be deployed safely in shallow water, and fish are killed during capture and cannot be used for tagging studies. In addition, scales are typically rubbed off during capture, limiting aging and growth rate analyses to more labour-intensive otolith processing. Given the relatively high tow speed, distance covered per tow is typically greater than 2 km (Beamish et al. 2000; Duffy and Beauchamp 2011), limiting the scale at which juvenile salmon distribution patterns can be resolved. Vessel availability also presents major challenges for trawl sampling programs due to high costs of chartering capable vessels and multipurpose-use requirements of government agency vessels.

Unlike trawling, purse seining allows fine-scale point sampling of juvenile salmon distribution. Also, fish are landed alive, meaning that they can be used for tagging studies (e.g.

Chittenden et al. 2009; Neville et al. 2015). Purse seines can also be deployed close to shore and in confined areas. However, a major problem with purse seines is that the small mesh needed to retain juveniles restricts where and when sets can be made, resulting in a non-random survey (D. Beamish personal communication), depth-stratified fishing is not possible, and sorting salmon from bycatch can be time consuming and result in mortality (for example if bycatch consists of large jellyfish). Purse seining also samples far less water than trawling and may not be an economical method to sample juvenile salmon at low densities, particularly as vessels capable of deploying a large purse seine are expensive to charter. Smaller, hand-hauled purse seines have been used effectively from small vessels, but they are only suitable for use in shallow water (e.g. Healy 1980), or to sample surface-oriented juvenile salmon (e.g. Godwin et al. 2015).

Hook and line methods have been used infrequently to sample juvenile salmon at sea. Rich (1920) used hook and line sampling, primarily from cannery wharves, as part of an investigation of juvenile Chinook Salmon *Oncorhynchus tshawytscha* life history in the Columbia and Sacramento River estuaries. Orsi (1987) assessed whether a commercial troller with scaled-down hooks and lures could be used to effectively sample juvenile Chinook and Coho Salmon *O. kisutch* in Southeast Alaska. Building on the success of this trial, Orsi and Wertheimer (1995) used trolling to study the vertical distribution of juvenile Coho and Chinook Salmon with respect to season and physical oceanography; and Orsi and Jaenicke (1996) investigated temporal and spatial patterns of age and origin for prerecruit Chinook Salmon in Southeast Alaska. Despite the success of these studies, trolling has not caught on as a sampling method for juvenile salmon.

Marine survival of Chinook and Coho Salmon in the Strait of Georgia, British Columbia and Puget Sound, Washington has declined dramatically since the 1980s (Beamish et al. 1995, Beamish et al. 2010, Zimmerman et al. 2015); providing the impetus for an ongoing binational research initiative, the Salish Sea Marine Survival Project. This initiative includes projects which investigate spatiotemporal patterns in diet, growth and predation exposure of juvenile salmon and tagging studies which seek to identify potential critical mortality periods. As part of this work, we identified the need for a low-cost method that could be used to capture, biologically sample, and apply passive integrated transponder (PIT) tags to juvenile Chinook and Coho

Salmon in the latter part of their first summer at sea. We therefore investigated the feasibility of using modified recreational fishing gear deployed from a small vessel (microtrolling) to non-lethally capture juvenile salmon. Specifically, we assessed the utility of microtrolling to investigate fine scale patterns in distribution; compared sizes of fish captured by microtrolling and alternative methods; and investigated short term (overnight) mortality resulting from hook and line capture in conjunction with sampling and tagging.

2.3 Methods

2.3.1 *Microtrolling*

Sampling occurred in the vicinity of Cowichan Bay, British Columbia, Canada (Figure 2.1) on 30 days between 9 August and 3 October 2014, using an open 4.9 m welded aluminum boat powered by a 37 kW outboard motor. Gear was deployed using Electric Downriggers (Scotty Depthpower, Scott Plastics, Victoria, British Columbia) spooled with 90 kg breaking strain braided dacron line and weighted with a 6.8 kg lead ball. These downriggers are equipped with a switch which automatically stops retrieving when activated by a plastic stopper on the line. Stoppers were placed on the line at measured intervals to allow each piece of gear (henceforward "leader") to be fished at a predetermined depth. Leaders consisted of a stainless steel clip for attachment to the downrigger line, 2 m of 18 kg breaking strain monofilament, a stainless steel swivel, and a piece of terminal gear attached with 50 cm of 2.4-3.6 kg breaking strain monofilament. This light line was used to allow any adult salmon encountering the gear to break free. Terminal gear consisted primarily of either a transparent pink and purple 2.5 cm "Apex" plastic lure ("UV Trout Killer" Hot Spot Lures Ltd. Victoria, British Columbia) or a 2 cm "fly" consisting of strands of red and pearlescent mylar tied in with thread at the front end of a mylar-wrapped hook (henceforward apex and fly respectively). To impart erratic movement, flies were tied 50 cm behind a 7 cm gold and chrome 'Super Diamond' salmon spoon (Gibbs-Delta Tackle, Delta, British Columbia) which was connected directly to the 2 m of heavy monofilament. Hooks for all gear types were #12 fly tying hooks with a 5 mm point to shank gap and 1.5 cm shank length (Mustad and Sons Inc., Doral, Florida). In general, barbs on hooks were crushed with pliers (to minimize hooking injury) and the two terminal gear types described above were fished on either side of the vessel. To assess the impact on catch per unit effort

(CPUE) of removing barbs, during the final eight sampling days (after 16 September) only flies were used, with barbless hooks on one side of the vessel and barbed hooks on the other. A schematic diagram of gear configuration is provided in Figure 2.2.

Gear was deployed in standardized fishing events. For each fishing event, the time of day was logged before beginning to deploy gear and the times required to lower gear to the desired fishing depth and to retrieve gear were measured with a stopwatch. Where two crew members were available, lines on both sides of the boat were dropped and retrieved simultaneously and gear was fished for 5 minutes. Where only one person was available, the two sides were dropped and retrieved sequentially and fished for only 4 minutes to compensate for the extra time required to lower and retrieve. The depth fished and number of leaders deployed depended on water depth; in general, up to five leaders were fished per side at 4 to 8 m intervals from depths of 2 m to 34 m. At shallower bottom depths, fewer leaders were deployed. Latitude and longitude were recorded at the beginning and end of each fishing event using a handheld GPS unit. The course and amount of throttle applied during gear deployment were adjusted based on topography and prevailing wind and current to maintain a relatively constant forward motion through the water (approximately 2.5 km/h). It was not possible to determine lure speed using GPS data as prevailing currents could result in speed over ground that was substantially greater or less than the speed through water. We targeted a speed through water that would result in erratic action of our lures without making them too difficult to catch. As gear was retrieved, presence (and species) or absence of fish on each hook was logged.

Some sampling effort (approximately 12 days) focused on testing the feasibility of pseudo-systematic spatial sampling across different habitats; with one or more fishing events occurring at each of a series of pre-determined waypoints between Cowichan Bay and Maple Bay. These included sites in open water, close to shore, and adjacent to Sansum Narrows, a narrow (500 m) passage with tidal currents reaching more than 4 knots. Most of the balance of the sampling days focussed on maximizing catch for the post-release mortality assessment. Fishing effort on these days occurred primarily in Maple Bay within 3.5 km of the net pen site at Octopus Point (Figure 2.1); and fishing events generally occurred consecutively without moving

to a different site. Some additional effort was expended on reconnaissance of additional areas, particularly Saanich Inlet.

2.3.2 *Fish processing*

Fish were lifted aboard and lowered directly into a 150 L cooler partially filled with seawater. Water in the cooler was periodically refreshed and temperature was monitored to ensure that it did not exceed 17 °C. All non-salmon were identified to species and immediately released. Using small mesh-bottomed containers, all juvenile salmon were gently transferred into an anaesthetic bath (80 mg/L Tricaine methanesulfonate) for unhooking and sampling.

Juvenile salmon were examined for the presence of an adipose fin clip and wanded with a metal detector (to assess coded wire tag presence) and PIT tag reader. Nose to fork length (FL) was recorded to the nearest millimeter and five scales (to be used for genetic stock identification, see below) were removed from the preferred area (just above the lateral line immediately posterior to the dorsal fin) using forceps and transferred to a gummed scale card. To express stomach contents (gastric lavage), a section of 3 mm diameter plastic tubing, glued to the outlet of a 250 mL wash bottle, was slid gently in and out of the stomach of fish held inverted above a plastic container while seawater was continually expressed from the bottle. Chinook Salmon that did not exhibit sustained bleeding or hook damage to the eye had a 12.5 by 2.1 mm PIT tag (HPT12 FDX-B; Biomark, Boise, Idaho) injected intraperitoneally in a posterior direction approximately 5 mm off the dorsal midline and just anterior to the pelvic girdle. Total handling time from first being placed in the anaesthetic bath was approximately 3 minutes. Fish were returned to the 150 L cooler and allowed to regain equilibrium before being released near the site of capture.

2.3.3 *Genetic stock identification*

To determine whether PIT tagged Chinook Salmon originated from the Cowichan River, and in turn which tags should be included in an ongoing (2014 to at least 2019) investigation of Cowichan River Chinook Salmon survival, scale samples were submitted to the Canadian Department of Fisheries and Oceans (DFO) molecular genetics laboratory at the Pacific

Biological Station. DNeasy® kits (Qiagen) were used for DNA extraction. Probabilities of belonging to 296 unique North American Chinook Salmon populations were assigned to each fish based on combinations of alleles at 15 highly variable microsatellite loci using methods similar to those described in Beacham et al. (2012).

2.3.4 *Fish size relative to other gear types*

To assess potential size bias relative to alternative sampling methods, we obtained FL data for juvenile Chinook Salmon captured in the same region by DFO researchers using a chartered purse seiner fishing a 300 m long, 20 m deep seine net with a 6 mm mesh bunt, and the research trawler CCGS WE Ricker using gear as described in Beamish et al. (2000). Purse seine sampling occurred between 8 May and 23 July 2014 in the vicinity of Cowichan Bay while trawling occurred on 10 June and 17 September throughout the Southern Gulf Islands (Figure 2.1). There was little temporal overlap between microtrolling and other methods of sampling, and Chinook Salmon FL increased during the study period. As sampling method was not independent of time, statistical comparison of the size of Chinook Salmon captured by alternative methods was not possible. To facilitate qualitative assessment of size bias we graphically report FL by date for microtrolling and alternative capture methods (Chinook Salmon greater than 300 mm FL were assumed to be in their second marine year and were excluded).

2.3.5 *Post-release mortality assessment*

To assess short-term capture, tagging, and handling related mortality, a subset of juvenile Chinook Salmon were maintained overnight in a 1.2 by 1.2 by 2.4 m net pen consisting of a wood frame covered with 2.5 cm galvanized wire mesh (to deter predators) and lined with 5 mm nylon netting. The pen was weighted and suspended just sub-surface from a concrete dock at Octopus Point near Sansum Narrows (Figure 2.1). Our original study design sought to compare mortality of fish subjected to tagging and all handling (gastric lavage and scale sampling), to a control group which was only anaesthetized and measured. However, as we observed negligible mortality in both groups, and as logistical challenges limited sample size, we switched to sampling and tagging all fish prior to transfer to the pen. We maintained a total of 66 juvenile Chinook Salmon overnight in the net pen (4-11 fish per night over eight nights). Forty-one of

these fish were anesthetized, PIT tagged, gastric lavaged and had scales taken; of these 10 were captured on barbed hooks and 31 on barbless hooks. The remaining 25 fish were anaesthetized and measured only.

2.3.6 *Statistical analyses*

All analyses were conducted in the R statistical language (R Core Team 2015). Analysis of CPUE was based on whether an individual hook deployed for one fishing event did (value = 1) or did not (value = 0) catch a juvenile Chinook Salmon. Catches of other species were too low for meaningful analyses.

To provide an example of how microtrolling could be applied to study spatiotemporal patterns in habitat use, we employed a generalized additive modelling (GAM) approach with a logit link function (binomial family) to describe how CPUE varied with hour of the day, tidal stage, and depth. Tidal stage was defined as hours after the most recent low slack at Active Pass in the Southern Gulf Islands as predicted by the Canadian Hydrographic Service. A GAM including all terms was fit using the unbiased risk estimator criterion (UBRE) and allowing for a maximum of 9 degrees of freedom for each covariate smooth term (i.e. basis dimension (k)=10), in the mgcv package in R (Wood 2011). To account for a lack of independence among hooks within fishing events, a random effect structure was included in the model with fishing event represented as a penalized regression term (Wood 2008), effectively resulting in a generalized additive mixed model (GAMM). A small number of hook deployments deeper than 35 m (n=150 or 3% of the total) were excluded from the analysis as these deployments did not occur throughout the study period. We assessed potential collinearity among covariates using variance inflation factors (VIF) calculated using the corvif function available at http://www.highstat.com/Book2/HighstatLibV6.R. For all three predictor variables VIFs were less than 1.5, suggesting no issues with multicollinearity.

To compare CPUE between the two primary lure types (apex and fly) and between barbed and barbless hooks, we generated subsets of data including only those fishing events where either the two lure types or barbed and barbless hooks were fished together in the same

event. We then fit a GAMM to each data set as described above, with the addition of either lure type or hook status (barbed or barbless) as a parametric fixed factor.

2.4 Results

2.4.1 *Microtrolling*

We conducted 557 fishing events on 30 days between 9 August and 3 October 2014: a total of 4,865 individual hook deployments. Straight line distance between starting and ending points for fishing events averaged 281 m (n = 496; SD = 102 m). Timed fishing event duration, including gear deployment and retrieval, averaged 7.73 minutes (n = 471; SD = 0.77 minutes). Based on this average we estimated a total gear deployment time of 71.8 hours. We captured 182 juvenile Pacific salmon: 168 Chinook, 13 Coho and 1 Chum Salmon *Oncorhynchus keta*, and a single adult Coho Salmon (approximately 45 cm). An additional four bent, broken, or missing hooks may have resulted from encounters with adult salmon. Bycatch was very limited, consisting of three Copper Rockfish *Sebastes caurinus*, three Pacific Sanddab *Citharichthys sordidus*, and five juvenile Pacific Sandfish *Trichodon trichodon*. Approximately 46% of total microtrolling effort was devoted to repeated sampling of predefined waypoints, 13% to reconnaissance outside the main survey area, and 41% to maximizing catch for the post-release mortality assessment. Respective Chinook Salmon CPUE (percentage of hooks with Chinook Salmon) during these activities was 3.0%, 1.6%, and 4.6%. This equated to approximately 1.9 Chinook Salmon per hour of active gear deployment time during the pseudo-systematic sampling portion of the study and 3.2 Chinook Salmon per hour for the period during which we were attempting to maximize catch. Overall Chinook Salmon CPUE was higher north of Sansum Narrows (4.4%) than at sites south of Sansum Narrows (1.9%; seeFigure 2.1).

2.4.2 *Fish Sampling*

Mean FL was 155 mm (range = 116-236 mm, n = 168) for microtroll-caught Chinook Salmon and 194 mm (range = 131-311 mm, n = 13) for Coho Salmon. A single adult Coho Salmon with an FL of approximately 450 mm was not measured and a single Chum Salmon captured on 17 September had an FL of 168 mm. The lengths of Chinook Salmon captured by microtrolling increased over the study period and were broadly consistent with the lengths of fish

caught by purse seining and rope trawling (Figure 2.3). No PIT tagged Chinook Salmon were detected during the study. While all Coho Salmon were wild (adipose fin intact and no cwt detected), 18 Chinook Salmon had a clipped adipose fin, for which a cwt was detected in 12 using the metal detector. A cwt was also detected in a single non-adipose clipped Chinook Salmon. This equated to a total hatchery Chinook Salmon proportion of 11.3%. The hatchery proportion in August (12.3%; N = 73) was similar to September (10.9%; N = 91); only four wild Chinook Salmon were caught in October. Gastric lavage was successful for sampling stomach contents; however, discussion of diet is beyond the scope of the present study and these data are not presented here.

Scales were collected from 148 Chinook Salmon for genetic stock identification and DNA was successfully amplified for all but two of these samples. Based on individual stock assignments, the majority of juvenile Chinook Salmon captured (64%) were from the Cowichan River. Other stock groups with significant representation were lower Fraser River (Chilliwack and Harrison River; 18%) and other East Coast Vancouver Island rivers (Nanaimo, Puntledge, and Big Qualicum Rivers; 10%). The remaining 8% consisted of West Coast Vancouver Island, Upper Fraser River, Howe Sound and Puget Sound stocks.

We successfully PIT tagged and released 138 Chinook Salmon, 89 of which were identified by genetic stock ID as being most likely of Cowichan River origin. One individual, tagged on 17 September in Maple Bay at 166 mm, was recorded on a PIT tag antenna at the fish fence in the lower Cowichan River on 7 October 2015 (Kevin Pellett, DFO, personal communication). This fish returned as an age-1 jack.

2.4.3 *Post-release mortality assessment*

The average time that juvenile Chinook Salmon (n = 66) spent in the net pen was 21.6 hours (SD = 2.8). A single PIT tagged fish, captured on a barbless hook, died in the net pen; one additional PIT tagged fish lost its tag prior to release. All other fish were observed to be active and apparently in good condition at release.

2.4.4 *Generalized additive modelling (GAM) of CPUE*

A GAMM including smooth terms relating log odds of catching a juvenile Chinook Salmon to depth, hour of the day and stage of the tide, and including fishing event as a random effect, explained 14% of the deviance in the data. Smooth terms for depth (edf = 4.19, χ^2 = 29.05, P < 0.001) and hour of the day (edf = 3.268, χ^2 = 13.54, P = 0.009) significantly reduced deviance of the model. Stage of the tide (edf = 2.70, χ^2 = 7.51, P = 0.082) marginally reduced model deviance (Figure 2.4). Reported P -values are approximate and are based on chi-squared tests of whether each smooth term significantly reduced model deviance. Catch per unit effort was lower through the morning and increased in the late afternoon; CPUE was highest during the first half of the flood tide, and then declined to a minimum in the middle of the ebb tide. The additive effect of hook depth on the log-odds of catching a Chinook Salmon was positive between six and nineteen meters and negative at shallower and deeper depths; modelled peak CPUE was at 12 m. The decline in modelled CPUE with depth appeared to level off below 25 m (Figure 2.4).

We fished with both of the two primary gear types on 17 days during the study period, a total of 2759 hook deployments (1306 apex and 1453 fly). The proportion of hooks which caught Chinook Salmon was 4.0% (52/1306) for apex and 3.2% (46/1453) for fly. A GAMM (see above) fit to this subset of data with lure type included as a parametric fixed effect did not detect a significant effect of lure type on CPUE (P = 0.267). During the final eight days of the study period we completed 177 fishing events (1742 hook deployments) using flies with barbed and barbless hooks on opposite sides of the vessel; 30 Chinook Salmon (3.4% of hooks) were captured on barbed hooks and 21 on barbless (2.4% of hooks). Including barb status as a parametric fixed effect in a GAMM for this subset of data did not detect a significant effect of barb status (P= 0.216). In total, 3 of 138 (2.2%) and 3 of 30 (10%) juvenile Chinook Salmon landed on barbless and barbed hooks respectively had hooking injuries that precluded tagging (3.6% total); this difference was marginally non-significant (Fisher Exact Test, df = 1, P = 0.07).

2.5 Discussion

Contemporary fishery-independent sampling methods for juvenile salmon represent trade-offs in terms of cost, flexibility, CPUE, and condition of the catch. Our results suggest that microtrolling has potential as an economical and flexible tool to non-lethally capture, sample and tag Chinook Salmon, and possibly Coho Salmon, during the latter part of their first summer at sea.

2.5.1 *Microtrolling CPUE*

Our overall catch rate (168 Chinook Salmon in 30 days, or just under 6 Chinook Salmon per day) was relatively low. Our initial trial of a spatial sampling design involved daily occupation of a number of predefined stations over a relatively large area (> 10 km linear travel between the most distant waypoints). This proved somewhat impractical due to the time required to repeatedly mobilize and demobilize gear, run between stations, and locate the vessel on station; combined with the low CPUE of an individual fishing event. Once we switched focus to the post-release mortality component of the study, we fished continuously within a given area, redeploying gear immediately after retrieval which was more efficient. However, we stopped fishing soon after capturing fish (within 1-2 fishing events) to run the fish approximately 3 km to the net pen site. Taken together these activities led to a misleadingly low total catch. The number of Chinook Salmon landed per hour of active gear deployment is a better reflection of CPUE (1.9/hour during pseudo-systematic sampling and 3.2/hour during the period where we attempted to maximize our catch). Indeed, in 2015 British Columbia Conservation Foundation personnel, working in the same area as the present study, achieved an ocean-age-0 (<300 mm FL) Chinook Salmon CPUE of approximately 7/hour in 19 days of microtrolling to capture fish for PIT tagging (K. Pellett, personal communication). Gear used differed from that described in the present study, with slightly larger barbed hooks (Gamakatsu Siwash #10005 size 10, 7 mm point-shank gap) and 10-20 cm plastic or metal flashers (designed to attract salmon and impart an erratic action to the lure) on all leaders.

It is unclear whether the very low juvenile Coho Salmon CPUE that we observed reflects a lack of vulnerability to microtrolling gear or low abundance in the study area. Holtby et al.

(1992) sampled the incidental juvenile salmon catch of sport fishermen in Saanich Inlet through the summer and fall of 1985 and reported data for 331 Coho Salmon and 133 Chinook Salmon, catches roughly in proportion to seine catches as part of the same study (3,117 Coho Salmon and 1,199 Chinook Salmon). This suggests similar vulnerability of the two species to hook and line gear. Despite the fact that juvenile Pink, Chum and Sockeye Salmon are present (the latter in very low numbers) in the Gulf Islands in the late summer and fall (Healey 1978), we caught only a single Chum Salmon and no Pink or Sockeye Salmon. Juvenile Pink, Chum and Sockeye Salmon do not prey on fish to the same extent as Chinook and Coho Salmon (Healey 1978; Brodeur et al. 2007), potentially making them less vulnerable to microtrolling. Unlike rope trawling, which facilitates studies of the entire community of juvenile Pacific Salmon and other pelagic species, we suspect that the potential applications of microtrolling will be limited to studies of Chinook and possibly Coho Salmon.

The lack of a significant difference in CPUE between the two primary gear types used (apex and fly), suggests that juvenile Chinook Salmon were equally vulnerable to these gears during the study period. It is likely that small sample size was responsible for our failure to detect a significant effect of barb status on both CPUE and frequency of serious hooking injury (we only evaluated the use of barbs towards the end of the study period). However, it is encouraging that even with barbed hooks, the incidence of serious hooking injuries was ≤ 10%.

One drawback of the present study was a failure to measure or control for lure speed through the water. Gear speed is challenging to accurately assess due to wind and tide which can result in speed over ground that is very different than speed through water. Future microtrolling work would benefit from the deployment of a flow logger to accurately measure the flow of water past the vessel and in turn the speed that the gear passes through the water.

2.5.2 *Fish size relative to other gear types*

Qualitative assessment of the FL of microtroll, trawl and purse seine captured juvenile Chinook Salmon did not indicate an obvious size bias. Nevertheless, the size distribution of purse seine and trawl caught Chinook Salmon in Figure 2.3 does suggest that fish below the minimum size captured by microtrolling (116 mm) were likely present in the study area in

August. The size distribution of microtroll caught Chinook Salmon prior to September (Julian date 244; Figure 2.3) also appears to be somewhat curtailed at the lower end. It is intuitive that there is some lower size below which juvenile Chinook Salmon are not vulnerable to hook and line sampling. It seems likely that the minimum size at which juvenile Chinook Salmon can be effectively sampled by microtrolling is somewhere between 120 and 150 mm FL.

2.5.3 *Post-release mortality assessment*

Our short-term post-release mortality assessment suggested that capture by microtrolling, combined with handling, PIT tagging, and gastric lavage, resulted in very low (<5%) short-term mortality of juvenile Chinook Salmon. Our holding period (mean = 21.6 hours) was short; however, Wertheimer et al. (1989) maintained 363 sublegal (< 65 cm FL) Chinook Salmon in net pens for four to six days after capture on troll gear and found that 89% of the total observed mortality (19%) occurred either immediately or on the first day. This suggests that extending the holding period would not have substantially changed our short-term mortality estimate. Our results contrast with those of Wertheimer et al. (1989) who estimated hooking mortality rates between 22.1% and 26.4% for sublegal Chinook Salmon captured in the commercial troll fishery, and of Gjernes et al. (1993) who estimated a mortality rate of 30% for first ocean-year Chinook Salmon captured and released in recreational fisheries. We suspect that the low mortality we observed was largely a consequence of using very small hooks which rarely penetrated the eye, gill, or other critical areas. Previous studies have suggested that the majority of short-term mortality for hook-and-line-captured salmon results from hooking injuries rather than capture or handling stress (Cox-Rogers et al. 1999; Wertheimer et al. 1989). Given the low sample size and low overall mortality rate (1 fish out of 66) it was not possible to separate the potential influence of handling, tagging and gastric lavage on mortality from that of capture alone. However, we believe the potential for tagging and gastric lavage related mortality was low. Dare (2003) observed a mortality rate of less than 1% for 145,000 PIT tagged Chinook salmon in the 28 days after tagging. Gastric lavage is also a minimally invasive procedure; Meehan and Miller (1978) found no effect of gastric lavage on the subsequent survival of juvenile Coho Salmon.

Assessment of post-release predation risk or delayed mortality resulting from stress or infection was outside the scope of the present study. These factors and their potential interactions in released Pacific salmon were recently reviewed by Raby et al. (2015). These authors point out the difficulty of assessing delayed mortalities in the marine environment where both tagging and extended net-pen-based holding approaches represent confounding stressors. Other methods of capturing juvenile salmon alive for sampling and tagging (e.g. purse seining) can also result in stress to fish (e.g. crowding in the bunt, pursuit with a dipnet, exposure to warm surface water during sorting) that may be of an equal or longer duration to that experienced by microtroll-caught fish. We did not observe evidence of predation on microtrolled fish; however, in areas where predators may be habituated to recreational fishing vessels, predation on hooked or recently released fish might pose a significant problem for microtrolling based studies.

2.5.4 *Microtrolling as a tool to investigate juvenile salmon ecology at fine spatiotemporal scales*

The relatively low proportion of deviance in the data (14%) explained by our GAMM approach was not unexpected given the low overall probability of catching a Chinook on any given hook (3.5%) and the large role presumably played by stochasticity. The purpose of this exercise was not to predict CPUE, but rather to demonstrate the potential of microtrolling for investigations of fine scale spatiotemporal patterns in distribution and feeding activity. To this end, GAMM results were informative, describing significant patterns in CPUE by depth and time of day. The positive effect of depth on CPUE we detected between 9 and 19 m was consistent with September 2008 trawl surveys in the Southern Gulf Islands where juvenile Chinook Salmon catches decreased by a factor of 3 to 4 with each increasing depth stratum (0-14, 15-29, and 30-44 m; Beamish et al. 2010). However, our results provided greater resolution of depth distribution by revealing that CPUE decreased sharply at depths shallower than 9 m (Figure 2.4). The greater CPUE we observed in the afternoon relative to the morning could reflect resumption of feeding after digesting food from a crepuscular dawn feeding period. Schabetsberger et al. (2003) found that stomach fullness of juvenile Chinook Salmon in the Columbia River plume peaked mid-morning and that at offshore stations the highest proportion of undigested stomach contents occurred early in the morning prior to peak fullness. Similarly, juvenile Chinook

Salmon stomach fullness in Puget Sound was greatest in the late morning (Duffy et al. 2010). In freshwater, Sagar and Glova (1988) found that dawn was the most important feeding period for juvenile Chinook Salmon (as indicated by stomach fullness) while late afternoon was the period of greatest feeding activity, with numerous small prey items consumed. Almost all of our fishing effort was after 0900 hours (Figure 2.4) and may therefore have missed a dawn feeding period. The observed patterns in CPUE by depth and time reflect both a strength and weakness of hook and line sampling, namely that CPUE reflects both distribution and feeding activity rather than one or the other. This has potential to result in different spatiotemporal patterns in CPUE, and potentially in different stomach fullness or diet composition, for fish caught by microtrolling versus net based gears. Conducting microtrolling in conjunction with net-based sampling or hydroacoustic surveys has potential to tease apart spatiotemporal patterns in distribution and feeding activity and reveal more than would be possible by any one method in isolation. While we detected only a marginally significant effect of tide on Chinook Salmon CPUE, our spatially and temporally unbalanced sampling did not allow us to tease apart how tide may have interacted with location to influence CPUE.

Equipment and vessel costs for microtrolling are low; outfitting a small vessel with downriggers and terminal gear should cost less than $2000 (estimated costs in CAD), operators do not require advanced marine certification, and fuel costs should be moderate (<$40 per day in the present study). This contrasts with daily charter costs for purse seiners running into several thousands of dollars and in excess of $10,000 for vessels capable of rope-trawling. Where large sample sizes are required, potential capture size biases cannot be tolerated, or there is a need to sample the entire pelagic fish community, trawling and purse seining remain the most robust methods to sample juvenile salmon at sea. However, the low cost and flexibility of microtrolling make it ideal for studies of juvenile Chinook Salmon that require high frequency sampling either in space or time. Non-lethal capture is also a benefit for tagging studies and where encounters with stocks of conservation concern are likely. Stakeholders including First Nations and non-profit stewardship groups have long been involved in Pacific salmon research in freshwater habitats. However, with some exceptions (e.g. Carr-Harris et al. 2015), the very high costs associated with vessel time have generally precluded these groups from taking the lead in studies of juvenile Pacific salmon as they disperse into the marine environment. Microtrolling provides

an example of a low-cost methodology with potential to enfranchise smaller stakeholders in the research process, thereby benefitting both fisheries science and fisheries management.

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2.7 Figures

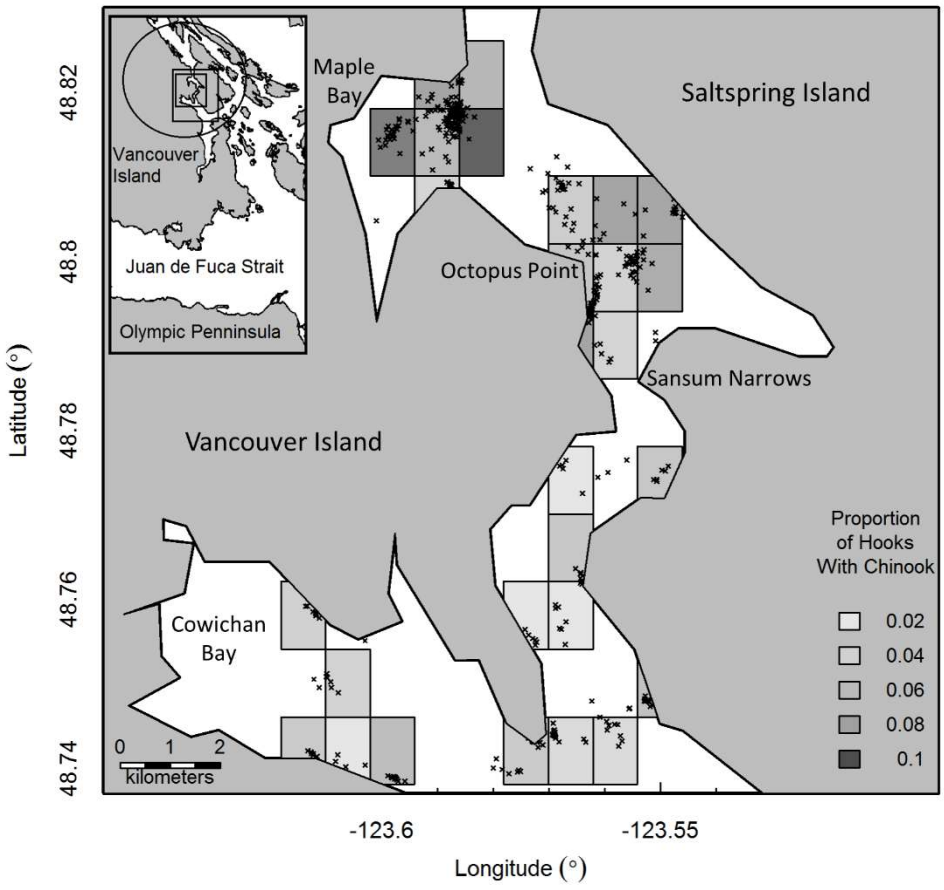

Figure 2.1. Fishing event locations (x) and CPUE (proportion of hooks with Chinook Salmon) for microtrolling in the vicinity of Cowichan Bay, British Columbia from 9 August to 3 October 2015; the inset map indicates expanded area (smallest rectangle); DFO purse seine sampling region (larger rectangle); and DFO rope trawl sampling region (ellipse). Catch per unit effort is averaged by a 0.48' x 0.48' grid and is shown only for grid references containing 30 or more hook records; shading represents CPUE on a continuous scale.

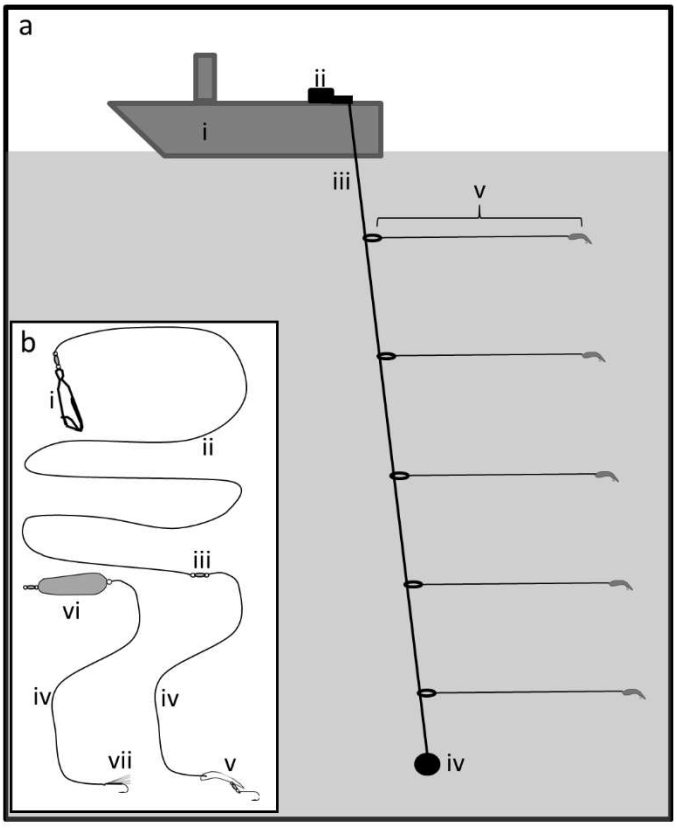

Figure 2.2. Schematic of microtrolling gear (not to scale) a. 4.9 m welded aluminum vessel (i) equipped with two (only one side shown) 'Scotty' electric downriggers (ii) with a mainline of 90 kg breaking strain braided dacron (iii) weighted with a 6.8 kg lead ball (iv); leaders (v) were deployed at measured intervals indicated by small plastic stoppers on the line; b. leaders consisted of a stainless steel clip for attachment to the downrigger line (i) and 2 m of 18 kg breaking strain monofilament (ii) connected to terminal gear consisting of either a stainless steel swivel (iii) 50 cm of 2.4-3.6 kg breaking strain monofilament (iv) and a 2.5 cm Hot Spot Apex "UV Trout Killer"(v) or a 7 cm gold and chrome 'Super Diamond' salmon spoon (vi) to provide action to a 2 cm mylar fly (vii).

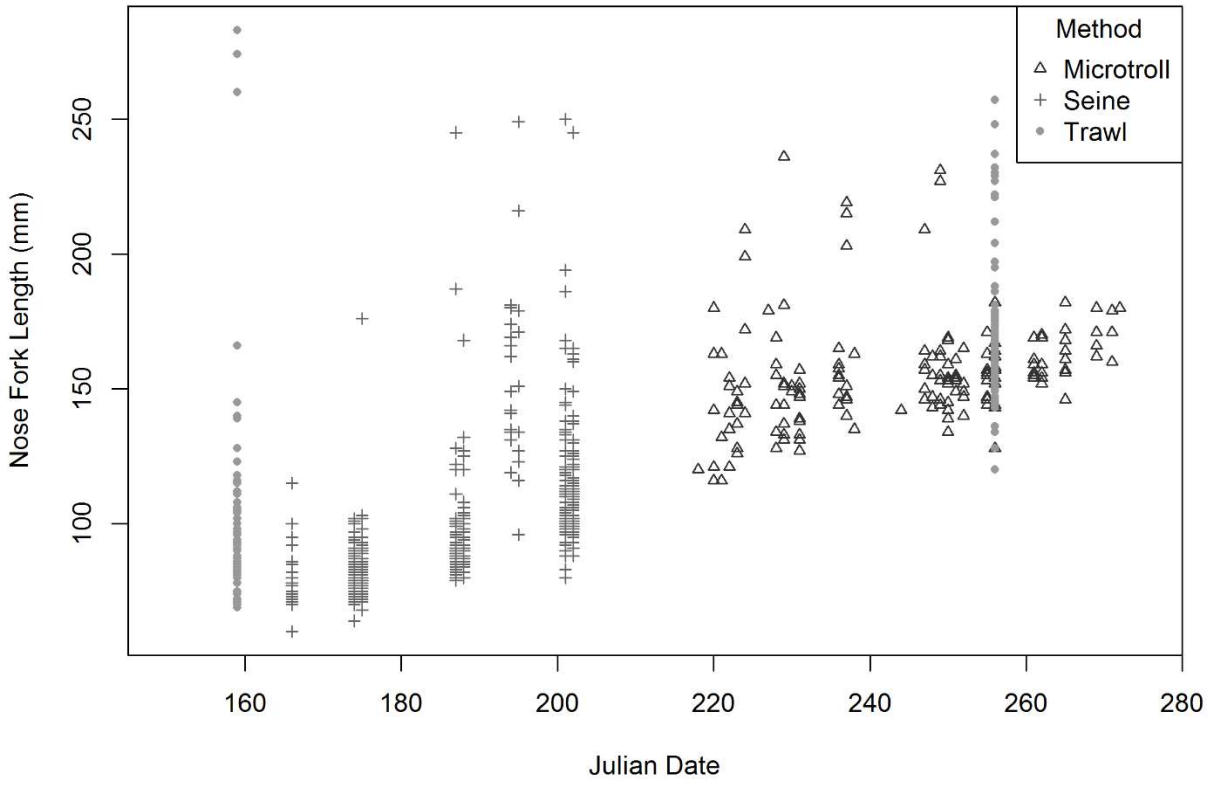

Figure 2.3. Nose-fork length in millimeters by Julian date for Chinook Salmon sampled by purse seining, rope trawling and microtrolling in the Southern Gulf Islands from 10 June to 3 October 2014.

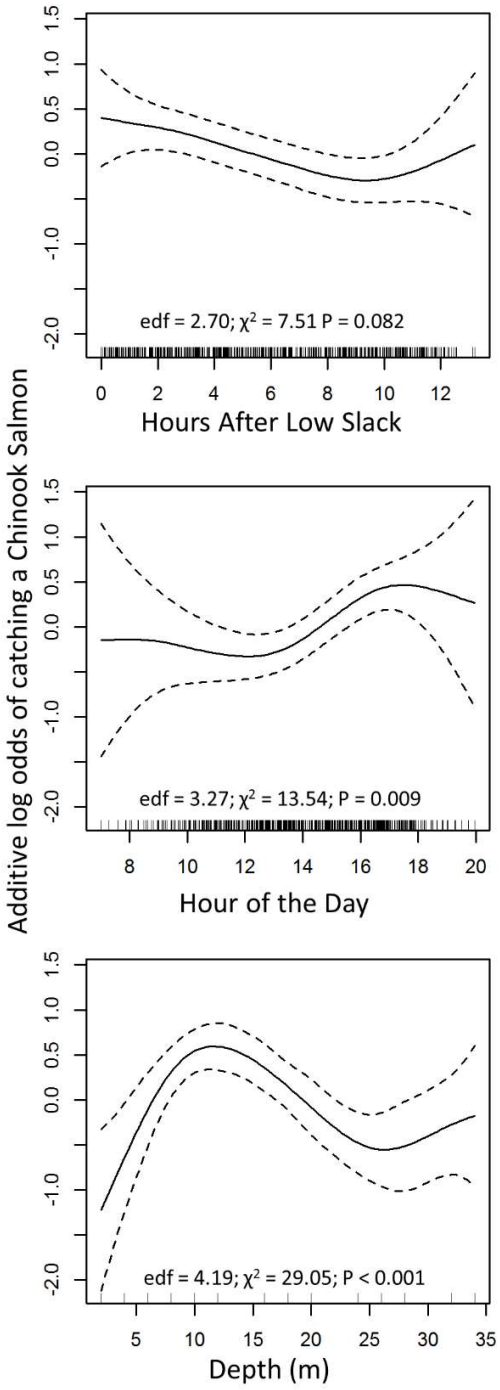

Figure 2.4. Additive log likelihood of catching a Chinook Salmon on an individual hook with respect to tidal stage, time of day, and depth as predicted by a generalized additive mixed model (GAMM) fitted with UBRE and default (9) maximum degrees of freedom and including fishing event as a random effect. Dashed lines indicate two standard errors from the estimate; rug plots on the x-axis indicate the distribution of predictors. Estimated degrees of freedom (EDF), Chi-squared statistics and P-values for the reduction in model deviance for each smooth term are inset on each graph.

Chapter 3 - Assessing indices of growth for field studies of juvenile salmon: an experiment and synthesis

Adapted from: William Duguid[a], Thomas Iwanicki[b], Meredith Journey[c], Amanda Noel[a], Brian Beckman[d] and Francis Juanes[a]. 2018. Assessing indices of growth for field studies of juvenile salmon: an experiment and synthesis. Marine and Coastal Fisheries 10: 204-223.

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Author contributions: W.D. conceived the study and designed it with support from F. J., T. I., M. J. and B. B. Lab analysis of RNA to DNA ratio, IGF1, and scale circulus spacing were led by T. I., M. J., and A. N. respectively, who all contributed to method development. Writing the manuscript was led by W.D. with support from all other authors.

3.1 Abstract

The hypothesis that size selective mortality in the first marine year is a major regulator of recruitment in Pacific Salmon has led to interest in assessing the recent growth of field-caught fish. Understanding differences in relative growth across years, regions, habitats and prey fields may provide insights into factors influencing survival. Plasma insulin-like growth factor (IGF1), muscle RNA to DNA ratio (RD) and scale circulus spacing have all been used as indices of recent growth in juvenile salmonids. We concurrently assessed these growth rate indices in a laboratory study of post-smolt, young-of-the-year, ocean-type Chinook Salmon. We synthesized results with previous work to inform selection of appropriate growth rate indices for field studies on juvenile salmonids. Muscle samples suitable for RD analysis were obtained non-lethally and without subsequent growth impacts even for very small juvenile salmon (75 - 99 mm nose to fork length). Plasma IGF1 concentration was strongly correlated with growth rate ($R^2 = 0.79$), while log(RD) and mean spacing of the outer two circuli were moderately correlated with growth rate ($R^2 = 0.47$ and 0.44 respectively). Relationships between the two biochemical indices and growth rate were independent of body size at the start of the experiment. Conversely, initially larger fish formed wider circuli for a given growth rate. Insulin-like growth factor and RD responded to a change in growth conditions within four and six days respectively. Rate of circulus formation varied positively with growth rate, meaning that outer circulus spacing indexed shorter periods of growth in faster growing fish. Our results confirm the value of plasma IGF1 as an index of recent growth in juvenile salmon. While scales (marginal circulus spacing) and white muscle (RD) can be both sampled non-lethally, scale sampling presents a number of practical advantages.

3.2 Introduction

Variation in survival of early life history stages has long been implicated in driving recruitment variability in marine fisheries (Hjort 1914; Lasker 1978). In the case of Pacific salmon (genus *Oncorhynchus*), size-selective mortality of juveniles is hypothesized to occur soon after marine entry (Parker 1965; Woodson et al. 2013), or subsequently during marine residence (Beamish and Mahnken 2001; Moss et al. 2005; Duffy and Beauchamp 2011). Size-selective mortality implies growth-selective mortality. This corollary has spurred extensive

research into factors influencing early marine growth rates of Pacific salmon (Fisher and Pearcy 1988; Tovey 1999; Litz et al. 2016; Wells et al. 2016). Prior growth trajectories of salmonids may be investigated by analysing the microstructure of hard parts including scales (Rich 1920; Ruggerone et al. 2005; Farley et al. 2007; Marco-Ruis et al. 2012) and otoliths (Neilson et al. 1985; Freshwater et al. 2015; Claiborne and Campbell 2016). However, retrospective analysis of growth presents challenges, as sampled fish are unavoidably the survivors of any previous selective mortality. To study factors influencing growth, it can be advantageous to compare relative instantaneous or recent growth rates of field-collected juvenile salmon across years, seasons, and habitats (Sommer et al. 2001; Fisher and Pearcy 2005; Ferriss et al. 2014; Journey 2015). A variety of methods are available to assess recent growth of fish, with different methods representing trade-offs in terms of accuracy and logistical feasibility.

Assessing the relative instantaneous or recent growth of juvenile fish captured in the field is a non-trivial endeavour. Growth may be assessed by repeated sampling of a fish population through time (eg. Fisher and Pearcy 1988; 2005). However, resulting 'apparent growth rate' estimates may be biased by size-selective mortality, immigration or emigration. A more robust approach is to repeatedly sample groups of marked fish of known release sizes (eg. Healey 1980a; Sommer et al. 2001; Fisher and Pearcy 1988; 2005). This method is also subject to the aforementioned biases, with the addition of potential size-selective recapture rates. Logistical challenges of releasing and recapturing adequate numbers of marked fish may also be limiting.

Recently formed regions (outer margins) of hard parts can provide an index of recent growth rate. Fish otolith growth is proportional to somatic growth and increments (rings) are generally deposited daily (Neilson et al. 1985; Zhang and Beamish 2000; Middleton 2011). This allows measurements near the otolith margin that correspond to recent growth periods of known duration. However, the relationship between otolith and somatic growth is not constant (Campana 1990). Changes in increment spacing may lag changes in somatic growth and be influenced by temperature and/or ration independently of growth (Bradford and Geen 1992; Stormer and Juanes 2016), calling into question increment spacing at the otolith margin as an index of recent growth conditions (Fey 2005). Otolith extraction and polishing is also labor intensive and requires lethal sampling of fish. Conversely, scale circulus spacing is simple to

measure and scales can be obtained non-lethally. As fish grow their scales also grow. In many species with ctenoid or cycloid scales, the circuli (concentric ridges) of the scale formed during periods of rapid growth are more widely spaced than those formed during periods of slower growth (Doyle et al. 1987; Fisher and Pearcy 1990). Circulus spacing at the outer scale margin may therefore be correlated with recent growth rate. Width of the scale's outer few circuli has been used as an indicator of recent growth in salmonids (Ball and Jones 1960; Thomas 1964; Fisher and Pearcy 2005). A limitation of this method is that circulus formation rate has been found to vary with growth rate (Fisher and Pearcy 1990), meaning that a given number of circuli may correspond to shorter recent growth periods in faster growing fish, and vice versa. Circulus formation intervals in salmon are also relatively long (several days to weeks); limiting the resolution of the pre-capture period for which they can index growth.

Biochemical indices can also be employed to infer relative rates of recent somatic growth. In fish, numerous potential biochemical growth indices have been evaluated including plasma insulin (Beckman et al. 2004a), insulin-like growth factor binding proteins (Beckman et al. 2004b; Kawaguchi et al. 2013), and RNA or DNA to protein ratios (Azuma et al. 1998; Caldarone et al. 2016). Perhaps the most well established and widely used biochemical growth index in fish is the ratio of RNA to DNA (Bulow 1970). Tissue growth requires protein synthesis. Messenger RNA (mRNA), transfer RNA (tRNA) and ribosomal RNA (rRNA) are all required for protein synthesis, with rRNA representing the great majority of total RNA in eukaryotic cells (>80% in yeast; Waldron and Lacroute 1975). While the DNA content of tissue is primarily a function of the number of cells (and hence nuclei), the total RNA content varies with protein synthesis requirements. If rapidly growing and dividing cells are synthesizing more protein than slowly growing cells, they will have a higher RNA to DNA ratio. The ratio of RNA to DNA (henceforward 'RD') has been most widely used as a growth index for larval fish (Buckley 1979; Clemmesen 1993), where small body size allows assays to be conducted on homogenized whole individuals or groups. In larger juvenile fish, liver and while muscle RD have also been assessed as growth rate indices (Bastrop et al. 1991). Recently, RD from a non-lethally obtained muscle biopsy has been correlated with individual growth rates of juvenile Atlantic Salmon, *Salmo salar* (Maclean et al. 2008; Caldarone et al. 2016). Significant responses in RD can occur as soon as the second day after a change in food availability in larval and

juvenile fish (Wright and Martin 1985; Malloy and Targett 1994) and response times of four to eight days have been observed in juvenile Atlantic salmon (Arndt et al. 1996; Caldarone et al. 2016). As with other growth indices, RD has drawbacks. Temperature may affect the relationship between RD and growth (Buckley 1982; Buckley et al. 2008) and the assumption that the DNA content of cells is constant only holds when growth is occurring by cell division (hyperplasia) rather than cell enlargement (hypertrophy; see discussion in Caldarone et al. 2016). `

Another well validated biochemical index of relative growth rate, particularly in salmonid fishes, is the plasma concentration of insulin-like growth factor (IGF1). The causal relationship between IGF1 and growth in vertebrates is well established. Growth hormone produced by the pituitary stimulates production of IGF1 in the liver and other tissues, which in turn acts directly to induce both cell growth (hypertrophy) in muscle cells (Vandenburgh et al. 1991; Adams and Hadad 1996) and cell proliferation (hyperplasia) in structural tissues in general (Lowe 1991; Lupu et al. 2001; Mommsen 2001; Castillo et al. 2004). The majority of studies on fish have found positive correlations between plasma IGF1 concentration and metrics of recent growth (Beckman 2011). Factors which may influence the relationship between IGF1 and growth rate include sexual maturation (Moriyama et al. 1997), stress (McCormick et al. 1998), and time of year (Beckman et al. 2004a). Plasma IGF1 has been found to be positively correlated with growth rate measured over periods ranging from days to months (reviewed by Beckman 2011). Levels of IGF1 have also been shown to change significantly in response to a change in growth conditions (ration) over periods as short as 4 days (Gabillard et al. 2006; Caldarone et al. 2016). While it is possible to draw blood from fish non-lethally for IGF1 assays (Pierce et al. 2001; Calderon et al. 2016), this may be problematic with very small fish. Also, the need to centrifuge blood and freeze plasma within hours of sampling may present logistical challenges where field facilities are limited.

Given the multiple external and intrinsic factors that can influence indices of recent growth, where possible they should be validated in the species and life stage of interest prior to application in the field. The present study evaluates three relative growth rate indices in post-smolt Chinook Salmon (*Oncorhynchus tshawytscha*). Scale and otolith microstructure have been used extensively to investigate Chinook Salmon growth trajectories over their entire life-cycle

and within selected stanzas (eg. Rich 1920; Reimers 1971; Neilson et al. 1985; Bradford and Geen 1992; Tovey 1999; Sommer et al. 2001; Middleton 2011; Woodson et al. 2013). Recent work has also investigated scale circulus formation in age-0 Chinook Salmon in freshwater (Walker and Sutton 2016). However, we are not aware of any work with this species that has validated or applied circulus spacing at the scale margin as an index of relative growth rate immediately preceding sampling. We are also not aware of any published work that has utilized RD as an index of Chinook Salmon growth in the field, although Hackmann (2005) did attempt to validate RD as an index of growth rate in age-0 Chinook Salmon parr. The relationship between IGF1 concentration, growth rate, and smoltification has been described for juvenile Chinook Salmon in freshwater (Beckman et al. 1998, 1999, 2003) and the relationship between nutritional state, IGF1 regulation, and growth has been characterized in some detail (Pierce et al. 2005). Insulin-like growth factor concentration has also been applied in the field to investigate spatio-temporal variation in growth conditions for Chinook Salmon during early marine residence (Ferriss et al. 2014; Journey 2015, Chamberlin et al. 2017).

There are many technical and logistical factors to consider when selecting the most appropriate indices of recent growth for ecological field studies on juvenile salmon. One obstacle to evaluating the relative merits of different approaches is that morphological and biochemical indices of growth are rarely directly compared on the same cohorts of fish. Here we examine the relationships of marginal circulus spacing, RD, and plasma IGF1 with individual specific growth rate over a 30-day period for ocean-type Chinook Salmon post-smolts, while accounting for the influence of initial size and ration level. We also quantified the integration time of the biochemical indices by assessing the time frame over which each index responded to an increase or decrease in ration. Performance of these growth indices is evaluated under feeding conditions selected to be ecologically relevant to those experienced in the wild (low, moderate and high ration), rather than to elicit a significant physiological response (fasted vs fed). We discuss our results in the context of previous studies on growth indices in juvenile salmonids and summarize the relative merits and drawbacks of different approaches.

3.3 Methods

3.3.1 *Animals*

Progeny of ocean-type Chinook Salmon broodstock spawned at the Nitinat River Hatchery (Canadian Department of Fisheries and Oceans) were transported as eyed eggs to the Goldstream Volunteer Salmonid Enhancement Hatchery near Victoria, British Columbia where they were reared in surface water-fed tanks. On 26 May 2015, pre-smolts were transported to the University of Victoria Outdoor Aquatics Unit, where they were housed in an outdoor, 390 L fiberglass round tank supplied with 12-16 ºC recirculating freshwater and covered with a lid fitted with a translucent window to admit dim, natural photoperiod light (this description applies to all tanks used in this study). Fish were fed by hand twice per day at an estimated total ration of 3% body weight per day (BW/day) on BioOregon 1.2 mm pelleted salmon feed. On 27 May, 10 individuals (mean mass = 4.57 g, SD = 0.68 g; mean nose to fork length = 75.0 mm, SD = 0.4 mm) were euthanized with 300 mg/L tricaine methanesulfonate (TMS), preserved in formalin, and shipped to the Animal Health Center of the BC Ministry of Environment for health surveillance histopathology. Aside from one acanthocephalan gut parasite in a single fish, no pathogens were detected. On 2 June, approximately 25% seawater by volume was added to the tank containing the juvenile Chinook Salmon before reconnecting to recirculating freshwater. This process was repeated with approximately 50% seawater on 3 June and on 4 June the tank was gradually brought up to 100% seawater and was thereafter supplied with 12-14 ºC recirculating bead-filtered and UV-sterilized seawater. Chinook Salmon continued to be fed twice per day at a ration of 3% BW/day, recalculated daily based on an assumed growth rate of 2.5% BW/day.

Tagging and pre-experimental sampling occurred on 22 June. The allocation of fish among tanks, numbers of fish sampled, and mortalities throughout the remainder of the study are illustrated in Figure 3.1. Anaesthesia occurred in aerated buckets containing 80 mg/L TMS in seawater, maintained at 12-14 ºC using ice-packs. Fish were individually weighed and measured for nose to caudal fork length (FL). Fine forceps were used to remove a smear of scales from the preferred area (just above the lateral line and immediately posterior to the dorsal fin) and these were spread across a single numbered square of a gummed scale card. Fish were individually

marked with a 12.5 by 2.1 mm passive integrated transponder (PIT) tag (Biomark HPT12 FDX-B) injected intraperitoneally in a posterior to anterior direction on the midline of the ventral surface just anterior to the pelvic fins. To assess potential growth and survival impacts of muscle biopsy, 145 fish were also subject to biopsies in conjunction with tagging. Fine forceps were used to remove scales from a small area of skin (~ 4 mm^2) on the left side of the dorsal surface 2-5 mm posterior to the dorsal fin. A Miltex® 1.5 mm biopsy punch was then inserted at this site at an anterior angle of approximately 45 degrees, while rotating between thumb and forefinger to cut through the skin. In cases where the muscle plug was not initially removed by the punch, the tip of a pair of fine forceps was pressed against the site of the biopsy in an anterior to posterior direction to extrude the plug from the hole. Fish were transferred to an aerated bucket of seawater until they regained equilibrium and were then returned to a single tank. Fish were subsequently maintained at a ration of 1% BW/day administered in a single morning feeding and calculated based on the remaining number of fish and the weight at the time of tagging (mean = 8.20 g, SD = 0.68 g), adjusted daily assuming growth of 1% BW/day. On 8 July 2015, all fish were again anaesthetized, weighed and measured as described above. Sixty fish were haphazardly selected for inclusion in the growth rate experiment while 226 were returned to a single tank and maintained on a continued ration of 1% BW/day in preparation for the start of the integration time experiment.

Daily percent growth rates in length and weight were calculated using the formula:

$$Growth\ (\%/d) = (ln(s_2)-ln(s_1))/(t_2-t_1)$$

where t_1 and t_2 are the experimental day numbers at the beginning and end of the period of interest and s_1 and s_2 are measurements of fish mass (in grams) or NFL (in mm) at these time points.

3.3.2 *Growth rate experiment*

On 8 July 2015, (day 0) 60 fish were measured and sampled for scales as described above and haphazardly distributed among three tanks (n = 20 per tank). Tanks were assigned as either high (3%), medium (1%), or low (0.5% BW/day) ration. To maximize individual variation in

growth rate (through within-tank competition for food) the ration was administered in four daily feedings between 0730 and 1530. Total ration was adjusted daily based on an assumption of 3%, 1.3% and 0.5% growth in weight per day respectively in the three treatments (1.3% was used for the 1% BW/day treatment as this was the observed growth rate between tagging and day 0 of the growth rate experiment). The original study design was to maintain treatments at these rations for three weeks prior to terminal sampling. However, on 13 July 2015, a pump failure caused mortality of multiple species in tanks connected to the UVic Outdoor Aquatics Unit recirculating seawater system. This mortality event included 18 juvenile Chinook Salmon in the high ration tank and three fish in the tank being held for the integration time experiment. Fish that survived this event showed no evidence of adverse effects, so 18 individuals were transferred from the integration time tank to the high feed tank and the end point of the growth rate experiment was extended to 7 August. The experimental period for the low and medium ration treatments and for two of 20 fish in the high ration treatment was therefore 30 days while for 18 of 20 fish in the high ration treatment it was 25 days. On 7 August, fish were haphazardly selected in groups of three from the three feeding levels for sampling. Each fish was euthanized in 300 mg/L TMS; scanned for a PIT tag number; and was weighed, measured, biopsied, and had scales sampled as described above. Fish were not fed on the morning of sampling. Biopsies were taken from the right side of the dorsal surface to avoid potential scar tissue associated with the original biopsy. Muscle plugs were transferred to a glass slide; trimmed with a scalpel if necessary to remove any visible skin; transferred to a microcentrifuge tube; flash frozen in liquid nitrogen; and stored at -80 °C for subsequent RD assays (see below). A razor blade was used to sever the posterior end of the fish at approximately a 45° anterior angle from the posterior tip of the anal fin to the dorsum. The fish was then held inverted and up to 0.1 mL of blood was drawn from the caudal vein using a heparinized Natelson capillary tube. Blood was blown from the capillary tube into a microcentrifuge tube and stored on ice for no more than 4 hours. To separate blood plasma, tubes were spun-down at 5000 rpm for five minutes in a chilled (1 °C) centrifuge. Up to 50 µl of plasma was drawn from each tube with a micropipette, taking care not to disturb the pellet. Plasma was transferred to clean tubes and frozen at -80 °C for subsequent IGF1 assay (see below).

3.3.3 *Integration time experiment*

On 30 July 2015 (day 0), 183 individually PIT tagged Chinook Salmon post-smolts which had been held together in a single tank were haphazardly divided among three tanks (n = 61 per tank). To minimize stress, fish were not anaesthetized and measured at this time. In order to provide baseline values for the integration time experiment, the remaining 20 individuals were euthanized and sampled as described for the growth rate study. The three tanks were designated as low, medium and high (0.5, 1.0, 3.0 % BW/day) feeding treatments with ration adjusted daily based on an assumption of 0.5, 1.3 and 3.0 % growth in weight per day. Ration was administered in four feedings per day to the high feeding treatment and in one morning feeding to the other two treatments. Twelve fish were removed from each tank for terminal sampling (as described for the growth rate experiment) on days 2, 4, 6, and 8; and the remaining 13 fish in each tank were sampled on day 14. On each sampling day, the fish to be sampled were caught in the morning prior to feeding and moved to a separate tank to minimize stress on fish remaining in each treatment. Due to a mistake on the final day of the experiment (day 14), fish were fed in the morning one to three hours prior to sampling.

3.3.4 *RNA:DNA assay*

An RNase free work environment was maintained by treating surfaces, glassware, and other equipment with RNaseZap™ (Ambion®). Nucleic acid quantification from muscle biopsies followed the assay outlined in Caldarone et al. (2001) with slight modifications. 100 µl 0.5% STEB (0.5% w/v N-lauroylsarcosine, 0.05 M Tris, 0.1 M NaCl, 0.01 M EDTA, pH 8.0, 0.1 mg/ml proteinase K) was added to 1.5 ml microcentrifuge tubes containing muscle biopsies. Samples were homogenized by vortex (Vortex Genie 2, Scientific Industries Inc.) for 30 minutes at room temperature. Samples were then diluted with 400 µl Tris-EDTA buffer (final concentration of N-lauroylsarcosine = 0.1%), centrifuged for 15 minutes (14000·g, 20ºC) to sediment out any undissolved particles, and a 300 µl aliquot was removed for fluorometry. Duplicate 75 µl aliquots of the centrifuged sample were added to an OptiPlate-96 black-walled opaque 96-well microtitre plate. Standard solutions of RNA (*E. coli* Total RNA, Ambion™ Catalog: AM7940) and DNA (Calf Thymus DNA, Invitrogen™ Catalog: 15633019)

were prepared at 10 µg/ml and two-fold serial dilutions (75 µl per well, minimum concentration = 0.63 µg/ml) of the standards were added to the plate. Every well then received 75 µl of Tris-EDTA buffer (containing 2 µg/ml Ethidium Bromide) and the plate was incubated for five minutes. Fluorescence was recorded on a PerkinElmer Victor3V 1420 microplate reader (excitation: 531 nm, emission: 600 nm) with the signal representing the combined fluorescence of RNA and DNA in each sample. Ribonuclease A (7.5 µl; Thermo Scientific™ Catalog: EN0531) was added to each well and incubated at room temperature for 30 minutes. Fluorometry was recorded again, and the remaining signal was empirically determined to be from DNA only. The RNA to DNA ratio was calculated for each well and samples where the coefficient of variation for either the RNA or DNA concentration in duplicate wells exceeded 15% were excluded from further analysis.

3.3.5 *Insulin-like growth factor-1 assay*

Frozen plasma was shipped on dry ice to the Northwest Fisheries Science Center, National Marine Fisheries Service, where concentration of plasma IGF1 for individual fish was measured using the time-resolved fluorescence immunoassay developed by Small and Peterson (2005) as modified by Ferriss et al. (2014). Uniformity and speed in processing samples was enhanced using an automated pipetting workstation (Perkin-Elmer). Across individual assays, all samples were standardized using inter-assay pools of juvenile Coho Salmon plasma at three known IGF1 concentrations (low, medium, and high), corresponding to approximately 75, 50, and 25 % binding in the immunoassay. Reported individual IGF1 concentrations are the standardized mean of duplicate measurements. In the event that duplication between wells was poor, classified by a percent coefficient of variation greater than 7, the sample was dropped from the final data set. Additionally, samples falling outside of the linear range of the immunoassay standard curve (greater than 80 % or less than 20 % binding) were dropped from the final data set. Data standardization and complete laboratory techniques are detailed in Ferriss et al. (2014).

3.3.6 *Scale circulus deposition and spacing analysis*

Impressions of Chinook Salmon scales were made at the Canadian Department of Fisheries and Oceans Pacific Biological Station by pressing scale cards onto acetate sheets using

a DK20SP 16X20 Automatic Digital Swinger swing-away heat transfer press following methods described in Hudson and Crosby (2010). Scale impressions were photographed at 8X magnification using bright field illumination with an Olympus DP26 digital camera mounted on an Olympus S2X16 stereomicroscope. Scale impressions were only analyzed when a clearly defined origin indicated that the scale was not regenerated. CellSense software was used to draw a line from the center of the origin to the scale margin in an anterior direction along the longest axis of each scale. The point tool was then used to place points sequentially beside this line at the center of the origin, margin of the origin, and at the outer margin of each circulus out to the edge of the scale Figure 3.2). The line length measurements and cartesian coordinates of points for each scale were exported as comma separated value (csv) files and custom code in the "R" statistical language was used to count the number of circuli and calculate the linear distance between sequential points. Where the sum of these linear distances (the radius of the origin and spacing of each circulus) differed by more than 2% from the scale radius measured using Cellsense software, the measurement process for the scale was repeated.

Up to three good scales (when available) were imaged and analyzed for fish sampled at the end of the growth study while one scale was imaged and analyzed for fish sampled at the time of tagging, and at the beginning of the growth rate study. In addition to the single scale analyzed for each fish at the time of tagging, visual circulus counts were made for up to two additional scales (where available) for those fish that were used in the growth rate experiment. Where more than one scale from a single fish was measured or counted for circuli, average values for each fish were used in analyses. For the growth rate experiment, circulus formation intervals for each fish were calculated as the elapsed days (46) divided by the difference between the mean circulus count at the time of terminal sampling and the time of tagging. Two fish for which the increase in circulus number over this period was calculated as being less than one were not included in the analysis.

3.3.7 *Analysis*

To assess relationships between individual growth rates and growth rate indices (growth rate experiment), we employed a small sample Akaike information criterion (AICc) model

selection approach which evaluated alternative multiple regression models. Identical candidate model sets (Table 3.1) were developed for each response variable (RD, plasma IGF1, spacing of the outermost one and two scale circuli, and circulus formation interval). The hypothesis of no relationship between response variables and individual growth was described by a 'Null' model. A 'Growth' model represented a monotonic relationship between each response variable and individual growth rate in percent length per day (henceforward "growth rate"). To account for non-independence of fish within tanks/ration levels, models including ration as a fixed factor either with ('Growth x Ration') or without ('Growth + Ration') an interaction with growth rate were also considered. Finally, to assess whether response variables were related to size at the beginning of the study, three additional models were specified that included a term for NFL on day 0 ('Growth + Day 0 NFL', 'Growth + Ration + Day 0 NFL', and 'Growth x Ration + Day 0 NFL'). Candidate models were fit using the "lm" function of the base stats package in the "R" statistical language. Heteroscedacity and normality of residuals were examined graphically, and where necessary response variables were natural-log transformed. Best models for each response variable were selected based on minimum AICc values using the "aictab" function in the "AICcmodavg" library. Goodness of fit of relationships between response variables and growth rate ('Growth Rate' model) were compared using the coefficient of determination.

To visualize the response of biochemical growth rate indices to a change in growth conditions (integration time experiment), we plotted 95% confidence interval-bounded, locally-weighted scatterplot smooths (loess; span = 0.8) of individual RD and plasma IGF1 against experimental day for each ration level (day-0 values were re-used for each ration level). We also generated loess smooths in the same manner for final mass and growth rate since day -22 (the most recent time point at which fish were measured prior to the experiment).

3.4 Results

3.4.1 *Survival and growth effects of muscle biopsy and PIT tagging*

Only six mortalities occurred over the 16 days between PIT tagging and remeasuring fish prior to the growth rate experiment. Of these, one resulted from a handling accident and one from a fish jumping from the tank. The other mortalities occurred when fish failed to recover

from anaesthesia at the time of tagging (n = 3) or remeasuring (n = 1). Two of these four mortalities were of fish which had been subjected to a biopsy in conjunction with tagging. Of the 21 fish which died at the time of the pump failure, ten had been subjected to a muscle biopsy at the time of tagging. Two fish lost their PIT tag between tagging on 22 June and remeasuring on 8 July, they were included in the 20 fish sampled at the beginning of the integration time experiment. Percent daily growth in length of Chinook Salmon post-smolts between tagging and remeasuring was almost identical for biopsied (mean = 0.43 %, n = 142, SD = 0.10 %) and non-biopsied (mean = 0.43 %, n = 143, SD = 0.11 %) fish.

3.4.2 *Analytical results*

All fish exhibited positive growth in length and weight between tagging and final sampling. During the growth rate experiment, individual daily growth rates were 0.46% (SD = 0.10%), 1.27% (SD = 0.13%), and 2.05% (SD = 0.14%) in weight and 0.18% (SD = 0.05%), 0.39% (SD = 0.07%), and 0.61% (SD = 0.07%) in length over 30 days for Chinook Salmon post-smolts reared for 25-30 days on estimated rations of 0.5% 1.0% and 3.0% body weight per day respectively. As ration calculations assumed growth rates of 0.5% 1.3% and 3.0% per day, the amount of food provided to the high ration group was slightly greater than 3% per day by the end of the study period. Estimated ration levels for the other two tanks were relatively accurate. Growth rate in length was highly correlated with growth rate in weight ($R^2 = 0.97$; Figure 3.3), and growth rate in length was used in all subsequent analyses. For the integration time experiment, overall mean growth rates from 22 days prior to the start of the experiment to final sampling (a period of between 22 and 36 days) was 0.43% per day (SD = 0.07%) in length and 1.27 % per day (SD = 0.27%) in weight.

A total of 263 muscle biopsies were assayed for RD on eight 96 well microplates. The DNA and RNA standard slope ratio (m_{DNA}/m_{RNA}) was 3.15 (SD = 0.11). Twenty-five samples (9.5%) were rejected due to high variation between duplicates. Values of RD averaged 3.47 (SD = 1.11, Range = 1.39 to 6.55) across all treatments in both experiments. Blood plasma was successfully obtained for 260 fish and assayed for IGF1 concentration, 228 (88%) of these assays met quality control standards for inclusion in analyses. Plasma IGF1 concentrations in ng/mL

averaged 29.62 (SD = 9.65, Range = 10.53 to 49.75) across all treatments in both experiments. For fish included in the growth rate experiment (n = 60) scales suitable for circulus counts were obtained for 56 and the average number of countable scales (target = 3) was 2.6. Scales were sampled again at the start of the growth rate experiment; however, due to the pump failure that occurred on day 5 and the need to transfer fish into the experiment, circulus formation interval was calculated over 46 days from the time of tagging to the end of the growth rate study. Nevertheless, circulus counts were obtained for 38 fish on both the day of tagging and at the start of the growth rate experiment. Mean circulus count over this 16-day period increased from 11.8 (SD = 1.0) to 12.8 (SD = 1.3). Scales suitable for analysis were obtained from all fish at the end of the growth rate experiment and the average number of countable scales (target = 3) was 2.85. Considerable scale loss was observed for some fish at the time of sampling.

3.4.3 *Growth rate experiment*

Residuals of linear models relating RD and circulus formation interval to growth rate were somewhat non-normal and heteroscedastic; therefore, both variables were log-transformed for the final candidate model set. Models including a growth rate term were strongly favored over null models for all response variables (ΔAICc > 25; Table 3.1). Model selection suggested that the relationship with growth was independent of ration level for all response variables except IGF1 concentration. The best model for IGF1 ('Growth + Ration'; Table 3.1) included independent intercepts for each ration level. Fish size (FL) at the start of the experiment was only retained as a term in the best models relating spacing of the outer one and two circuli to growth rate (Table 3.1). Initial FL was marginally significant for the spacing of the outermost circulus (P = 0.0575; Figure 3.3) but was highly significant for the mean spacing of the outer two circuli (P = 0.0005).

Of the growth rate indices, IGF1 concentration correlated most strongly with growth rate ($R^2 = 0.79$), followed by log RD ($R^2 = 0.47$), mean spacing of the outer two circuli ($R^2 = 0.44$), and spacing of the outermost circulus ($R^2 = 0.29$; Table 3.2). There was also a relatively strong correlation between growth rate and the log of circulus formation interval ($R^2 = 0.45$), indicating that the effect of fish growth rate on scale growth was not limited to circulus spacing. Circulus

spacing declined over the initial ten circuli and remained low after the beginning of the experiment (mean circulus number 12.8) in the low and medium ration treatments; in the high ration treatment, circulus spacing increased by the end of the experiment (Figure 3.4).

3.4.4 *Integration time experiment*

The sizes (fork lengths) of low, medium, and high ration groups of Chinook Salmon post-smolts were not clearly different by the end (day 14) of the integration time study (Figure 3.5). However, growth rates measured over 22-36 days (depending on sampling day) had separated by day 8 of the experiment (Figure 3.5). Mean IGF1 of fish sampled on day 0 of the integration time experiment (26.14 ng/mL; SD = 7.05 ng/mL) was lower than that of fish fed at 1% BW/day in the growth rate experiment (34.95 ng/mL; SD = 8.94 ng/mL). In the high ration treatment, IGF1 increased rapidly, and by day 4 was higher than in both the medium and low ration treatments, remaining relatively constant through day 14. Concentrations of IGF1 for the low and medium ration fish remained low initially, but on day 14 had increased to levels similar to the high ration treatment. Unlike IGF1 concentration, mean RD of fish sampled on day 0 (3.82; SD = 1.13; N = 17) was higher than that of fish fed at 1% BW/day in the growth rate experiment (2.55; SD = 0.66; N = 19). The RD values of fish sampled from low and high ration treatments had separated by day 6, and remained so until the end of the experiment. The ratio of RNA to DNA graded with ration level from day 6 to day 14; however, 95% confidence intervals of the medium ration loess smooth overlapped with those of high and low ration smooths throughout this period.

3.5 Discussion

Factors to consider when selecting indices of relative growth rate for fish ecology studies include the strength of the relationship with growth, integration time, logistical feasibility, and potential for non-lethal sampling. Couture et al. (1998) and Beckman et al. (2004a) further suggested that an ideal growth rate index should be required for growth (causal) rather than a result of growth (correlational). The growth rate indices evaluated in the present study fall on a causal to correlational spectrum with respect to their theoretical relationship to somatic growth. Insulin-like growth factor 1 is a proximal cause of growth, elevated RNA content (and hence

RD) is required for growth, and scale circulus spacing is correlated with the growth rate at the time of circulus formation.

3.5.1 *IGF1 relation to growth*

Given a direct causal relationship to growth, it is perhaps unsurprising that of the indices evaluated, plasma IGF1 concentration showed the strongest correlation with recent growth rate in Chinook Salmon post-smolts. The coefficient of determination for this relationship (0.79; Table 3.1) compared favourably with literature values, falling above the values reported in 21 of 25 studies of IGF1 and fish growth reviewed by Beckman (2011). While our model selection approach suggested that this relationship was not independent of ration level (Table 3.1), the slope coefficients were very similar whether or not ration was included in the model (60.8 and 58.1 respectively). The intercepts for treatment levels also did not grade with ration level (Figure 3.3) indicating no consistent relationship between ration and IGF1 independent of growth rate. The fact that fork length on day 0 was not included in the best model suggested that IGF1 was independent of initial size in our experiment. This contrasts with the results of Shimizu et al. (2009) who found that for fasted juvenile Coho Salmon (*Oncorhynchus kisutch*), basal IGF1 levels were dependent on fish size. On the other hand, Beckman et al. (1998 and 2003) sorted juvenile Chinook Salmon at the same developmental stage into small and large individuals, and then induced different growth rates using differences in temperature and ration respectively. In both cases, faster growing small fish achieved higher IGF1 values than slower growing large fish, indicating that IGF1 concentration was more strongly related to growth than size. Concern that a relationship between IGF1 and size could confound the ability of IGF1 to resolve differences in growth has led some authors to standardize IGF1 values to fish length for field studies (Ferriss et al. 2014). One drawback of this approach is that it may reduce the significance of results if differences in size are in part a consequence of differences in recent growth rates. While challenging, more research to tease apart the relations among growth rate, size and IGF1 concentration is warranted.

The absolute values of plasma IGF1 concentration we observed (10-50 ng/mL; Figure 3.3) cannot be directly compared with most literature values for juvenile Chinook Salmon (eg.

Pierce et al. 2005; Beckman et al. 1998, 1999), as IGF1 standards and methodologies have varied. However, samples from the present study were run in the same lab using the same standards, inter-assay pools and protocols as two recent field studies (Ferriss et al 2014 and Journey 2015). For age 0.0 and 1.0 Chinook Salmon sampled in early summer across eight regions of the British Columbia coast over three years, Ferriss et al. (2014) observed year-by-region mean IGF1 concentrations ranging from 38 to 64 ng/ml. Similarly, Journey (2015) reported year-by-region-by-life history type mean concentrations ranging from 43 to 92 ng/mL for age 0.0 and 1.0 Chinook Salmon sampled over three years in three coastal regions of BC. The higher IGF1 concentrations observed for these post-smolt Chinook Salmon in the marine environment than in our laboratory study could reflect more rapid growth rates in the wild. Based on change in size frequency distributions of Chinook Salmon caught from June to October in the Gulf Islands of BC in 1976, Healey (1980b) reported a consistent increase in size of 0.75-0.85 mm/day for three distinct modes corresponding to June FL of 80mm, 140-160 mm, and 320-360 mm (likely corresponding to age 0.0, 1.0, and 0.1 fish respectively). A very similar estimate of growth rates for age 0.0 Chinook Salmon (0.7-1.0 mm/day) was derived by Trudel et al. (2007) based on sizes of fish caught in summer trawl surveys from California to the Bering Sea. Applying a growth rate of 0.8 mm/day to the range of FLs observed at the end of our growth rate study (89 mm to 106 mm) yields growth rates of 0.6 to 0.9 % length per day, at or above the growth rates observed for the high ration treatment.

3.5.2 *IGF1 integration time*

Plasma IGF1 concentrations responded to an increase in ration (improved growth conditions) within 4 days. However, IGF1 concentration did not decrease for fish on a reduced ration (Figure 3.5). This may have been because the mean IGF1 concentration for fish on Day 0 was already quite low (lower than for fish fed at the same ration level - 1% BW per day - in the growth rate study). This lower IGF1 level could have been a consequence of providing food in a single daily feeding while fish in the growth rate study were fed four times per day. Shimizu et al. (2009) detected higher plasma IGF1 in juvenile Coho Salmon two to ten hours after receiving a meal relative to unfed controls (although this pattern was not significant in fish that had previously been fasted for a week or longer). Peddu et al. (2009) found that IGF1 in juvenile

Mozambique Tilapia (*Oreochromis mossabicus*) was elevated one hour after a scheduled feeding time whether or not feeding occurred, suggesting that IGF1 regulation could become conditioned to diel food availability. Fish in the medium ration treatment of the growth rate study had been fed over a longer diel period and more recently prior to sampling than those at the beginning of the integration time study, possibly resulting in elevated levels of IGF1. Short term effects of feeding may also explain the increase in plasma IGF1 concentration observed on day 14 for both the low and intermediate ration treatments (Figure 3.5). Unlike on other sampling days, these fish were fed (in error) one to three hours prior to sampling. Shimizu et al. (2009) measured IGF1 values that were approximately 50% higher in fed fish than controls two hours after a meal. A similar response could explain the elevated IGF1 for low and medium ration fish on day 14, although it is not clear why a similar elevation was not observed for high ration fish. If elapsed time since a previous meal, or conditioned diel feeding chronology, have large effects on plasma IGF1 this could have implications for field study design in cases where fish exhibit diel periodicity in feeding behaviour (eg. Schabetsberger et al. 2003).

Notwithstanding the results on day 14, the observed four-day response time to a change in ration for IGF1 concentration is consistent with results of other studies. Pierce et al. (2005) reported that fasted Chinook Salmon parr had significantly lower IGF1 than control or increased ration individuals after 4 days and Gabillard et al. (2006) and Caldarone et al. (2016) reported increases in IGF1 4 days after refeeding fasted juvenile Rainbow Trout (*Oncorhynchus mykiss*) and Atlantic Salmon (*Salmo salar*) respectively. Slower responses have also been reported. Shimizu et al. (2009) measured IGF1 concentration in juvenile Coho Salmon 1, 7 and 21 days after withdrawing food; while a slight decline occurred by day 7, a much larger and statistically significant decline was evident by day 21. A more extended period for IGF1 values to stabilize (two weeks) was also observed by Pierce et al (2005) and Gabillard et al. (2006). This contrasts with our results where IGF1 values in the high ration treatment remained constant after day 4. Overall, the period over which IGF1 level is able to resolve differences in growth conditions probably ranges from about four days to two weeks.

3.5.3 *IGF1 logistical considerations*

Sampling blood plasma to assay IGF1 concentration is a somewhat delicate operation that could be challenging in certain field conditions. While blood may be drawn from the caudal vein using a syringe in larger fish, this is difficult in small individuals (< 120 mm; Ferriss et al. 2014). In the present study, we removed the caudal fin and drew blood using heparinized Natelson capilliary tubes. Obtaining an adequate blood sample (~50 µl) using this method requires a steady hand on smaller fish. Plasma must be separated by centrifuging blood within four hours of collection, requiring a centrifuge suitable for use in the field. Plasma must then be frozen as soon as possible at -80 °C. Nevertheless, plasma samples for IGF1 have been obtained successfully under remote field conditions (eg. Bond et al. 2014). While blood may be collected from recently killed fish, for example those brought on deck during trawling (Ferriss et al. 2014, Journey 2015), it is necessary to process fish quickly before clotting begins. It is possible to draw blood non-lethally using a syringe in larger juvenile salmonids (Pierce et al. 2001, Caldarone et al. 2016); however, this would not be possible in smaller fish. Furthermore, in any field study design where non-lethal sampling was important (e.g. tagging studies), drawing a significant blood volume could impair feeding and predator avoidance behavior and result in delayed mortality or abnormal behavior. Of the three evaluated growth indices, IGF1 analysis was the most complex (and therefore expensive) requiring a well-equipped lab, and specialized reagents (antibodies and IGF1 standards) and training.

3.5.4 *RD relation to growth*

The significant, positive relationship we observed between RD and growth rate was consistent with a large body of previous work on larval and juvenile fish (Buckley 1979, 1982; Rooker and Holt 1996; Caldarone 2005; and many others). While the use of RD as an index of relative growth rate in fish is well established, results for juvenile salmonids have been more equivocal. Moderate to strong positive correlations between muscle RD and growth have been reported for Arctic Char (*Salvelinus alpinus*) (Miglavs and Jobling 1988), Rainbow Trout (Suresh and Sheehan 1998a), Brook Trout (*Salvelinus fontinalis)*, and Atlantic Salmon (Wilder and Stanley 1983). Maclean et al. (2008) found a positive and highly significant relationship

between RD and individual growth rate for Atlantic Salmon smolts, a result which was confirmed by Caldarone et al. (2016). On the other hand, Ferguson and Danzmann (1990) investigated relationships between RD and growth (measured over periods of 7 to 21 days) for individual yearling Rainbow Trout held at temperatures from 5 to 11 °C and found significant relationships in less than 50% of cases (8 of 18 regressions). Even where relationships were significant, the coefficients of determination reported by these authors were relatively low (0.21-0.39). Kawaguchi et al. (2013) did not find a significant relationship between growth rate and RD in yearling Masu Salmon (*Oncorhynchus masou*), and observed no decrease in RD even after 6 weeks of fasting. In the only previous work we are aware of investigating RD in juvenile Chinook Salmon, Hackmann (2005) found only a very weak correlation between RD and individual growth rate ($R^2 = 0.06$).

Size at the beginning of the experiment was not included in our top model relating RD to growth rate, suggesting that RD was independent of size over the range of sizes in our study. As fish grow, the importance of hypertrophy relative to hyperplasia may increase, resulting in a decrease in the DNA concentration of tissues (Koumans et al. 1994; Suresh and Sheehan 1998b). This can result in a violation of the basic assumption of constant DNA content of tissues that underpins the use of RD as a growth rate index (discussed by Caldarone et al. 2016). While our results appear to confirm that RD is related to growth rate and not size for fish at the same stage of development, the question of size and developmental stage should be considered carefully before applying RD as an index of relative growth rates in the field.

While previous studies have generally described a linear relationship between RD and growth rate (eg. Suresh and Sheehan 1998a; Maclean et al. 2008; Caldarone et al. 2016) we fit a regression to log-transformed RD, which improved normality of residuals. It is unclear if the somewhat nonlinear and heteroscedastic relationship that we observed between RD and growth rate reflected the actual distribution of RD values for experimental fish, or if it was an artifact of sampling technique. Our study was intended as a trial of a technique which would have minimal growth and mortality impact on age 0.0 Chinook Salmon which would be tagged and released. We therefore used a smaller biopsy punch (1.5 mm diameter) than the 2 mm diameter punch used by Maclean et al. (2008) on relatively larger (160-220 mm) Atlantic Salmon smolts. This

approach was successful in that it apparently resulted in no increased mortality or decreased growth for the small (75-99 mm) fish in our study. However, the resulting plug of tissue was only 56% of the cross-sectional area that would be produced by a 2 mm biopsy. Fish muscle is not homogenous, rather it is organized into myotomes separated by myosepta. These myosepta consist primarily of connective tissue and have a higher lipid content than the muscle fibres themselves (Zhou et al. 1995). Maclean (2008) found that for juvenile Atlantic Salmon, tissues other than muscle (scale, fin and gill) had low and consistent RD ratios that were not related to growth rate. It seems plausible that our very small biopsy punch may have risked non-representative samples of muscle tissue (relatively more or less muscle fibers relative to connective tissue). This could have resulted in greater variance and artificially low RD values for some high growth rate fish (but not vice versa if myosepta had consistently low RD). Alternatively, it is possible that there is a minimum RNA concentration (ribosome density) for fish exhibiting non-negative growth, and that RD values converge as growth rate decreases.

3.5.5 *RD integration time*

RD responded to a change in ration within 6 days, and continued to track ration level until the end of the experiment (Day 14). However, given the high variance and small sample size, RD values were only able to differentiate high and low ration treatments from each other, and not from the medium ration treatment. Interestingly, RD values in the integration time experiment were elevated when compared to corresponding ration levels in the growth rate experiment. The time required for RD to respond to a change in growth conditions was relatively consistent with results for previous work on Atlantic Salmon. Working with post-smolts, Caldarone et al. (2016) documented a consistent decrease in individual RD after 7 days of fasting, and a consistent increase 8 days after refeeding fasted fish (previous measurements at 3 and 4 days respectively). Treatment means were significantly different after 12 days in both cases. Similarly, Arndt et al. (1996) reported that RD of Atlantic Salmon fry responded to changes in ration within 4-8 days. Faster RD response times of two days or less have been reported for larval fish (eg. Buckley 1980; Wright and Martin 1985; Rooker and Holt 1996). It is likely that RD response time is partially a function of energetic reserves (Caldarone et al. 2016),

with greater reserves corresponding to a longer response time. It seems safe to conclude that RD responds to changes in growth conditions within one to two weeks in juvenile salmonids.

3.5.6 *RD logistical considerations*

Muscle biopsies for RD analysis are simpler to obtain from small fish in the field than blood plasma for IGF1. The only special requirement is the capacity to flash freeze samples and maintain them at -80 °C. Our results, and those of Maclean et al. (2008) and Caldarone et al. (2016), also confirm that biopsies can be obtained non-lethally and with little if any growth impairment. Nevertheless, as discussed above, we are uncertain whether the heteroscedacity that we observed for the relationship between RD and growth was a consequence of difficulty obtaining a representative muscle sample with a very small biopsy punch.

Another major consideration impacting the validity of RD as an index of recent growth in the field is temperature. At lower temperatures, RD values may be higher for a given growth rate (Buckley et al. 1999, 2008), possibly due to the need to compensate for reduced catalytic activity of RNA at low temperature (Goolish et al. 1984). Models have been developed that attempt to derive a common RD, growth and temperature relationship across multiple species of larval fish (Buckley 1984, Buckley et al. 2008). This challenge may be more acute for juvenile fish, where greater mobility may facilitate movement between habitats with very different temperatures over a relatively short time scale (e.g. above or below a thermocline in lakes or the ocean or into tributaries with different thermal regimes in a riverine system). Laboratory experimental work should therefore seek to determine whether the influence of temperature and growth rate on RD integrate over common or differing timeframes in juvenile fish. Even if such details can be worked out, researchers will still be challenged by situations where it is not possible to be confident of the thermal regime experienced by a juvenile fish immediately prior to capture.

3.5.7 *Circulus spacing relation to growth*

We observed a significant, positive correlation between mean spacing of the two outermost circuli and growth, and a negative correlation between circulus formation interval and growth. The coefficients of determination for these relationships (0.44 and 0.46 respectively)

were only slightly lower than for log(RD) and growth (0.47). An assumption of variation in circulus spacing with growth rate in salmonids underpins widely used aging techniques that differentiate summer growth zones with widely spaced circuli from winter zones with closely spaced circuli (eg. Gilbert 1912; Ricker 1962; Bilton and Ludwig 1966). A number of studies have also explicitly demonstrated positive correlations between growth rate and scale circulus spacing (Fisher and Pearcy 1990, 2005; Fukuwaka and Kaeiryama 1997).

The relationship between the spacing of the outermost circulus and growth ($R^2 = 0.29$) was weaker than that for the outer two circuli, likely due in part to measurement uncertainty. When measuring circuli on acetate scale impressions it is not always clear whether the visible scale margin corresponds to the edge of a fully or only partially formed circulus. Our outermost circulus spacing measurement might better be considered a 'penultimate circulus to scale margin' measurement. In studies of wild fish, averaging the spacing of a subset of outer circuli not including the scale margin could reduce error due to incompletely formed circuli (providing the time period reflected was relevant for the study design, see below). Additionally, scale circuli are irregular in spacing, and in some cases split (Figure 3.2). Averaging spacings of multiple circuli reduces the effect of this variability. The relatively strong relationship between growth rate and circulus spacing observed by Fisher and Pearcy (1990) for laboratory-reared age-0 Coho salmon (R^2=0.64) likely reflected averaging across a greater number of circuli than in the present study (up to 16 based on a formation rate of 0 - 0.25 circuli per day over 63-66 days). Given the challenges discussed above, the strength of correlation between circulus spacing and growth that we observed when averaging only two circuli (including the outermost) was encouraging.

Our best models relating spacings of the outer one and two circuli to growth both included terms for FL on day 0. This relationship was positive in both cases (initially larger fish formed wider circuli relative to growth rate). Chinook Salmon scales exhibit a pattern of initially wide circuli close to the origin which then become narrower (Koo 1967, Figure 6 Campbell et al. 2015, Figure 2; and the present study, Figure 3.2,Figure 3.4). Often a minimum is reached with a series of closely spaced circuli (generally between circulus 10 and 20), which may be interpreted as an annulus or ocean entry check depending on life history type. A subsequent increase in circulus spacing has been interpreted as a consequence of rapid growth rate in marine

waters (Koo 1967; Reimers 1971; Tovey 1999). Recent work employing scale and otolith microchemistry has called into question the ability of scale morphology to accurately identify habitat transitions in juvenile Chinook Salmon (Campbell et al. 2015). Our results suggest that early changes in circulus spacing are to some degree independent of growth rate and the phenological events which influence it. Further experiments on fish over a wider range of sizes are necessary to determine if the relationship between circulus spacing and growth rate becomes independent of size in larger Chinook Salmon.

3.5.8 *Circulus spacing integration time*

The duration of the integration time experiment (14 days) was less than the estimated time required to form a single circulus at the growth rates exhibited by many of the fish in the study (see below). We therefore inferred potential integration times for this index from the relationship between circulus formation interval and growth rate observed in the growth rate experiment. The positive relationship between growth rate and circulus formation rate for Chinook Salmon post-smolts was consistent with previous results for Sockeye Salmon (Bilton and Robins 1971), Steelhead (anadromous *Oncorhynchus mykiss*) (Beakes et al. 2014), Coho Salmon (Fisher and Pearcy 1990, 2005) and Atlantic Salmon (Haraldstad et al. 2016). This relationship has the important implication that circulus spacing, averaged over the same number of circuli for fish growing at different rates, will reflect different periods of growth. The nonlinear relationship between circulus formation interval and growth rate (Figure 3.3) was consistent with the observation that scale growth ceases (circulus formation rate approaches 0) in fish that are not growing (Suzuki and Kaeriyama 1990 as cited by Fukuwaka 1998). Heteroscedasticity in the relationship between circulus formation interval and growth rate was likely a consequence of error structure. Circuli were counted as integers and formation interval was calculated by dividing a constant number of days (46) by the number of circuli deposited (mean of up to three scales). Variance in the number of circuli deposited therefore generated far greater variance in estimated circulus formation interval where the increase in circulus number was small.

The observed relationship between circulus formation interval and growth equated to formation of an individual circulus over 9 to 17 days at growth rates of 0.6 to 0.2 % length per day. As previously discussed under 'IGF1 relation to growth' typical growth rates for juvenile Chinook Salmon are likely greater in the field than we observed in the lab. Extrapolating the relationship in Figure 3.3, growth rates of 0.9 to 0.6% length per day would equate to deposition of one circulus every 6 to 9 days. This agrees well with formation interval estimates of 6.8 days during early marine residence of Roberson Creek ocean-type Chinook Salmon (Tovey 1999) and 4.6 to 8.3 days across different stocks of Puget Sound Chinook Salmon (Gamble et al. in press). Based on these literature values for growth and circulus formation rate, circulus spacing averaged over the outermost 2 to 4 circuli could be expected to index growth over the preceding 10 to 20 or 18 to 36 days respectively. Likely growth rates of field-sampled fish must therefore be considered if using circulus spacing as an index of relative recent growth rate, and the potential that very slow growing fish could confound analyses should be taken into account.

3.5.9 *Circulus spacing logistical considerations*

A great advantage of using scale pattern analysis as an index of relative recent growth rates is that scales can be collected easily and non-lethally in the field without the need for specialized equipment. Scales can also be obtained from dead or frozen fish, and can be stored and archived dry for many years. Processing and measuring scales for growth rate analysis requires less specialized labor than aging, as fixed protocols can be established for obtaining digital measurements that do not require subjective assessment of check and annulus locations. Nevertheless, scale processing is time consuming and subject to error. An added benefit of scales relative to biochemical indices of growth is that they can also provide information on life history or growth trajectories prior to the period immediately preceding capture (eg. Ball and Jones 1960; Beamish et al. 2004; Pearcy and Fisher 2005; Gamble et al. in press).

One challenge is that when fish are caught using net-based gear, particularly trawling, most scales are often lost during capture. Recent work by Beaks et al. (2014) has also suggested that temperature may have a significant effect on the relationship between circulus spacing and growth rate. Specifically, at lower temperatures, Steelhead formed wider circuli despite a lower

growth rate. If future work confirms this relationship between temperature and circulus spacing in other salmonids, similar considerations will apply as discussed above for RD and growth.

3.5.10 *Conclusions*

The relative growth rate indices evaluated here differ in terms of theoretical basis, strength of relationship to growth rate, integration time, and logistical constraints (Table 3.2). Plasma IGF1 concentration has a causal theoretical relationship to growth and our results confirm that it is strong indicator of relative recent growth rates in post-smolt Chinook Salmon. This index has been well validated in salmonids and other fish (reviewed by Beckman 2011) and successfully applied to study recent growth of salmon in the field (Ferriss et al. 2014; Journey 2015; Chamberlin et al. 2017). We found that IGF1 responded to a change in growth conditions (ration) within 4 days; earlier than differences in growth rate could be measured directly. This is consistent with the causal role of IGF1 in somatic growth. Where fish may be sampled lethally (or are large enough to permit non-lethal sampling of blood plasma), IGF1 provides a robust index of recent relative growth rates. Muscle RNA to DNA ratio has been less comprehensively validated in juvenile salmonids than IGF1; nevertheless, our results confirm that RD values are positively related to recent growth rate in juvenile Chinook Salmon and respond quickly (within 6 days) to changes in growth conditions. We confirmed and extended the results of Maclean et al. (2008) and Caldarone et al. (2016) by demonstrating that non-lethal sampling of RD was possible even in very small fish (< 10 cm); however, it is possible that use of a very small (1.5 mm diameter) biopsy was responsible for high variability around the relationship between growth rate and RD. The well documented effect of temperature on the relationship between RD and growth (Buckley et al. 1999, 2008) could be problematic where fish may differ in thermal regimes experienced prior to sampling. Nevertheless, RD represents an analytically simple, non-lethal approach to assessing recent relative growth rates. Mean spacing of the outer two scale circuli was almost as strongly related to recent growth of Chinook Salmon post-smolts as RD. Morphometric analysis of scales is non-lethal, simple and inexpensive, but the dependence of circulus formation rate on growth rate means that this metric will index different periods of growth for fish growing at different rates. This is a particular concern where some fish may be

growing very slowly. Scales can also provide additional information on prior growth trajectories and life history.

3.6 References

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3.7 Tables

Table 3.1. Log likelihood, regression statistics, and small sample Akaike information criterion (AICc) for candidate multiple regression models relating muscle RNA to DNA ratio, plasma insulin-like growth factor concentration, circulus formation interval, and mean spacing of the outermost 1 and 2 circuli, to daily percent growth in length for Chinook Salmon post-smolts (n = 60) reared for 25-30 days at rations of 0.5% 1.0% and 3.0% BW/day. Models including fork length (FL) on day 0 were included to account for possible size-based differences in growth indices that were independent of growth rate. Models including ration level and the interaction of ration level and growth rate were included to account for possible non-independence of individuals with each tank/ration level. Growth rates were measured over 30 days while circulus formation interval was measured over 46 days (25-30 days of differential rations following 16-21 days of 1.0% BW/Day. Best models (based on AICc) are indicated in bold.

Response	Model	Log Likelihood	N	K	AICc	ΔAICc	R^2	P
RNA to DNA Ratio								
	Null	-19.9	53	2	44.0	31.6	NA	NA
	Growth	**-2.9**	**53**	**3**	**12.4**	**0.0**	**0.47**	**<0.0001**
	Growth + Ration	-1.7	53	5	14.7	2.3	0.50	<0.0001
	Growth x Ration	-1.5	53	7	19.5	7.1	0.50	<0.0001
	Growth + Day 0 FL	-2.8	53	4	14.5	2.1	0.47	<0.0001
	Growth + Ration + Day 0 FL	-1.6	53	6	16.9	4.6	0.50	<0.0001
	Growth x Ration + Day 0 FL	-1.4	53	8	22.0	9.7	0.50	<0.0001
(ng/mL)								
	Null	-186.8	47	2	377.9	79.6	NA	NA
	Growth	-146.4	47	3	299.3	0.9	0.79	<0.0001
	Growth + Ration	**-143.5**	**47**	**5**	**298.4**	**0.0**	**0.81**	**<0.0001**
	Growth x Ration	-141.8	47	7	300.4	2.1	0.83	<0.0001
	Growth + Day 0 FL	-146.0	47	4	301.0	2.6	0.79	<0.0001
	Growth + Ration + Day 0 FL	-143.2	47	6	300.4	2.0	0.82	<0.0001
	Growth x Ration + Day 0 FL	-141.2	47	8	302.1	3.7	0.83	<0.0001
Circulus Formation Interval (days)								
	Null	-28.9	53	2	61.9	30.0	NA	NA
	Growth	**-12.7**	**53**	**3**	**31.9**	**0.0**	**0.45**	**<0.0001**
	Growth + Ration	-11.9	53	5	35.1	3.2	0.47	<0.0001
	Growth x Ration	-11.6	53	7	39.7	7.9	0.48	<0.0001
	Growth + Day 0 FL	-12.0	53	4	32.9	1.0	0.47	<0.0001
	Growth + Ration + Day 0 FL	-11.3	53	6	36.5	4.6	0.48	<0.0001
	Growth x Ration + Day 0 FL	-10.8	53	8	40.9	9.0	0.49	<0.0001
Outer Circulus Width (μm)								
	Null	-187.1	59	2	378.4	25.9	NA	NA
	Growth	-173.8	59	3	354.0	1.5	0.29	<0.0001
	Growth + Ration	-172.8	59	5	356.7	4.3	0.32	<0.0001
	Growth x Ration	-171.2	59	7	358.6	6.1	0.35	0.0003
	Growth + Day 0 FL	**-171.9**	**59**	**4**	**352.5**	**0.0**	**0.34**	<0.0001
	Growth + Ration + Day 0 FL	-170.4	59	6	354.5	2.0	0.37	<0.0001
	Growth x Ration + Day 0 FL	-169.3	59	8	357.6	5.1	0.39	0.0002
Mean Width of Outer 2 Circuli (μm)								
	Null	-181.3	59	2	366.8	48.1	NA	NA
	Growth	-161.3	59	3	329.1	10.4	0.44	<0.0001
	Growth + Ration	-160.2	59	5	331.6	12.9	0.46	<0.0001
	Growth x Ration	-157.3	59	7	330.8	12.1	0.52	<0.0001
	Growth + Day 0 FL	**-155.0**	**59**	**4**	**318.7**	**0.0**	**0.55**	**<0.0001**
	Growth + Ration + Day 0 FL	-153.0	59	6	319.7	1.0	0.58	<0.0001
	Growth x Ration + Day 0 FL	-150.9	59	8	320.7	2.0	0.61	<0.0001

Table 3.2. Theoretical, technical and logistical comparison of indices of relative recent growth rate in juvenile salmon; italic text indicates interpretation of results of the present study.

	Plasma IGF1	**RNA:DNA Ratio**	**Mean spacing of the outer scale circuli**
Theoretical relationship to tissue growth rate	Proximal Cause	Corollary of Mechanistic Requirement	Conditional Consequence
Correlation with recent growth rate	*Strong*	*Moderate*	*Moderate*
Linear relationship with growth rate	*Yes*	*No*	*Yes*
Independent of initial size	*Yes*	*Yes*	*No*
Able to detect very slow or zero growth	*Yes*	*Yes*	*No*
Response time for a change of growth conditons	*4 Days* [a]	*6 Days* [a]	*> 14 Days*
Provides information on prior growth history	No	No	Yes
Non-lethal sampling possible	Not on small fish	*Yes*	Yes
Useable on dead fish	No[b]	No[b]	Yes[c]
Feasibility for remote field work	Moderate	Moderate	High

[a] Our results were consistent with some response by these indices over the time frames indicated; however, biologically meaningful results will depend on scale of differences in growth rate

[b] In fish dead for an extended period (>30 minutes) blood will clot and become impossible to draw and nucelic acids will be subect to degredation, sampling freshly killed fish should be possible

[c] While sampling of scales from dead fish is possible, a caveat is that fish killed by trawl gear or other mechanical injury may have lost their scales

3.8 Figures

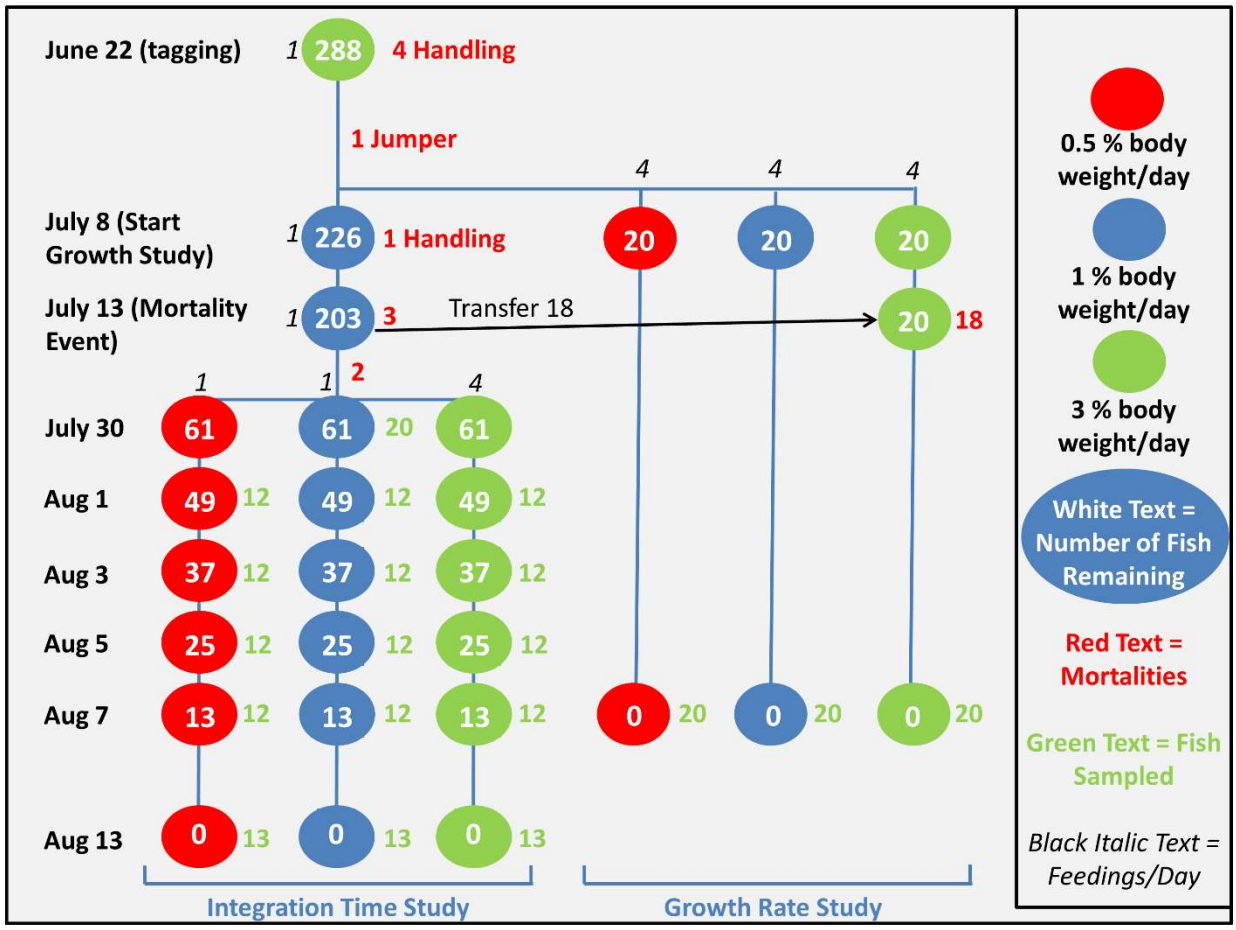

Figure 3.1. Schematic describing the disposition of Chinook Salmon post-smolts among tanks (ellipses) prior to, and during, experiments to evaluate the relative value of plasma IGF1, RNA:DNA ratio, and spacing of the outer scale circuli as indices of recent growth.

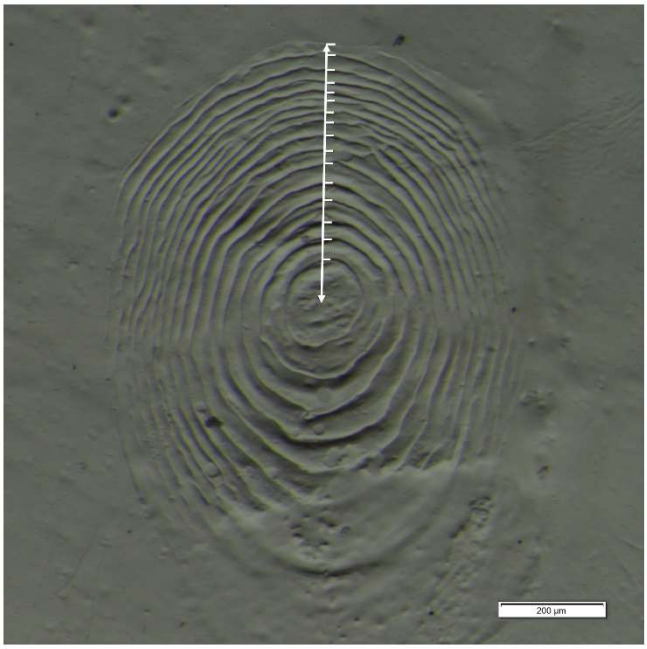

Figure 3.2. Acetate impression of a post-smolt Chinook Salmon scale from an individual 120 mm long and 20.68 g, sampled at the end of the growth rate experiment from the high growth rate treatment (3% BW/day). The measurement radius (double ended arrow) and location of points used to calculate circuli spacings (hatch marks) are indicated.

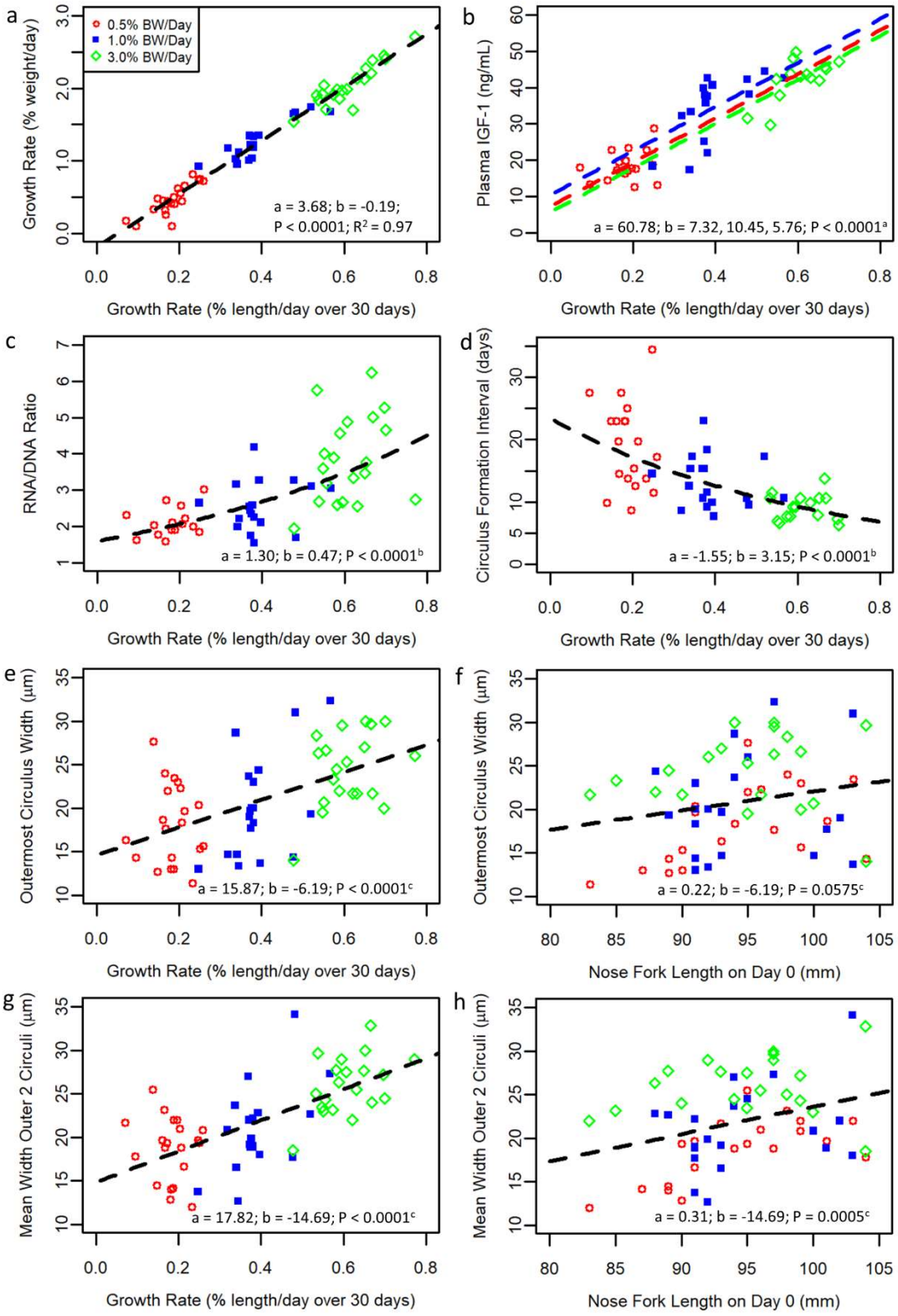
a
0.5% BW/Day
1.0% BW/Day
3.0% BW/Day
Growth Rate (% weight/day)
a = 3.68; b = -0.19;
P < 0.0001; R² = 0.97
Growth Rate (% length/day over 30 days)
b
Plasma IGF-1 (ng/mL)
a = 60.78; b = 7.32, 10.45, 5.76; P < 0.0001[a]
Growth Rate (% length/day over 30 days)
c
RNA/DNA Ratio
a = 1.30; b = 0.47; P < 0.0001[b]
Growth Rate (% length/day over 30 days)
d
Circulus Formation Interval (days)
a = -1.55; b = 3.15; P < 0.0001[b]
Growth Rate (% length/day over 30 days)
e
Outermost Circulus Width (µm)
a = 15.87; b = -6.19; P < 0.0001[c]
Growth Rate (% length/day over 30 days)
f
Outermost Circulus Width (µm)
a = 0.22; b = -6.19; P = 0.0575[c]
Nose Fork Length on Day 0 (mm)
g
Mean Width Outer 2 Circuli (µm)
a = 17.82; b = -14.69; P < 0.0001[c]
Growth Rate (% length/day over 30 days)
h
Mean Width Outer 2 Circuli (µm)
a = 0.31; b = -14.69; P = 0.0005[c]
Nose Fork Length on Day 0 (mm)

Figure 3.3. (previous page) Plots of best regression models (see Table 3.1) of a. instantaneous growth rate (mass) in percent per day over 30 days, b. plasma IGF1, c. RNA to DNA ratio, and d. rate of circulus formation over 46 days (since tagging) against instantaneous growth rate (length) in percent per day over 30 days for post-smolt Chinook Salmon maintained on rations of 0.5% 1.0% and 3.0% body weight per day for 25-30 days. Rate of circulus formation and RNA to DNA ratio were log transformed to improve normality and reduce heteroscedasticity of residuals; however, model fits to untransformed data are plotted here to facilitate comparison to other indices. As best models for the mean spacing of the outermost circulus (e-f), and the mean spacing of the outermost two circuli (g-h) against instantaneous growth rate (length), included a term for FL at the time of tagging, these relationships are plotted separately with initial FL (e and g) and individual growth rate (f and h) held at their respective means (94.5 mm and 0.39% length/day). Regression parameters are a = slope and b = intercept. [a] As the best model for IGF1 included intercepts for each ration level, b-values listed are for rations of 0.5% 1.0% and 3.0% body weight per day respectively. [b] Regression parameters listed are for the linearized form of the illustrated relationships with the response variable log transformed. [c] Regression parameters provided are for the complete model including both variables, therefore b-values do not correspond to those for the illustrated partial regression lines.

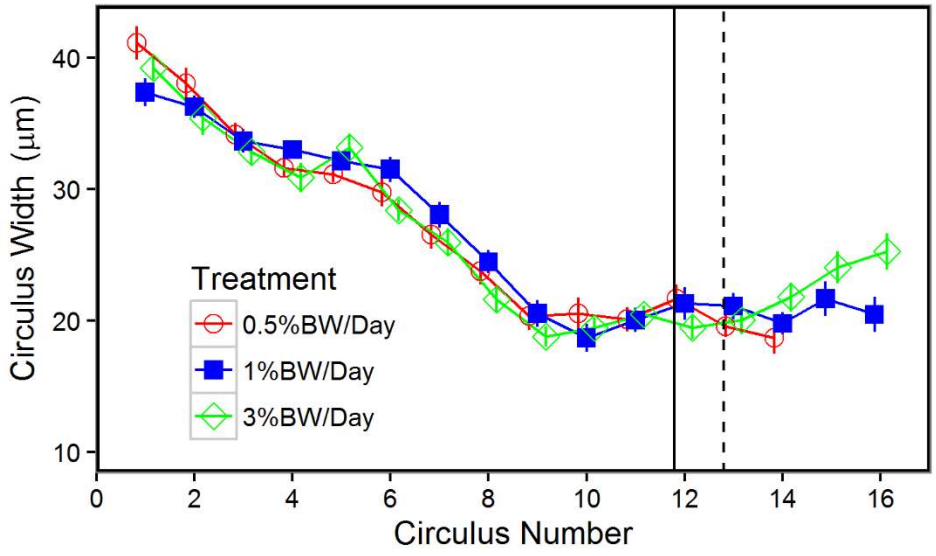

Figure 3.4. Circulus spacing by circulus number for post-smolt Chinook Salmon reared for 25-30 days on rations of 0.5% 1.0% and 3.0% body weight per day. Points are not shown where circulus measurements were available for fewer than 8 fish in any treatment; error bars indicate standard errors of the mean. The vertical solid line indicates the mean number of circuli (11.8) for these fish at the time of PIT tagging (day -15) and the dashed line indicates the mean number of circuli (12.8) at the start of the experiment (day 0).

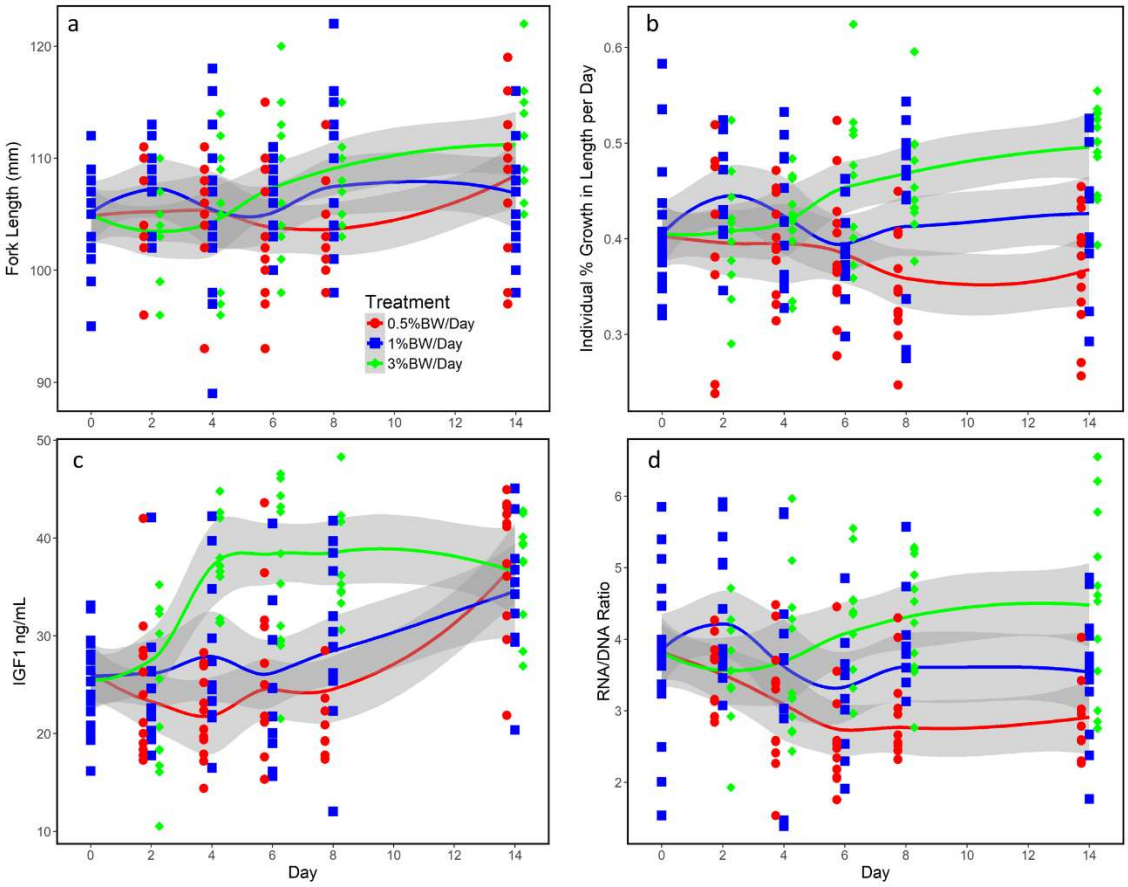

Figure 3.5. Locally weighted scatterplot smooths (loess; span = 0.8) of a. fork length; b. growth rate (length) in percent per day since day -22 (ie. integrates a period of 22 to 36 days); c. Plasma IGF1 concentration; and d. RNA to DNA ratio, for post-smolt Chinook Salmon maintained at a ration of 1.0% BW/day up to the beginning of the experiment (day 0) and subsequently split into treatments of 0.5% 1.0% and 3.0% BW/day and subsampled (n=12-13 per treatment) on days 2, 4 ,6, 8 and 14. Shaded regions indicate 95% confidence intervals of loess smooths. Smooths were fitted by replicating these day 0 values for each ration level. Note that fish were last fed no later than 24 hours prior to sampling in the low and medium ration treatments and 17 hours prior to sampling in the high ration treatment on all days except day 14 where all fish were fed one to three hours prior to sampling.

Chapter 4 - Fine-scale spatiotemporal variation in juvenile Chinook Salmon distribution, diet and growth in an oceanographically heterogeneous region

Adapted from: William Duguid[a], Thomas Iwanicki[b], Jessica Qualley[a] and Francis Juanes[a], (in review). Fine-scale spatiotemporal variation in juvenile Chinook Salmon distribution, diet and growth in an oceanographically heterogeneous region. Progress in Oceanography (in review as of 22 December 2020).

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4.1 Abstract

The existence of fine-scale structure in the abiotic and biotic characteristics of pelagic habitats is widely recognized, but the ecological significance of that structure is understudied. Logistical considerations have meant that research on the ecology of commercially and ecologically important marine species generally occurs at relatively coarse spatial and temporal scales. Many populations of Chinook Salmon (*Oncorhynchus tshawytscha*) in the Northeast Pacific are currently experiencing low productivity. The hypothesis that survival, and hence recruitment, of Chinook Salmon is related to growth early in marine residence has led to intensive research on the trophic ecology of this species during the first year at sea. We employed a small vessel-based methodology to simultaneously characterize fine-scale spatial and temporal variation in physical and biological oceanography, and juvenile Chinook Salmon distribution, size, diet, temperature exposure, and growth from July through October at five sites within the Southern Gulf Islands of the Salish Sea. Densities of zooplankton prey of Chinook Salmon declined to very low levels by the end of the study period. Juvenile Chinook Salmon stomach fullness and growth also declined by early fall while frequency of empty stomachs and importance of fish in diets increased. We found that both oceanographic conditions and trophic ecology of juvenile Chinook Salmon varied among sites only a few (2-23) kilometers apart. Juvenile Chinook Salmon were larger and faster growing at sites where fish (generally Pacific Herring *Clupea pallasii*) constituted a larger proportion of the diet. Overall, the most important prey of juvenile Chinook Salmon by mass proportion (25.6%) was Pacific Herring; however, only 8.4% of individuals contained *C. pallasii*. Analysis of co-occurrence of diet items suggested alternate foraging strategies, with some individuals specializing on Pacific Herring while others targeted a variety of small crustacean zooplankton. Juvenile Chinook Salmon which had consumed Pacific Herring had greater mean stomach fullness than those which had not. Predation on Pacific Herring was strongly related to juvenile salmon length, suggesting that age-0 Pacific Herring may have been too large to be consumed by smaller Chinook Salmon. Our results reinforce the importance of the transition to piscivory in the trophic ecology of juvenile Chinook Salmon. Further research is necessary to determine if fine-scale distribution of larger, piscivorous juvenile salmon is linked to the distribution of their forage fish prey and to understand the role of prey to predator size ratios in limiting the ability of juvenile salmon to transition to piscivory.

4.2 Introduction

Historical research efforts and conservation strategies for anadromous salmonids focused primarily on freshwater life history stages (Hayes and Kocik, 2014, Flitcroft et al. 2019), likely due to ease of observation and the existence of evident anthropogenic impacts on rivers and streams (e.g., Hartman et al. 1996, Williams et al. 2005). This focus has shifted as evidence grows that ocean conditions play a key role in controlling recruitment (Beamish and Bouillon 1993, Welch et al. in review) and as we learn more about the potential of anthropogenic climate change to alter the capacity of marine ecosystems to support salmonids (Abdul-Aziz et al. 2011). The hypothesis that first year survival of juvenile Pacific Salmon (genus *Oncorhynchus*) may be strongly linked to growth (Parker 1971, Beamish and Mahnken 2001, Beamish et al. 2004), and in turn to diet, has led to interest in how the trophic ecology of juvenile salmon varies spatially and temporally (Brodeur et al. 2007, Duffy et al. 2010, Peterson et al. 2010, Hertz et al. 2015, Davis et al. 2020).

Despite this focus on early marine growth, knowledge of the spatial and temporal scales at which juvenile salmon trophic ecology is structured in the ocean still lags that for freshwater, where studies of fine-scale processes have a long history (e.g. Lister and Genoe 1970, Everest and Chapman 1972, Sagar and Glova 1988, Nislow et al. 1998, Metcalfe et al. 1997, Gries and Juanes 1998). Recent work has demonstrated differences in diet and growth of juvenile salmon among estuarine, nearshore and offshore habitats (Duffy et al. 2010, Chittenden et al. 2017, Gamble et al. 2018, Davis et al. 2020). For estuarine and nearshore habitats, fine-scale studies have also attempted to link habitat structure, habitat use, and trophic ecology (e.g. Levy and Northcote 1982, Munsch et al. 2016, Chalifour et al. 2019, Davis et al. 2019). Marine sampling programs for juvenile salmon which have dispersed from estuaries and littoral habitats generally employ large, expensive vessels capable of deploying seine or trawl nets. The cost and availability of such vessels typically limit investigations to seasonal snapshots, with spatial analyses limited to region, basin, or sub-basin comparisons (e.g. Beamish et al. 2000, Ferriss et al. 2014, Hertz et al. 2015, Journey et al. 2016). Trawl sampling integrates linear tracks generally measured in kilometers, limiting inference about fine-scale spatial processes (Peterson et al

2010). While such studies have provided valuable insights, it is also important to understand finer scale processes in these epipelagic habitats.

Most pelagic marine organisms cannot survive on average prey densities and rely on aggregating mechanisms on various scales to generate foraging patches (Steele 1980). Such patches may occur at convergent fronts, where water masses of different densities meet, concentrating buoyant particles or zooplankton which swim actively against downwelling currents (Wolankski and Hamner 1988, Genin 2004). Internal waves (gravity waves occurring at density interfaces within the ocean rather than at the surface) may also concentrate surface-oriented zooplankton by a similar mechanism (Jillett and Zeldis 1985, Shanks and Wright 1987). In a stable water column, zooplankton may concentrate at the depth corresponding to a chlorophyll maximum (Harris 1988) potentially facilitating more efficient predation by planktivores. The interaction of ocean currents with topography may also generate localized foraging opportunities by concentrating and changing the vertical distribution of zooplankton prey and providing an increased flux of prey past waiting predators (Dower and Mackas 1996, Zamon 2002, Genin 2004). Where physical mechanisms concentrate zooplankton prey, zooplanktivorous fish and their predators may also become aggregated, leading to trophic energy transfer becoming focused in space (Zamon 2000, 2003, Genin 2004).

While limited, previous attempts to link fine-scale oceanography to juvenile salmon trophic ecology have provided intriguing results. Sampling inside, outside and at the interface between river plumes and oceanic water has suggested that both prey and juvenile salmon densities may be elevated within or at the edge of plumes (St. John et al. 1992, de Robertis et al. 2005). However, the latter authors did not detect fuller stomachs or different prey in juvenile salmon sampled in frontal regions and suggested that the transient nature of plume fronts might prevent their exploitation by salmon. Off California, stomach fullness of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) was positively related both to recent upwelling and proximity to thermal fronts detected by remote sensing (Sabal et al. 2020). Moulton (1997) also encountered larger and more diverse catches of juvenile salmon within tidal rip lines in Cook Inlet, Alaska. More work is needed to elucidate linkages between fine-scale physical oceanography and juvenile salmon trophic ecology.

Chinook Salmon, a species of particularly high cultural, economic and ecological value, have exhibited declines in marine survival throughout their North American range (Welch et al. in review). Juvenile Chinook Salmon may migrate to sea in the year that they emerge from the gravel (ocean-type) or spend one or more years rearing in freshwater (stream-type). They generally then spend 2-4 years in the ocean before returning to their river of origin to spawn (Quinn 2005). Marine survival of Chinook Salmon is calculated by marking smolts with coded wire tags and measuring the subsequent catch and return to the river of surviving adults; the smolt to adult survival. Within the Salish Sea (Strait of Georgia, Strait of Juan de Fuca, and Puget Sound), perception of synchronous declines in smolt to adult survival of Chinook Salmon (Riddell et al. 2009), along with those of Coho Salmon (*O. kisutch*, Beamish et al. 2010, Zimmerman et al. 2015) and Steelhead Trout (*O. mykiss*), led to the inception of the Salish Sea Marine Survival Project (SSMSP), a binational, five year initiative to understand factors influencing marine survival of these species. While detailed analysis of survival time series suggests that Chinook Salmon survival trends are quite variable within the Salish Sea (Ruff et al. 2017), low abundance of many stocks relative to historical levels led to unprecedented restrictions on Canadian recreational, commercial and First Nations fisheries beginning in 2019.

A considerable body of research has investigated factors influencing diet and growth of juvenile Chinook Salmon during their first summer in the Salish Sea. Much of this work has occurred in Puget Sound, where the average size achieved by July is positively related to survival to adulthood of Chinook Salmon cohorts (Duffy and Beauchamp 2011). Individuals in offshore habitats (defined as generally greater than 30 m bottom depth) consume more decapod larvae and fish (Duffy et al. 2010) and grow more rapidly (Gamble et al. 2018) than those in estuarine or nearshore habitats. For fish in offshore habitats, diet and growth also vary by sub-basin, with greater growth associated with greater consumption of fish prey (Davis et al. 2020). Chamberlin et al. (2017) found that larger juvenile Chinook Salmon grew faster than smaller individuals in regions of Puget Sound where small Pacific Herring (*Clupea pallasii)* were abundant, suggesting that larger size may facilitate a transition to piscivory. To date, no research has investigated the potential role of fine-scale (kilometers to tens of kilometers) variation in physical and biological oceanography in structuring the diet, distribution and growth of juvenile Chinook Salmon during the first summer at sea.

We employed hook and line sampling (microtrolling; Chapter 2) to conduct a fine-scale investigation of size, diet, and growth of juvenile ocean-type Chinook Salmon through summer and early fall in an oceanographically heterogeneous region (the Southern Gulf Islands in the Strait of Georgia; Figure 4.1). Concurrent with fish sampling we used small vessel-based oceanography to characterize spatiotemporal variation in physical (temperature) and biological (zooplankton composition and abundance) oceanography. Within a framework of three specific hypotheses, we sought to determine whether variability in Chinook Salmon diet and growth was present at finer spatial scales than typically considered in studies of juvenile salmon at sea. We hypothesized that locations with a more stratified water column would be selected by juvenile salmon and support faster growth due to generation of prey patches through mechanisms such as internal waves (Jillett and Zeldis 1985, Shanks and Wright 1987) and stable chlorophyll maxima (Harris 1988), and for the potential ability of salmon to select optimum temperatures for growth (Burke et al. 2013). Our study region in the Southern Gulf Islands included a narrows (Sansum Narrows; Figure 4.1) and we hypothesized that the tidal jet generated at this location on the flood tide might also represent a 'hot spot' of juvenile abundance and growth if upwelling and/or flux of zooplankton concentrated forage fish (primarily Pacific Herring) and their predators (Dower and Mackas 1996, Zamon 2002, Genin 2004). We also hypothesized that juvenile Chinook Salmon foraging could be influenced at fine temporal scales by tidal shifts in water column properties and zooplankton availability. Our results will facilitate an improved understanding of how juvenile Chinook Salmon use the topographically complex coastal waters during the latter part of their critical first summer at sea.

4.3 Materials and Methods

4.3.1 *Study Area*

The Southern Gulf Islands region (Figure 4.1) is oceanographically diverse. It adjoins the strongly tidally mixed waters of Haro Strait and the seasonally stratified waters of the Southern Strait of Georgia and Saanich Inlet (Harrison et al. 1983). This region contains Stuart Channel, a well stratified basin (Waldichuck et al. 1968), and a number of passages with strong tidal currents. Sansum Narrows, within our study area, is a narrow (500 m) passage with tidal currents reaching more than 4 knots. Interpretations of the quality of the Southern Gulf Islands

as juvenile salmon habitat are inconsistent. Healey (1978), using seine surveys to collect juvenile salmon throughout the Strait of Georgia, concluded that this region was an important nursery area. Journey (2015) found poor recent growth (as indexed by low IGF-1 concentrations and negative residuals of an IGF-1 to nose to fork length relationship) of Coho and Chum (*O. keta*) Salmon in the Southern Gulf Islands and suggested that this could be due to a lack of stratification resulting in low primary, and hence secondary, productivity. The Southern Gulf Islands has also been identified as a potential model system to study early marine survival of juvenile Chinook Salmon, as smolts from the Cowichan River, a Pacific Salmon Commission indicator stock, apparently rear almost exclusively in this region during their first summer at sea (Beamish et al. 2012).

4.3.2 *Oceanographic sampling*

Each sampling day spanned two tidal phases at one of five sites in the Southern Gulf Islands of the Strait of Georgia (Figure 4.1). Sampling occurred between 9 July and 23 October 2015 with 11 to 12 days at each site. Where possible, successive days at the same site alternated between ebb to flood and flood to ebb transitions (Table 4.1). A single station within each site (Figure 4.1) was occupied twice on each sampling day, once on the ebb and once on the flood. Oceanographic sampling generally occurred between the middle and the end of each tidal phase. A CastAway conductivity, temperature and depth profiler (CTD) was deployed from the surface to within 10 m of bottom (up to a maximum depth of 90 m) to record temperature and salinity. A 50 cm diameter, 2 m long, 350 µm mesh zooplankton net weighted with a 4.5 kg lead ball and equipped with a TSK flowmeter was towed vertically from 30 m to the surface using an Ace Brutus electric line hauler capable of retrieving at ~0.5 m/s. The weight was suspended from the tow line to prevent damage to the net and the cod end was clipped to the weight to ensure the net would sink vertically and not capture zooplankton on the downcast. While deploying and hauling the net, the vessel maneuvered to maintain as close to a vertical cable angle as possible. On the initial five sampling days (10 tows) the CastAway CTD was deployed below the weight (2.5 m below the net rim), to confirm that the target depth was reached. Zooplankton were washed down to the cod end of the net from the outside using pumped surface water and preserved in 10% formalin in seawater.

4.3.3 *Zooplankton Processing*

In the laboratory, zooplankton retained on a 1 mm Nitex sieve were examined in a Bogorov Chamber using a stereomicroscope. Organisms were identified to taxonomic and life-stage groups (see Table 4.2) with taxonomic resolution varying by group based on a combination of ease of identification and frequency of occurrence. For example, hyperiid amphipods were identified to species, brachyuran megalopae were identified to family, and brachyuran zoeae were treated as a single group. Prey items were separated into groups, blotted on Kimwipes, and weighed to the nearest 0.00001 g. Where very high numbers of a given taxon were observed (11/116 samples) the sample was split using a Folsom plankton splitter and the total number and weight of that taxon in the sample was extrapolated from the subsample.

4.3.4 *Fish sampling*

4.3.4.1 Salmon capture

Fish sampling occurred over two tidal phases on all sampling days in the interval between occupation of oceanographic stations. Two Chinook Salmon captured on a reconnaissance day in Cowichan Bay on 6 July are also included in the analyses. Juvenile salmon were captured by 'microtrolling' (Chapter 2) using a 6.7 m vessel and modified recreational fishing gear. Up to six lines per side (12 lines total) were deployed at 5 m intervals from 5 m to up to 30 m (depending on water depth) using Scotty electric downriggers weighted with 6.8 kg lead balls. For the majority of sampling, terminal gear consisted of 2.5 cm "Trout Killer" Apex plastic lures (Hot Spot Fishing & Lures Ltd.) modified to accept small #12 barbed fly-tying hooks with a 5 mm point-shank gap. In general, a translucent pink Apex (finish #138: pink haze/UV) was fished on one side of the boat while an opaque white, black, white and silver (finish # 304: black n' white) Apex was fished on the other.

Fishing activity occurred haphazardly within predefined sites (Figure 4.1). On each day, as much of the sampling site was covered as possible on both tidal phases. Microtrolling occurred in standardized gear deployments (Chapter 2). Start time was logged at the beginning of each gear deployment. Once all lines were at the intended depth, a five-minute period was

timed on a stopwatch. At the end of five minutes, gear was retrieved, and the end time was recorded when all lines were out of the water. To record actual speed through water a General Oceanics Flowmeter weighted with a 0.5 kg weight was suspended 1 m below the surface at the start and retrieved at the end of each fishing event. The vessel track during the fishing event was logged with GPS and the event location was assigned as the location at the mid-point between the start and end time. Hobo Tidbit thermistors were deployed at each depth on the clip connecting the leader to the downrigger cable to provide *in situ* temperature data. As temperature was inversely related to depth over the study period, the minimum temperature recorded between the start and end time of the gear deployment was taken to be the temperature-at-depth. Data were manually screened to exclude the limited periods where air temperature was colder than water temperature at the end of the season. Salmon catch was logged at the level of the individual hook (Chapter 2).

4.3.4.2 Catch processing

All salmon were landed directly into a 150 L insulated live well partially filled with seawater aerated and maintained at ≤ 17 °C using ice blocks. Fish were individually transferred into an anaesthetic bath (5 L of 80 mg/L Tricaine methanesulfonate) for sampling. All salmon were assessed for an adipose fin clip and checked for coded wire tag and PIT tag presence. Nose to fork length (FL) was measured to the nearest millimeter. Scale sampling (for genetic stock ID and growth analysis) and PIT tagging (Chinook Salmon which did not exhibit obvious hooking damage) followed methods described in Chapters 2 and 3. Chinook Salmon stomach contents were sampled non-lethally by gastric lavage (Chapter 2) and then preserved in ≥ 5% formalin in 50 mL tubes for quantitative laboratory analysis (see below). Total time under anesthesia was approximately 3 minutes. Fish were returned to the live well and allowed to regain equilibrium before being released near the site of capture.

4.3.4.3 Chinook Salmon genetic stock identification

As we passive integrated transponder (PIT) tagged all uninjured Chinook Salmon as part of a separate study of Cowichan River Chinook Salmon survival (Pacific Salmon Foundation 2017), genetic stock identification was required to determine which fish originated from the

Cowichan River. After pressing (see 2.3.5 below), scale books were transferred to the Molecular Genetics Laboratory at the DFO (Fisheries and Oceans Canada) Pacific Biological Station where DNA was extracted using Qiagen DNeasy kits. Fish were assigned probabilities of belonging to each of 296 stocks of North American Chinook Salmon following methods similar to those of Beacham et al. (2012). All Chinook Salmon samples were analyzed as a single mixture using the program cBayes (Neaves et al. 2005), which estimates the stock composition following Pella and Masuda (2001). Highest probability stock assignments for each fish were grouped by region and primary life history type (supporting Table 7.1). To avoid confounding effects of life history type and the tendency of larger fish within a stock to disperse more quickly from natal areas (Freshwater et al. 2016), analyses of size, diet, growth, and patterns of catch per unit effort (CPUE) were limited to ocean-type stocks from river systems draining into the Strait of Georgia. Ocean-type Chinook Salmon from the South Thompson stock aggregate were also excluded as these fish have an unusual late ocean entry timing (Beamish et al. 2010).

4.3.4.4 Chinook Salmon diet

Laboratory analysis of samples followed methods described for Zooplankton under 4.3.3 above. For samples with very numerous, small prey (8/325 samples), only a subsample was examined. The remainder of these samples was blotted and weighed in bulk, and weight proportions and counts were assigned in proportion to results for the subsample. Given the importance of cancrid megalopae in Chinook Salmon diets that became evident over the course of processing samples, up to 10 cancrid megalopae per stomach were re-examined from a subsample of stomachs (N = 44) *post hoc* to determine species composition (312 individual megalopae). Where possible, heavily digested fish were identified on the basis of bone morphology using index collections maintained in the Anthropology Bone Lab at the University of Victoria.

4.3.4.5 Chinook Salmon growth indices

Determination of Chinook Salmon circulus spacing followed methods described in Chapter 3. Impressions were produced at the DFO Pacific Biological Station by pressing scale cards onto acetate sheets using a heat-transfer press following Hudson and Crosby (2010).

Acetate impressions of up to three scales per fish were photographed under brightfield illumination with a stereomicroscope-mounted camera. Only scales with a clearly defined origin (non-regenerated) were photographed. The anterior scale radius and width of all circuli along the long axis of the scale were measured using a combination of CellSens software and custom code in the R language. Where the independently measured scale radius differed by more than 1% from the sum of the radius of the origin and all circuli, the scale was remeasured. Where residuals from linear regressions of scale diameter on fork length and circulus count exceeded 200 μm, scales were excluded from analysis. Scales with a measured radius of the origin of < 40 μm or > 110 μm were also excluded. As it was not always possible to tell if the outermost measured circulus was partially or completely formed, the average of the second and third to last circuli were used as an index of growth rate over the preceding 12-27 days (assuming outermost circuli ranging from negligible to fully formed and a circulus formation duration of 6-9 days as discussed in Chapter 3). Where more than one good scale was measured for the same fish this circulus spacing based growth index (henceforward "circulus spacing") was averaged across scales.

4.3.5 *Data Visualization and Statistical Analyses*

4.3.5.1 Oceanographic Sampling

Temperature, salinity, and density data for both the downcast and upcast of the CTD were integrated using CastAway software. For plotting and analysis, data were averaged for each meter of depth (1 m therefore represents the average of data from 0 to 1 m). To visualize spatiotemporal variation in thermal stratification we averaged temperature profiles across the two daily tows and interpolated temperature across dates using the 'interp' function in the package 'akima' in R. We plotted heatmaps of temperature by depth and date for all five sites. To visualize flood vs. ebb shifts in water column properties at each site we calculated the within-day difference of flood tide vs. ebb tide values of temperature, salinity, and density within each meter of depth and plotted the mean and standard deviation of these values over the study period for each site. We also employed generalized additive modelling (GAM) to examine the relationships between stratification and date, site, and tidal phase. The response variable for this analysis was

an index of stratification calculated as the density difference between the second and fiftieth meter of the water column. Models were fit in the package 'mgcv' in R with the identity link and using maximum likelihood (ML) to estimate smoothing parameters (Wood 2011). We specified our model based on the *a priori* hypotheses that stratification would differ among sites, would change non-linearly through time, would change differently among sites, and would exhibit site-specific differences between tidal phases (ebb vs. flood). Our model therefore included a global smooth term for day of the year (DOY), separate smooth terms for DOY by site, and parametric terms for site, phase of the tide (flood vs. ebb), and the interaction of site and phase of the tide. To allow non-linear, site-specific changes in stratification with date to be compared to global changes in stratification with date, we applied a first derivative penalty to the site-specific smoothers rather than the default second derivative penalty (coded as m = 1 in the 'gam' function in the package 'mgcv'). Rather than penalizing the degree of curvature of the smooth, this approach penalizes deviance from a flat function. In the presence of a global smooth for the same variable, this is effectively penalizing deviance from this global smooth (Pedersen et al. 2019). Deviation coding of the categorical variable 'site' facilitated comparison of stratification at each site to the average across sites. Model fit was validated using function 'gam.check' which indicated that the model was under-smoothed using the default (10) maximum degrees of freedom (k) in 'mgcv'. We therefore increased the maximum degrees of freedom until the p-values of the k-index of all smoothers (an indication of patterns in the residuals of that smooth) was > 0.05. The final maximum degrees of freedom selected by this process for smooth functions of day of the year was 13. To visualize the fit of our model we used the function 'gam.predict' to generate predicted stratification indices and associated standard errors at the five sites over the study period and plotted these predictions against observed values. Residual diagnostics for all gams implemented in this study employed a residual simulation approach using the 'DHARMa' package (Hartig 2018).

Prior to analysis of spatiotemporal variation in composition, zooplankton groups were aggregated into categories (Table 4.2). To reduce the influence of rarely encountered taxa, zooplankton categories were only included in analyses of spatiotemporal patterns in community composition if they occurred in more than 10% of tows. All analyses used an index of biomass density calculated as the mass of each category in each tow divided by the average volume

sampled per tow, yielding an approximate biomass/m^3 (but see section 3.1.2 for issues with quantitative zooplankton sampling). To compare zooplankton composition among sites while accounting for seasonal changes we employed permutational multivariate analysis of variance (PERMANOVA) on a Bray-Curtis dissimilarity matrix of averaged (two tows) daily biomass density indices for each category. Using the 'adonis' function in the package 'vegan' (Oksanen et al. 2019) with 999 permutations, we assessed whether the factors month and site, and their interaction, significantly influenced zooplankton composition. In the case of a significant interaction, we ran separate one-way PERMANOVA analyses to compare sites within each month. As PERMANOVA can be sensitive to differences in dispersion among groups, we tested for heterogeneity of group dispersion using the function 'betadisper' in 'vegan'. As the order in which variables are arranged can also influence PERMANOVA results, we ran models with variables in both possible orders. Where significant differences were detected by PERMANOVA, we employed similarity of percentages (SIMPER) analysis to investigate which taxa contributed the most to pairwise dissimilarities between groups. We also visualized differences in zooplankton composition by site and month using non-metric multidimensional scaling (nMDS) on the Bray-Curtis dissimilarity matrix implemented using the function 'metaMDS' in the R package 'vegan'.

To examine the relationships between date, site, and tidal phase and the aggregate biomass concentration of important zooplankton prey of juvenile Chinook Salmon we employed a generalized additive modeling approach corresponding to that used for stratification (section 2.4.1.1). The response variable for this analysis was an overall index of zooplankton biomass concentration derived by summing the category-specific indices in each tow (see previous paragraph). Prey categories included in this analysis were those which represented > 2% of Chinook Salmon diets by weight (see prey biomass analysis column in Table 4.2). To account for the positively skewed nature of the response, the GAM was fit with a gamma distribution and log link. As k-index p-values did not suggest undersmoothing, default (k = 10) maximum degrees of freedom were used.

4.3.5.2 Chinook Salmon diet, size and growth

Analysis of spatial and temporal variation in Chinook Salmon diet followed the same framework as described for zooplankton composition under section 2.4.1.2 (above). Aggregation of prey groups into categories for analysis is outlined in Table 4.3. Only prey groups which occurred in at least 10% of non-empty stomachs were included in analyses of diet composition. As we did not weigh live fish we were not able to convert the weight of diet components into fullness values (i.e. prey weight/predator weight). In order to prevent stomach contents of large fish disproportionately influencing analyses we converted the mass of each diet category in each fish into an index of partial stomach fullness (PF) following Magnussen (2011). The PF index for a given prey category in an individual juvenile Chinook Salmon was calculated as $PF = 100(w)/L^3$ where w is the weight of that prey category in grams and L is the length of the juvenile Chinook Salmon in centimeters.

For analysis of spatial and temporal patterns in diet composition, diet data were grouped by site and period (July to August and September to October) for Chinook Salmon with non-empty stomachs. Diets were not analyzed by month due to limited sample size. Within each site and period, Chinook Salmon diets were randomly grouped into sampling units of 5-7 individuals (6 individuals where possible) and PF indices were averaged for each prey category. Analyses of diet composition (nMDS, PERMANOVA, and SIMPER) were conducted on these sampling units. Grouping diets into sampling units overcame the analytical challenges posed by individual diets where PF indices were zero for several prey categories and facilitated interpretable nMDS results (Platell and Potter 2001). Random grouping also prevented the loss of information entailed in calculating daily averages where sample sizes differed considerably between days.

To visualize volumetric contribution of different prey groups we also aggregated prey into coarse categories (herring, other fish, decapod larvae, other crustacean zooplankton, euphausiid, cephalopod and other) and plotted the means of aggregate partial fullness scores for these categories across months and sites. To investigate foraging selectivity of individual fish we employed a distribution-free, probabilistic model that compared the incidence of pairwise co-occurrence of prey categories within individual stomachs to the expected incidence of co-

occurrence given that prey categories occurred randomly and independently from each other (Veech 2013). This analysis was implemented using the package 'cooccur' in R (Griffith et al. 2016). As our goal was to observe patterns of co-occurrence among prey categories, we did not apply a correction for multiple comparisons to the significance level of the co-occurrence analysis ($\alpha = 0.05$).

To test how juvenile Chinook Salmon length, stomach fullness, occurrence of empty stomachs, capture temperature, and growth varied by site and through the season we employed a GAM approach similar to that applied to stratification and zooplankton biomass. In each case the response variable – FL in mm, total stomach fullness index (the sum of PF scores for each prey type in each fish), binomial occurrence of empty stomachs, temperature at capture depth in °C, and mean spacing of second and third outermost circuli - was related to a parametric term for site and both global and site-specific smooth terms for day of the year. To test for an effect of stratification, a smooth term for the density stratification between 2 and 50 m was included in each model based on the average of density stratification values derived for the flood and ebb on each sampling day (see section 2.4.1.1). As stratification data were not available for all sampling days, this term was dropped from the model when non-significant ($P > 0.05$). To prevent over-fitting where simple non-linear relationships were anticipated, smooth terms were constrained to a maximum of three knots. Where all site-specific smoothers for day of the year were non-significant ($P > 0.05$), site-specific smoothers were dropped from the model. Given the importance of Pacific Herring in diets which became evident in the course of this work (see results) we also included diet groupings as a parametric term in each model (except the empty stomach model). We grouped juvenile Chinook Salmon as having empty stomachs, having preyed on Pacific Herring, or not having preyed on Pacific Herring. As juvenile Chinook Salmon scale circulus spacing has been demonstrated to be related to FL independently of growth rate (Chapter 3), we included a smooth term for FL as a covariate in the scale circulus spacing (growth rate) model. To accommodate positively skewed distributions, FL, stomach fullness, and capture temperature were modelled using the gamma distribution with a log link. Occurrence of empty stomachs was modelled as a binomial response (empty = 1, non-empty = 0) with a logit link and circulus spacing was modelled with a normal distribution and identity link.

Finally, as an independent test of how salmon size was related to piscivorous behavior we investigated lure preference. We subset the data to include only fish caught on our two standard gear types (a translucent pink or an opaque black, white and silver apex lure) and modelled the relationship of salmon length with lure-type and day of the year.

4.3.5.3 Analysis of catch per unit effort

Catch per unit effort of first ocean year Chinook Salmon was analyzed at the level of the individual hook deployment based on a modification of the method describe in Chapter 2. Each hook where a Chinook Salmon was captured was scored as a 1 while all other hooks were scored as 0s. To investigate how CPUE varied across sites, depths, time of day, DOY, and stage of the tide we specified a binomial GAM on the basis of *a priori* hypotheses. Specifically, we hypothesized that Chinook Salmon CPUE would differ among sites, and would vary globally and non-linearly by depth, DOY, density stratification, vessel speed through water, and hour of the day. We also hypothesized that site-specific non-linear relationships might exist between CPUE and depth, DOY, and stage of the tide. Our binomial GAM included a parametric term for site; global smooth terms for hour of the day, depth, and DOY; and site-specific smooth terms for DOY, depth, and tide. Speed through water and stratification data were available only for subsets of fishing events. To determine if these variables influenced Chinook Salmon CPUE, we fit separate models including the aforementioned variables and smooth terms for either speed or stratification to the subset of fishing events that included these variables. We calculated a continuous variable for stage of the tide (tide) based on hour relative to predicted low slack at Active Pass, the nearest tidal prediction site of the Canadian Hydrographic Service. This variable was negative during the ebb tide and positive during the flood tide. As minimum values of the variable 'tide' approximated high slack, and were therefore theoretically continuous with maximum values, we modelled the site-specific relationship between CPUE and tide using cyclic cubic splines (bs = "cc" in gam model formula) which have matching end points. Other smoothers employed default thin plate splines. Models were fit using maximum likelihood (ML). As discussed in section 2.4.1, where both a global smooth and site-specific smooth were included in the model (DOY and depth), a first derivative penalty was applied to the site-specific smoothers. We limited the maximum degrees of freedom (knots) to 5 for smoothers of DOY,

tide, and hour of the day, and 3 for depth. The clustering of hooks within an individual gear deployment represented a potential violation of the assumption of independence in our modelling approach. The GAM function in 'mgcv' allows the inclusion of random effects modelled similarly to smoothers as penalized regression terms (bs = "re" in 'gam' model formula; Wood 2008). We used this approach to include fishing event as a random effect in our model, thereby generating a generalized additive mixed model (GAMM). Due to the relatively large size of the dataset (15,905 individual hooks deployed) this GAMM was fit using the function 'bam' rather than the function 'gam' in the package 'mgcv' in R. The function 'bam' is optimized for more computationally efficient fitting of generalized additive models to large datasets (Wood et al. 2015).

4.4 Results

4.4.1 *Oceanographic sampling*

4.4.1.1 Physical

Cast depths with the CTD varied by site due to differing bottom depth at the oceanographic sampling station. Plotting and analyses included only data down to the shallowest maximum depth reached by any cast at each site. These depths were Cowichan Bay: 50 m; Maple Bay: 84 m; Saanich Inlet: 89 m; Sansum Narrows: 82 m; and Satellite Channel: 68 m. The conductivity sensor on the CTD failed on a single cast on the flood tide at Satellite Channel on 11 July; this cast was excluded from analyses. A cast in Cowichan Bay on 7 October encountered a shallow (< 3 m) layer of low salinity water, likely a consequence of localized input from the Cowichan River, this date was also excluded from generalized additive modeling of stratification.

The warmest water temperatures were observed in Maple Bay and Sansum Narrows, with maximum temperature in the top 1 m reaching 20.3 °C and 18.9 °C, respectively. Temperatures in the top 1 m also reached 18.6 °C in Saanich Inlet, but the layer of warm water was shallower than at the former two sites and the deep water was cooler (Figure 4.2). Maximum temperatures in the top 1 m were lowest at Cowichan Bay (16.9 °C) and Satellite Channel (15.5 °C). Across sites, temperature in the top 1 m declined from 16.3 °C in July (SD = 1.4 °C) to 12.8 °C in

October (SD = 0.60 ℃). A decrease in surface water temperature and thermal stratification was evident at all sites at the end of August. The most pronounced within-day differences between flood tide and ebb tide water column properties occurred at Cowichan Bay and Satellite Channel. At Cowichan Bay the flood tide was associated with warmer, lower salinity and lower density water below about 5 m, while at Satellite Channel the opposite pattern was observed (Figure 4.3). At Maple Bay there was a slight shift towards warmer, lower salinity, lower density water on the flood tide, particularly in the top third of sampled depths. Sansum Narrows showed a similar pattern, but in the bottom third of sampled depths, and exhibited high variability in flood to ebb differences in water column properties in the top third of sampled depths. Water column properties varied little between flood and ebb in Saanich Inlet (Figure 4.3).

A GAM including parametric terms for site, phase of the tide, and their interaction, and global and site-specific smooth terms for day of the year, explained 93.5% of the deviance in density stratification between 2 m and 50 m. Relative to the global mean, density stratification was significantly higher at Maple Bay and Sansum Narrows and significantly lower in Satellite Channel (regression statistics provided in Figure 4.4). The global smooth term for day of the year was significant ($p = 0.010$) but was penalized to a straight line with a negative slope (edf = 1). Site-specific smoothers differed significantly from this global trend for all sites and density stratification exhibited strong cyclic periodicity at all sites except Saanich Inlet. We detected no global effect of phase of the tide, and the interaction of site and phase of the tide was significant only for Cowichan Bay and Satellite Channel, with Satellite Channel more stratified on the flood and Cowichan Bay more stratified on the ebb (Figure 4.4).

4.4.1.2 Biological

Zooplankton tows were successful in sampling the intended depth (30 m) with trial CTD deployments (N = 10) 2.5 m below the net mouth ranging from 32.1 m to 33.3 m (mean = 32.7 m). Line hauling speed averaged 0.55 m/s (SD = 0.05 m/s; based on 106 timed 30 m tows). The retrieval speed through water was close to the threshold required to initiate recording by the TSK flowmeter, and in 34/116 tows the flowmeter either did not begin to spin or recorded implausibly low values (< 50% of the mean value). Due to the very full and tide-dependent daily program of

oceanographic sampling and fish capture it was not practical to repeat tows with problematic flowmeter readings. Zooplankton biomass values must therefore be considered relative indices rather than absolute estimates. Where flowmeter readings were plausible (N = 82 tows) the volume sampled averaged 5.6 m^3 (SD = 0.7; range = 3.4 to 10.0 m^3; net mouth area = 0.2 m^2; flowmeter calibrated at 6.57 revolutions/m).

Decapod zoeae, calanoid copepods, decapod megalopae, and gammarid amphipods collectively made up more than 90% by weight of the potential juvenile Chinook Salmon food sampled in our tows (Table 4.3). Of the decapod megalopae, almost half were of a single species, *Lophopanopeus bellus*, while almost all gammarid amphipods examined were *Cyphocaris challengeri*. Zooplankton categories encountered in a very low number of tows and therefore not included in analyses of species composition included decapod post-larvae (7 tows), *Hyperia medusarum* (2 tows), insects (10 tows), pteropods (1 tow), and unidentified amphipods (2 tows). The category with the minimum numbers of tows that was included in the analysis was larval fish which occurred in 30 tows.

Cumulative densities of zooplankton prey important to juvenile Chinook Salmon declined dramatically over the course of the study period, reaching very low levels in October (Figure 4.4). A GAM model containing both global and site-specific smooth terms for day of year and parametric terms for site, phase of the tide, and the interaction of phase of the tide and site explained 77.1% of the variance in zooplankton density. Relative to the overall average, zooplankton densities were significantly lower at Sansum Narrows, and significantly higher in Cowichan Bay. We did not detect a global effect of phase of the tide on zooplankton density; however, at Sansum Narrows densities were significantly lower on the flood tide (P = 0.003).

Composition of potential zooplankton prey of juvenile Chinook Salmon varied by site and month (Figure 4.5, Table 4.4). As PERMANOVA indicated a significant interaction of site and month (P = 0.005; Table 4.4) we ran separate PERMANOVA analyses comparing sites within each month, and detected significant differences among sites in July (P = 0.004), August (P = 0.001), and September (P = 0.028), but not October (P = 0.262). Maple Bay and Sansum Narrows showed greater overlap with each other in zooplankton composition than with the three

other sites, which in turn were more similar to each other (Figure 4.5). Where zooplankton composition differed by more than 50% between sites in a given month, differences were driven primarily by decapod zoeae, gammarids, copepods, and *Hyperoche sp.* (Table 4.5). Biomass densities for decapod zoeae were particularly high in Cowichan Bay in July and August and were consistently lowest at Sansum Narrows across months (Supplementary Table 7.2). Gammarids represented a larger proportion of biomass at Sansum Narrows and Maple Bay than at other sites while copepods were most important in Satellite Channel and Saanich Inlet (Figure 4.5, Supplementary Table 7.2). Highest biomass densities of *Hyperoche sp.* consistently occurred in Saanich Inlet and Cowichan Bay across months (Supplementary Table 7.2).

4.4.2 *Fish Sampling*

We conducted a total of 1,459 fishing events totaling 15,905 hook deployments over 58 sampling days. The number of fishing events per day ranged from 15 to 33 (Table 4.1). Fishing event duration averaged 8.0 minutes (SD = 0.7 min), mean speed through water as logged by the flowmeter averaged 0.55 m/s (SD = 0.02 m/s). In the field we identified our catch as 382 Chinook Salmon, 92 Coho Salmon, 1 Chum Salmon, 3 Copper Rockfish (*Sebastes caurinus*), 5 Spiny Dogfish (*Squalus acanthias*), and 1 Pacific Sandfish (*Trichodon trichodon*).

4.4.2.1 Chinook Salmon stock, origin, and size

In the course of genetic stock identification (GSI), one fish originally identified as a Chinook Salmon was revealed to be a Coho Salmon and 12 fish identified as Chinook Salmon were revealed to be Chinook Salmon-Coho Salmon hybrids. A manuscript investigating the phenomenon of Chinook-Coho Salmon hybridization in this region and including data for these fish is in preparation (Araujo et al. in prep). Of the 369 confirmed Chinook Salmon, 362 were < 300 mm FL and assumed to be in their first ocean year, and 7 were likely second ocean year fish ranging from 320-381 mm FL. Genetic stock identification (GSI) indicated that 58% of first ocean year Chinook Salmon were of Cowichan River origin (See Table 7.1 for detailed GSI results); the proportion of Cowichan River origin fish ranged from 51% to 68% among sites (Figure 4.6). The remainder were primarily from East Coast Vancouver Island, Puget Sound, and the lower Fraser River. Small proportions of the catch were West Coast Vancouver Island ocean-

type (2%) and middle and upper Fraser River ocean-type (2%) and stream-type (6%) stocks. All subsequently reported results and analyses refer to the 289 first year ocean-type juveniles originating from Strait of Georgia systems including the Cowichan River (N = 209), Lower Fraser River (N = 55), and other East Coast Vancouver Island rivers (N = 25).

Hatchery origin was confirmed for 101/289 fish (36.7%) based on adipose clip, coded wire tag, or both; total hatchery proportion could not be determined as marking of Chinook Salmon is not universally employed at Canadian hatcheries. For Cowichan River-origin Chinook Salmon, where universal marking of hatchery fish did occur in 2015 (Kevin Pellett, DFO, pers. comm.) the overall hatchery marked proportion was 44% and remained relatively constant through the season (Supporting Figure 7.1).

Mean FL was 176 mm (SD = 27 mm), increasing from 145 mm (SD = 19 mm) in July to 202 mm (SD = 23 mm) in October. A GAM detected a non-linear apparent rate of increase in FL which levelled off after mid-September (Figure 4.7). Fork length differed significantly among sites with the largest fish at Sansum Narrows and the smallest fish in Cowichan Bay ($P = 0.024$; Figure 4.7). Both fish with empty stomachs and those which had consumed Pacific Herring were significantly larger than fish which had consumed other diet items ($P < 0.001$; Figure 4.7). A smooth term for stratification and site-specific smooth terms for day of the year were all non-significant and were not included in the final model.

4.4.2.2 Diet

Quantitative diet data were obtained for 262 of 265 juvenile Strait of Georgia-origin ocean-type Chinook Salmon with non-empty stomachs; 23 individuals had empty stomachs and 1 individual was not lavaged. Juvenile Chinook Salmon consumed a diverse assemblage of prey, with the most important prey categories by weight being Pacific Herring (25.6%; 62% of all fish prey) and cancrid megalopae (15.2%; Table 4.3). This diet proportion for Pacific Herring was a minimum estimate as unidentified post larval fish and fish fragments constituted an additional 6% of diets by mass. When diets were aggregated for all juvenile Chinook Salmon, including stock groups not included in analyses (n=322), Pacific Herring represented 38.5% of diets by mass and 73.4% of fish prey (Table 7.4). Despite having the greatest importance by weight,

Pacific Herring occurred in only 8.4% of non-empty stomachs, while cancrid megalopae occurred in 69.5%. For a subset of cancrid megalopae identified to species (N = 312), the majority (88.8%) were *Cancer productus,* with the balance being *Cancer oregonensis* (10.6%) and *Cancer gracilis* (0.6%). Of the zooplankton categories dominating our zooplankton tows (Table 4.2), calanoid copepods, decapod zoeae, and gammarid amphipods were relatively far less important in juvenile Chinook Salmon diets (Table 4.3). Quantitative stomach data were also collected from an additional 60 juvenile Chinook Salmon from non-focal stocks. A taxonomically nested, hierarchical summary (Buckland et al. 2017) of gravimetric composition and frequency of occurrence of prey identified in all 322 diets is provided in Supplementary Table 7.4).

Diet composition was significantly related to site, period and the interaction of site and period (PERMANOVA; see Table 4.4). Dispersion was not homogenous either between sites (P = 0.005) or periods (P = 0.003), meaning that significant PERMANOVA results may have reflected differences in dispersion as well as, or rather than, differences in diet composition. Reduced diet variation at Maple Bay relative to other sites was evident from nMDS (Figure 4.8); but differences in diet composition were also evident, particularly between Sansum Narrows and Maple Bay. Similarly, September – October diets were globally more variable than July – August diets, but were also shifted away from crustacean larvae and other small crustacean zooplankton (copepods and hyperiid amphipods) and towards Pacific Herring, euphausiids and cephalopods (Figure 4.8). Overall, the importance of crustacean zooplankton prey (with the exception of euphausiids) declined dramatically from July to October, while fish (primarily Pacific Herring) became more important after July (Figure 4.9). Crustacean zooplankton dominated diets at Maple Bay and Saanich Inlet into September while fish became the most important prey at Sansum Narrows and Satellite Channel in August and September (Figure 4.9). Cephalopods and euphausiids were more important at Sansum Narrows than at other sites (Figure 4.8, Supplementary Table 7.3). Sample sizes in October were very low (≤ 3) at all sites except Saanich Inlet and Sansum Narrows where fish dominated diets (along with euphausiids at Sansum Narrows; Figure 4.9).

Several categories of small zooplankton prey including copepods, decapod larvae, and hyperiid amphipods all occurred together in diets more often than would be expected by chance. Only cephalopods and Pacific Herring occurred with any other prey categories significantly less often than expected by chance (2 and 7 of 15 potential pairings respectively; Figure 4.10).

Overall stomach fullness declined significantly over the study period ($P = 0.019$) while the occurrence of empty stomachs increased ($P = 0.036$; Figure 4.7). Neither overall fullness nor occurrence of empty stomachs differed significantly between sites. Juvenile Chinook Salmon which had consumed Pacific Herring had significantly fuller stomachs than fish with non-empty stomachs which did not contain Pacific Herring ($P < 0.001$). Smooth terms for stratification and site-specific smooth terms for day of the year were non-significant in models explaining both stomach fullness and occurrence of empty stomachs and were not included in final models.

Lure selection by fish was also related to size, with the opaque, silvery "cop car" apex lure catching significantly larger fish for a given date than an identically sized translucent pink apex ($P = 0.002$; Figure 4.11). When juvenile Chinook Salmon had fed on Pacific Herring the stomach would typically contain the remains of a single age-0 individual. While Pacific Herring remains were too digested for meaningful measurement, many individuals were evidently quite large relative to the size of their predator (Figure 4.12).

4.4.2.3 Capture Temperature

Temperature at the depth and time of capture was successfully measured for 267 of 289 juvenile ocean-type, Strait of Georgia-origin Chinook Salmon of which 264 were captured on days for which stratification data were available. The mean *in situ* capture temperature was highest in August at 14.0 ℃ ($N = 111$; $SD = 1.0$ ℃) and declined to 12.3 ℃ ($N=29$; $SD = 0.3$ ℃) by October (Figure 4.13). Capture temperature also increased significantly with density stratification. The relationship between capture temperature and date differed significantly from the global linear decline at Maple Bay ($P = 0.004$; Figure 4.13) and Sansum Narrows ($P = 0.001$; Figure 4.13); both of which exhibited relatively lower capture temperatures in the first part of the sampling period and relatively higher capture temperatures in the middle of the sampling period. Capture temperatures did not differ significantly by site or diet grouping.

4.4.2.4 Growth

A total of 458 scale impressions from 247 juvenile Chinook Salmon were measured, and 450 of these from 243 fish met quality control criteria. For individual Chinook Salmon with usable scale data a mean of 1.85 scales per fish were analyzed. Circulus spacing decreased linearly over the study period ($P < 0.001$) and was significantly different between sites ($P = 0.030$), being lowest in Maple Bay (Figure 4.14). Circulus spacing did not differ significantly among coarse diet groupings for juvenile Chinook Salmon (Pacific Herring, other items, or empty stomachs; $P = 0.212$). A term for FL was also highly significant in the model relating circulus spacing to site and DOY ($P < 0.001$). A smooth term for stratification and site-specific smooth terms for day of the year were all non-significant and were not included in the final model.

4.4.2.5 CPUE with respect to location, date, depth, time, and tide

Preliminary GAMMs fit to the 1350 fishing events for which speed through water data were available and 1430 fishing events for which stratification data were available, suggested weak, linear, positive relationships between both of these variables and CPUE. However, neither relationship was significant ($P = 0.12$ and $P = 0.07$ respectively) and we therefore omitted these variables and fit the model to all fishing events. Overall, this GAMM explained 8% of the deviance in juvenile Chinook Salmon CPUE. We did not detect significant overall effects of site or hour of the day on Chinook Salmon CPUE (Table 4.6). Chinook Salmon CPUE was lowest at 5 m and significantly elevated from 15 m to 25 m (Figure 4.15). Only Sansum Narrows differed significantly from the global trend, exhibiting lower CPUE for hooks less than 15 m and higher CPUE for hooks deeper than 20 m (Figure 4.15b). The global relationship between day of the year and CPUE was dome shaped, with significantly lower CPUE at the end of the sampling period and a peak in the middle of August (Figure 4.15c). Relative to the global relationship Saanich Inlet had lower CPUE during the middle of the sampling period (late August and early September) and higher CPUE from late September into October (Figure 4.15d). At Sansum Narrows CPUE was slightly elevated late in the sampling period relative to the global trend (Figure 4.15e). We detected significant effects of stage of the tide on Chinook Salmon CPUE

only at Sansum Narrows and Maple Bay (Table 4.6, Figure 4.15f, g). At Maple Bay, CPUE was elevated from the late flood tide through most of the ebb but declined to a minimum in the two hours after low slack. At Sansum Narrows CPUE was elevated during the middle of the flood tide and reached a minimum during the late ebb.

4.5 Discussion

We characterized spatial and temporal variation in water column stratification; zooplankton composition and abundance; and the diet, size, growth, temperature experience and CPUE of juvenile ocean-type Chinook Salmon within a small (< 25 km x 10 km; Figure 4.1) area of the Southern Gulf Islands in the Salish Sea in late summer and fall. We found little evidence that juvenile Chinook Salmon size, growth, diet, or temperature exposure was directly related to local water column properties or zooplankton composition or availability. Nevertheless, our results suggested that individual fish were exhibiting different patterns of foraging behavior, with diet, size and growth varying at a fine spatial scale. Larger juvenile Chinook Salmon were able to transition from a diet of crustacean zooplankton to age-0 Pacific Herring. Forage fish distribution may play an important and size-dependent role in structuring the trophic ecology of juvenile Chinook Salmon in space and time.

4.5.1 *Seasonal Changes*

Near surface water temperature, density stratification and abundance of zooplankton prey of juvenile Chinook Salmon all declined over the study period (Figure 4.2, Figure 4.4), with densities of zooplankton prey reaching very low levels by October. Mean monthly capture temperatures (range = 12.3 ℃ to 14 ℃) were very close to optimal growth temperatures for first ocean year Chinook Salmon feeding at 50% - 100% of C_{max} (Myers et al. 2010). Our results suggest that juvenile Chinook Salmon growth rates decreased over the study period. Plateauing of the non-linear relationship between FL and date (Figure 4.7) could also have been a consequence of size selective mortality (Thomas et al. 2017; Gamble et al. 2018; Nelson et al. 2019) or emigration (Neville et al. 2015); however, circulus spacing also decreased with date (Figure 4.14), suggesting that the decline in growth rate was genuine. One possible explanation for decreasing growth was a shift in energy budget from somatic growth to lipid storage, a

common phenomenon in temperate fish prior to winter (reviewed by Martin et al. 2017). Alternatively, if the decline in growth rate was due to physiological limitation, it was more likely a consequence of decreasing food availability than decreasing temperature. This interpretation was supported by decreasing stomach fullness and increased occurrence of empty stomachs over the study period (Figure 4.7; but see discussion of link between empty stomachs and piscivory under *4.3*). The decrease in crustacean zooplankton abundance (Figure 4.4) was mirrored by a decrease in the importance of crustacean zooplankton in the diet of juvenile Chinook Salmon (Figure 4.9).

It is important to note that our zooplankton tows represented just an index of zooplankton community composition and abundance rather than a representative sampling of zooplankton prey available to juvenile Chinook Salmon. The limitations of plankton nets for representative sampling of juvenile salmon prey has been documented (Brodeur et al. 2011) and was demonstrated in the present study by the absence or near absence from plankton tows of some zooplankton prey which were frequently encountered in juvenile Chinook Salmon stomachs (e.g. adult euphausiids and *Hyperia medusarum*; Table 4.2, Table 4.3). Nevertheless, our zooplankton sampling detected a dramatic decline in biomass density of decapod larvae through the study period (Figure 4.4, Supporting Table 7.2). These larval forms collectively represented 29.5% of juvenile Chinook Salmon diets by mass (Table 4.3). Previous work has found that decapod larvae are at times an important summer diet component for juvenile Chinook Salmon in the Strait of Georgia (Riddell et al. 2018) and on the continental shelf (Brodeur et al. 2007). Decapod larvae are particularly important in some regions of Puget Sound, where they are thought to drive increased growth of juvenile Chinook Salmon as they move offshore (Duffy et al. 2010, Davis et al. 2020). The declining abundance of decapod larvae that we observed in autumn was expected given the strong seasonal links between phytoplankton and meroplankton production in high latitude oceans (Thorson 1946, Highfield et al. 2010). The biomass of euphausiids within the Strait of Georgia peaks in late fall (Heath 1977), while biomass of predatory amphipods (including hyperiids and the gammarid *Cyphocaris challengerii*) is highest during spring and summer (Harrison et al. 1983). Declining partial fullness scores for crustacean zooplankton from July to September indicate that euphausiids were not able to compensate for declining abundance of decapod larvae and other small crustacean zooplankton in Chinook

Salmon diets. Partial fullness scores for fish, primarily driven by Pacific Herring, also increased after July but were not able to compensate for decreased meroplankton abundance (discussed further in *4.3*). The planktonic larval duration of decapods and other meroplankton is strongly inversely linked to water temperature (Lindley 1998, O'Connor et al. 2007). This relationship has the potential to curtail the availability of meroplankton earlier in the season during warmer years when food demands of juvenile salmon may be higher (Daly and Brodeur 2015).

The dome shaped relationship that we observed between CPUE and date (Figure 4.15) likely resulted from increasing catchability of juvenile Chinook Salmon from July to August followed by emigration and mortality between August and October. Chinook Salmon below approximately 150 mm FL are less vulnerable to microtrolling than larger fish (Chapter 2 which may have lowered July CPUE. Some mortality will also have occurred throughout the study period. Beamish et al. (2012) attributed ~80% July to September declines in swept volume-based abundance estimates for Cowichan River Chinook Salmon in the Southern Gulf Islands in 2008 to mortality. The modest decline in CPUE that we observed was inconsistent with mortality on this scale. Preliminary results for Cowichan River Chinook Salmon PIT-tagged in May-June (collected via purse seine) and August-September (microtrolling) show only 3-4 fold greater survival for the latter group (Pellett et al. in prep), suggesting a lower summer mortality rate than inferred by Beamish et al. (2012). Consistent with Beamish et al. (2012) we did not detect a decline in the proportion of hatchery origin Cowichan River Chinook Salmon from July to October (Figure 7.1), suggesting that any differential survival of hatchery and natural origin fish occurs outside of this period. The results of Beamish et al. (2012) suggest dramatically lower survival of hatchery origin Chinook Salmon prior to July, while those of Pellett et al. (in prep) suggest that much lower survival of hatchery fish occurs after September. As discussed above for seasonal changes in length, it is also possible that differential emigration of hatchery and wild-origin fish may confound inferences of differential mortality (or lack-thereof) from changes in hatchery and wild catch proportions.

Many juvenile ocean-type Chinook Salmon are thought to migrate out of the Salish Sea and onto the continental shelf in autumn of their first year at sea (Neville et al. 2015), although some also exhibit residence through at least part of their life history (Chamberlin and Quinn

2014, Rechisky et al. 2019). Healey (1982) suggested that some distributional shifts of juvenile Pacific Salmon at sea may be linked to foraging success. Our results suggest that declining meroplankton availability in fall may decrease the value of the Southern Gulf Islands as rearing habitat. Unfortunately, few data are available on diets of first ocean year Chinook Salmon after October. On the West Coast of Vancouver Island, Hertz et al. (2017) found that euphausiids, amphipods and fish were important diet components in autumn (October-November) and winter (February-March), with stomach fullness higher in winter. Future work on summer to winter shifts in prey availability and diet of juvenile Pacific Salmon may clarify mechanisms driving migration phenology.

4.5.2 *Distribution, size and growth in relation to physical and biological oceanography*

Our results did not provide support for the hypothesis that juvenile Chinook Salmon abundance (as reflected by CPUE) was directly related to local scale water column stratification or zooplankton composition and abundance. Stratification and zooplankton abundance differed significantly between sites (Figure 4.4), as did zooplankton composition (Table 4.4, Figure 4.5). However, we did not detect significant differences in mean CPUE between sites, although Saanich Inlet and Sansum Narrows had relatively higher CPUE at the end of the sampling period. Consistent tidal patterns in density stratification were detected only at Satellite Channel and Cowichan Bay (more and less stratified during flood respectively; Figure 4.3, Figure 4.4), while significant tidal patterns in CPUE were detected only at Sansum Narrows and Maple Bay (Figure 4.15). Only Sansum Narrows exhibited a significant relationship between zooplankton biomass density and stage of the tide (Figure 4.4) with biomass density counterintuitively lower on the flood tide when Chinook Salmon CPUE was elevated.

Our failure to detect strong spatial patterns in CPUE suggest that juvenile Chinook Salmon were broadly distributed in epipelagic habitats within the Southern Gulf Islands. Despite this, we feel our results are inconsistent with random distribution of juvenile Chinook Salmon through the study area. Juvenile Pacific Salmon are highly mobile and are capable of rapid directed migrations, although Chinook Salmon exhibit more milling and consequently lower migration rates than other species (Welch et al. 2011). The shortest distance between our two

most separate sites (Saanich Inlet and Maple Bay) was approximately 24 km. At the travel speed reported by Welch et al. (2011; 0.33 body lengths per second) it would take a 176 mm juvenile Chinook Salmon (the overall mean for the present study) 4.8 days to cover this distance. This is lower than the median local movement rate of 18.9 km/day reported by Rechisky et al. (2019) for juvenile Chinook Salmon tagged in September 2017 in the same region as the present study. Given these movement rates, some mixing of juvenile Chinook Salmon among the sites in our study region almost certainly occurred. Nevertheless, we detected significant differences in juvenile Chinook Salmon size (Figure 4.7), growth (Figure 4.14), and diets (Tables 7, 8, Figure 4.8) among sites, suggesting that individual juvenile salmon were using the seascape in ways which influenced their likelihood of being caught at a given site.

While characteristics of juvenile Chinook Salmon differed between sites, clear cut linkages to local scale physical and biological oceanography were not evident. Specifically, we found no support for the hypothesis that juvenile Chinook Salmon captured at sites with greater water column stratification experienced faster growth. This was exemplified by Maple Bay and Sansum Narrows, which had warmer near-surface temperatures (Figure 4.2) and significantly greater density stratification (Figure 4.4) than the global mean. These two sites also had similar zooplankton composition (Figure 4.5), with SIMPER indicating < 50% dissimilarity in July, August, and September (Table 4.5). Despite these similarities and their physical adjacency, characteristics of juvenile Chinook Salmon differed more between Sansum Narrows and Maple Bay than between other sites. Sansum Narrows had the largest (Figure 4.7) and fastest growing (Figure 4.14) juvenile salmon of any site, while Maple Bay had smaller fish which were the slowest growing of any site. These results were surprising given that Sansum Narrows also had the lowest zooplankton biomass density of any site (*see 4.4*). Sansum Narrows was also the only site to differ from the global relationship between depth and CPUE; the deeper distribution of juvenile Chinook Salmon at Sansum Narrows (Figure 4.15) may explain why capture temperature was considerably lower for fish at Sansum Narrows than Maple Bay despite similar thermal stratification (Figure 4.2). The low growth rate of juvenile Chinook Salmon at Maple Bay was inconsistent with the hypothesis that stratification promotes higher growth rates by allowing selection of optimal temperatures (Burke et al. 2013). Our failure to detect a clear link between local-scale variability in water column stratification and juvenile Chinook Salmon

abundance, size or growth does not contradict evidence for the importance of stratification to juvenile Chinook Salmon growth at larger spatial scales (Burke et al. 2013, Journey 2015).

4.5.3 *Size and growth in relation to diet and the importance of Pacific Herring*

While biological characteristics of juvenile Chinook Salmon were not clearly linked to local biological and physical oceanography, linkages to diet were apparent. Juvenile Chinook Salmon which had preyed on Pacific Herring were larger and had greater stomach fullness than those which had not (Figure 4.7). Scale circulus spacing based growth rates of Chinook Salmon which had eaten Pacific Herring were also higher than those which had fed on other items, although this difference was not significant (Figure 4.14). Juvenile Chinook Salmon size and growth were elevated at sites where fish formed a greater proportion of the diet. The lowest growth rate was observed at Maple Bay (Figure 4.14), which had the least variable diets of any site, dominated by small crustacean zooplankton (Figure 4.8 Figure 4.9). The largest, fastest growing juvenile Chinook Salmon were captured at Sansum Narrows, where diets included more Pacific Herring, euphausiids and cephalopods. Cowichan Bay, Saanich Inlet and Satellite Channel were intermediate between Maple Bay and Sansum Narrows in Chinook Salmon growth rates (Figure 4.14) and the relative importance of crustacean zooplankton and fish in diets (Figure 4.8, Figure 4.9, Table 7.3). The smallest juvenile Chinook Salmon were observed at Cowichan Bay, where diets were dominated by small crustacean zooplankton in July and August and mean partial fullness indices were lower than other sites after August despite fish constituting most of the diet. Smaller size of Chinook Salmon in Cowichan Bay may also have been partially due to proximity to the mouth of the Cowichan River, as smaller individuals in a population may disperse more slowly from their point of ocean entry (Freshwater et al. 2016). Our results were consistent with evidence that the transition to piscivory provides an important growth advantage to juvenile fish (Juanes and Conover 1994, Olson 1996, Juanes et al. 2002). The growth advantage provided by piscivory has also been demonstrated for juvenile Chinook Salmon in other regions. In the Northern California Current, growth and condition of juvenile Chinook Salmon were elevated during periods when Northern Anchovy were abundant in trawl samples and salmon diets (Litz et al. 2017). In Puget Sound, stomach fullness and growth were

greater for piscivorous juvenile Chinook Salmon and growth was higher in regions where fish dominated diets (Davis et al. 2020).

Our growth rate results were likely influenced by the inclusion of FL as a predictor in the scale circulus spacing model. This conservative approach was based on lab results suggesting that circulus spacing varies with fish size independently of growth rate (Chapter 3). As pointed out by Ferriss et al. (2014), correcting growth indices for possible independent relationships with fish size can reduce risk of type I error but may increase risk of type II error. Chapter 3 discusses the possibility that scale circulus spacing becomes independent of length as Chinook Salmon grow, but more work is required to confirm this. Our approach may have underestimated the effect of diet and location on growth as both variables were also strongly related to fish size (Figure 4.7).

The strong relationship that we observed between juvenile Chinook Salmon size and consumption of Pacific Herring may have important implications. Failure to reach the size threshold necessary to transition to piscivory on a dominant prey species can dramatically reduce growth of juvenile fish (Olson 1996). Pacific Herring are the dominant forage fish in the surface waters of Georgia Strait in summer (Riddell et al. 2018) and were historically the dominant forage fish in Puget Sound (Greene et al. 2015). Juvenile Chinook Salmon become more piscivorous as they grow but are only able to consume prey < 50% of their body length, with the vast majority being < 40% (Brodeur 1991, Daly et al. 2009). In our study region, age-0 Pacific Herring were the primary fish prey of juvenile Chinook Salmon (at least 62.0% of fish prey for focal stocks and 73.4% for all stocks combined). While no individual Pacific Herring were intact enough for accurate measurements, they typically appeared close to the size threshold for consumption (Figure 4.12). Chamberlin et al. (2017) found that IGF-1 concentration (a proxy for growth rate) of juvenile Chinook Salmon in Puget Sound was more strongly related length in sub-basins where relatively small (relative to Chinook Salmon length) Pacific Herring were abundant. These authors concluded that this pattern could result from a size dependent shift to piscivory where only larger juvenile Chinook Salmon were able to use Pacific Herring as prey. The size dependence of juvenile Chinook Salmon predation on Pacific Herring is also evident in the Northern Bering Sea where Pacific Herring are the dominant fish by weight in surface trawl

surveys, but are able to outgrow the prey size threshold of Chinook Salmon in their first year at sea and are rarely encountered in diets (Murphy et al. 2014). In the present study Pacific Herring did not become important in diets until August. Working in the same region, Chittenden et al. (2017) reported that fish prey were relatively unimportant in diets of juvenile Chinook Salmon from April to June 2010-2013, and that Pacific Herring represented only 24% of the fish that were consumed. These recent results contrast with historical data from the same region. In 1973, fish dominated (≥ 50% by mass) juvenile Chinook Salmon diets in every month from May to September in Cowichan Bay, with Pacific Herring representing 54% of diet by mass over this period (Argue et al. 1986). These authors also report that in 1976 Pacific Herring represented 85% of hatchery-origin Chinook Salmon diets in Cowichan Bay in July. Similarly, Pacific Herring dominated Chinook Salmon diets off the nearby Nanaimo River estuary from May through October in the mid-1970s (Healey 1980).

Could changes in the predator-prey size ratio over time explain this apparent shift from consumption of Pacific Herring throughout the first summer at sea to a late season, size dependent shift to piscivory? Pacific Herring in the Northeast Pacific primarily spawn in March and early April, although genetically distinct late and early spawning populations also occur (Beacham et al. 2008, Petrou 2019). Chamberlin et al. (2017) hypothesized that late (April to June) spawning Pacific Herring could be particularly important as prey to juvenile Chinook Salmon due to their presumed smaller size. The primary late spawning population in the Salish Sea (Cherry Point) was historically the largest stock within the inside waters of Washington State but has declined precipitously since the 1990s (Sandell et al. 2019). Interannual changes in temperature and density dependence can also influence the size of age-0 Pacific Herring in the Salish Sea (Reum et al. 2013). The Strait of Georgia is warming (Chandler 2019) and warm spring temperatures may result in relatively larger age-0 Pacific Herring in summer (Reum et al. 2013). Density dependent growth also plays a role in the size and condition achieved by age-0 Pacific Herring by fall (Reum et al. 2013; Boldt et al. 2018). It is likely that Pacific Herring population diversity, cohort abundance, and environmental conditions are all interacting with juvenile Chinook Salmon size to regulate predator-prey dynamics, potentially at multiple spatial and temporal scales. Given the importance of piscivory to growth (Litz et al. 2017, Davis et al. 2020) and growth to survival (Moss et al. 2005, Duffy and Beauchamp 2011), changes in the

predator to prey size ratios of Pacific Herring and Chinook Salmon may explain part of both interannual variability and long term trends in Salish Sea Chinook Salmon survival.

Our results support a defined shift in foraging behaviour of juvenile Chinook Salmon from feeding on a mixed assemblage of zooplankton to targeting age-0 Pacific Herring, with individuals which had consumed Pacific Herring containing a number of other prey taxa significantly less often than would be expected by chance (Figure 4.10). Reduced diversity of diet items in juvenile Chinook Salmon which had fed on Pacific Herring may have been partly a seasonal effect given the observed decline in zooplankton abundance and increase in occurrence of piscivory over the study period. However, it is also likely that Chinook Salmon diets become more specialized as they transition to piscivory, as has been described for other predatory fish (e.g. Sánchez-Hernández et al. 2016). If specialization is occurring, a reduction in occurrence of zooplankton prey could result from piscivorous juvenile Chinook Salmon selecting against these prey when encountered, or from a shift in behaviour and habitat use that increased encounters with Pacific Herring at the expense of encounters with alternative prey. For piscivorous fish, Juanes (1994) suggested that apparent selection of small (relative to the available size distribution) prey was generally a function of prey vulnerability rather than predator selection. The larger size of juvenile Chinook Salmon which were captured on silver lures (similar to juvenile Pacific Herring) relative to those captured on equivalently sized pink lures (Figure 4.11) suggests that active prey selection plays some role in the transition to piscivory by juvenile Chinook Salmon. One possible explanation for differences in the size and growth of juvenile Chinook Salmon between sites is that larger, piscivorous fish spent more time in areas where age-0 Pacific Herring were abundant. In historical purse seine surveys conducted in the Strait of Georgia, Chinook and Coho Salmon CPUE became correlated with age-0 Pacific Herring CPUE in late summer and fall (Tanasichuck et al. 2008). If larger, faster growing juvenile Chinook Salmon actively associate with age-0 Pacific Herring this could have implications for predation exposure, competition, and the impacts of Pacific Herring recruitment on Chinook Salmon survival.

Interestingly, size and growth of juvenile Chinook Salmon with empty stomachs were more similar to those of individuals containing Pacific Herring than to those of individuals

containing other prey (Figure 4.7, 14). While non-significant, the occurrence of empty stomachs was also greater at sites with larger, faster growing juvenile salmon. Empty stomachs occur more frequently in piscivorous fish (particularly those that engulf their prey whole) than in those with other habits (Arrington et al. 2002). It seems likely that fish captured with empty stomachs in the present study were disproportionately those which had transitioned to piscivory. This could be explained by fish maintaining empty stomachs between large, high value meals. Alternatively it is possible that gastric lavage sometimes failed on individuals containing large prey (although we believe that this is unlikely) or that juvenile Chinook Salmon containing age-0 Pacific Herring were more likely to completely regurgitate their stomach contents prior to landing than those containing zooplankton. In Puget Sound, the frequency of empty stomachs and occurrence of fish in diets of juvenile Chinook Salmon was elevated in offshore relative to nearshore habitats (Duffy et al. 2010) and in Southeast Alaska juvenile Chinook Salmon had more empty stomachs and were more piscivorous than juvenile Coho Salmon (Weitkamp and Sturdevant 2008). Caution should be used when interpreting empty stomachs of juvenile Pacific Salmon as an indicator of unsuccessful feeding (e.g. Brodeur et al. 2007, Weitkamp and Sturdevant 2008).

4.5.4 *Tidal jets as foraging hotspots*

Support for the hypothesis that the tidal jet at Sansum Narrows would represent a foraging and growth hotspot was equivocal. While Sansum Narrows did have the largest, fastest growing juvenile Chinook of any site, CPUE was not significantly higher than the global mean. Size and growth at Sansum Narrows were also very similar to those at Satellite Channel and Saanich Inlet. Pacific Herring were important in Chinook Salmon diets at Sansum Narrows, and qualitative sonar observations suggested elevated occurrence of forage fish schools (Duguid et al., unpubl. data). One striking result was the significantly lower biomass density of crustacean zooplankton at Sansum Narrows relative to other sites, with densities also significantly lower on the flood tide. Satellite Channel, which was upstream of Sansum Narrows on the flood tide, exhibited the opposite pattern of tidal zooplankton abundance, although this difference was non-significant (Figure 4.4). Low zooplankton densities ‘downstream’ from the constriction of Sansum Narrows could be a consequence of disruption of a concentrated zooplankton layer (possibly at a chlorophyll maximum; Harris 1988) by turbulent mixing in the narrows and

homogenization of zooplankton through the water column. Testing this hypothesis would require depth stratified zooplankton sampling. An alternative explanation for low zooplankton densities at Sansum Narrows in general, and downstream of the narrows in particular, would be that locally abundant forage fish schools, possibly age-0 Pacific Herring, graze down zooplankton as they pass through the tidal passage. Pacific Herring consume many of the zooplankton crustacean taxa that were included in our index of zooplankton biomass density (Kemp 2014). Local predation pressure has been suggested as a mechanism of reduced zooplankton abundance or altered zooplankton community composition over or downstream of seamounts (Genin et al. 1988, Dower and Mackas 1996). Why might age-0 Pacific Herring consistently occupy Sansum Narrows? Zamon (2002) demonstrated that flood currents increased copepod densities in near-surface waters in San Juan passage through upwelling of deeper water. This in turn led to changes in distribution of Pacific Sandlance (*Ammodytes hexapterus*) and Pacific Herring and concentration of their avian and pinniped predators (Zamon 2000, 2003). The lower biomass density of zooplankton that we observed in the top 30 m of the water column at Sansum Narrows was inconsistent with advection of a zooplankton subsidy from depth, although it is possible that such an effect could have been masked by intense local predation. Elevated water velocities associated with abrupt topographies can increase flux of prey particles available to waiting predators, providing an energetic advantage even if prey densities in the water column are not elevated (the "feed-rest" hypothesis reviewed by Genin 2004). Tidal narrows also generate turbulence that may modulate predator-prey interactions. Turbulence reduces the ability of calanoid copepods to evade predation (Clarke et al. 2005, Gilbert and Buskey 2005) which could provide a foraging advantage to planktivorous Pacific Herring. Turbulence may also impact the ability of fish to detect their own predators or may make prey capture more challenging for predatory fish (Higham et al. 2015). It is possible that turbulent flows influence predatory interactions between age-0 Pacific Herring and juvenile Chinook Salmon, however; it is uncertain whether predator or prey would be at an advantage. Tidal narrows are conspicuous features of the Salish Sea and other coastal areas of the Northeast Pacific. More work is required to understand the role of such sites in the trophic ecology of juvenile Chinook Salmon and their prey.

4.5.5 *Conclusion*

Juvenile Chinook Salmon are broadly distributed in coastal marine waters. Our results suggest that this distribution is not homogenous, even at fine spatial scales. Our failure to detect clear linkages between CPUE or characteristics of juvenile Chinook Salmon and local water column stratification and zooplankton abundance suggest that other factors may be more important in structuring juvenile Chinook Salmon habitat use at fine scales. Specifically, the importance of Pacific Herring in diets, combined with linkages between size, growth, catch location and piscivory, suggest that the distribution of forage fish may play a size dependent role in structuring how juvenile Chinook Salmon use their environment.

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4.7 Tables

Table 4.1. Oceanographic and fish sampling times and effort at five sites (Cow = Cowichan Bay, Map = Maple Bay, Saan = Saanich Inlet, Sans = Sansum Narrows, Sat = Satellite Channel) in the Southern Gulf Islands of the Salish Sea (see Figure 4.1). CTD casts were conducted immediately before or after twice-daily zooplankton tows. Tide data are Canadian Hydrographic Service predictions for Active Pass while sunrise and sunset times were accessed from https://sunrise-sunset.org/ on 14 March 2019.

Date	Site	First Tow	Second Tow	First Fishing Event	Last Fishing Event	Fishing Events	Tide Transition	Slack	Sunrise	Sunset
09-Jul-15	Cow	9:47	16:20	10:28	16:35	20	Flood to Ebb	12:03	5:22	21:17
11-Jul-15	Sat	11:54	18:30	12:40	17:48	19	Flood to Ebb	14:41	5:24	21:16
12-Jul-15	Sans	12:29	18:56	12:53	18:40	24	Flood to Ebb	15:43	5:25	21:15
17-Jul-15	Map	11:22	16:10	11:51	15:51	15	Ebb to Flood	12:19	5:30	21:11
18-Jul-15	Sans	10:35	17:13	11:05	16:32	29	Ebb to Flood	12:57	5:32	21:10
19-Jul-15	Cow	11:13	17:46	11:47	18:22	27	Ebb to Flood	13:33	5:33	21:09
20-Jul-15	Sat	11:59	18:27	12:32	17:54	24	Ebb to Flood	14:11	5:34	21:08
22-Jul-15	Saan	13:31	20:15	13:52	19:45	23	Ebb to Flood	15:35	5:36	21:05
25-Jul-15	Cow	10:23	17:02	10:53	16:44	27	Flood to Ebb	13:13	5:40	21:02
26-Jul-15	Saan	11:04	19:09	11:24	18:42	27	Flood to Ebb	14:20	5:41	21:00
27-Jul-15	Map	12:00	19:25	12:17	18:22	19	Flood to Ebb	15:15	5:43	20:59
28-Jul-15	Sat	12:36	19:37	12:55	19:17	30	Flood to Ebb	16:03	5:44	20:58
29-Jul-15	Sans	13:15	19:58	13:30	19:28	28	Flood to Ebb	16:47	5:45	20:56
02-Aug-15	Map	10:36	17:39	10:53	17:05	27	Ebb to Flood	12:50	5:51	20:51
04-Aug-15	Cow	12:30	19:30	12:57	19:00	27	Ebb to Flood	14:30	5:53	20:47
05-Aug-15	Sat	13:00	19:08	13:28	18:45	23	Ebb to Flood	15:26	5:55	20:46
06-Aug-15	Saan	13:52	20:29	14:17	20:08	22	Ebb to Flood	16:30	5:56	20:44
09-Aug-15	Sans	10:34	17:38	11:03	17:15	24	Flood to Ebb	14:23	6:00	20:39
10-Aug-15	Cow	12:17	17:24	12:48	19:01	29	Flood to Ebb	15:24	6:02	20:38
11-Aug-15	Map	13:30	19:38	13:22	19:08	26	Flood to Ebb	16:15	6:03	20:36
12-Aug-15	Saan	13:28	20:15	13:55	19:35	29	Flood to Ebb	16:57	6:04	20:34
13-Aug-15	Sat	13:45	20:27	14:06	20:08	27	Flood to Ebb	17:34	6:06	20:32
17-Aug-15	Cow	10:39	17:32	11:04	16:54	24	Ebb to Flood	13:13	6:11	20:25
18-Aug-15	Map	11:18	18:38	11:36	18:11	28	Ebb to Flood	13:49	6:13	20:23
19-Aug-15	Sat	11:58	18:29	12:35	17:36	25	Ebb to Flood	14:28	6:14	20:21
21-Aug-15	Saan	14:18	19:00	14:33	18:41	23	Ebb to Flood	16:04	6:17	20:18
22-Aug-15	Sans	13:40	20:12	13:54	19:52	30	Ebb to Flood	17:11	6:18	20:16
24-Aug-15	Map	10:27	17:39	10:44	16:52	22	Flood to Ebb	13:36	6:21	20:12
25-Aug-15	Sat	10:57	17:46	12:12	17:22	24	Flood to Ebb	14:36	6:23	20:10
27-Aug-15	Cow	12:52	19:13	10:51	18:21	26	Flood to Ebb	16:12	6:25	20:06
30-Aug-15	Saan	9:28	15:23	9:51	15:02	25	Ebb to Flood	11:50	6:30	20:00
31-Aug-15	Sat	11:01	16:26	11:24	16:01	17	Ebb to Flood	12:39	6:31	19:58
01-Sep-15	Map	11:15	17:07	11:38	16:47	26	Ebb to Flood	13:29	6:32	19:56
02-Sep-15	Sans	12:59	18:03	9:02	17:36	33	Ebb to Flood	14:22	6:34	19:54
03-Sep-15	Cow	13:02	19:11	13:30	18:51	25	Ebb to Flood	15:21	6:35	19:52
09-Sep-15	Sat	12:38	18:36	12:58	18:17	30	Flood to Ebb	15:41	6:44	19:39
10-Sep-15	Map	13:21	19:11	13:50	18:52	24	Flood to Ebb	16:21	6:45	19:37
11-Sep-15	Saan	8:32	15:21	8:53	14:43	27	Ebb to Flood	10:28	6:47	19:35
12-Sep-15	Sans	10:16	16:34	10:47	15:54	19	Ebb to Flood	11:08	6:48	19:33
14-Sep-15	Cow	11:03	17:35	11:53	17:07	22	Ebb to Flood	12:21	6:51	19:28
16-Sep-15	Sat	10:43	17:04	11:02	16:30	30	Ebb to Flood	13:34	6:54	19:24
17-Sep-15	Map	12:32	18:07	12:57	17:56	25	Ebb to Flood	14:15	6:55	19:22
19-Sep-15	Saan	8:22	13:47	9:09	15:52	20	Flood to Ebb	9:37	6:58	19:18
22-Sep-15	Sans	10:05	16:34	10:27	15:56	25	Flood to Ebb	12:51	7:02	19:11
23-Sep-15	Map	10:51	17:23	11:08	16:16	20	Flood to Ebb	13:53	7:04	19:09
24-Sep-15	Cow	11:25	17:58	11:57	17:36	27	Flood to Ebb	14:45	7:05	19:07
25-Sep-15	Sat	12:56	18:31	13:10	18:11	26	Flood to Ebb	15:31	7:06	19:05
29-Sep-15	Saan	10:04	15:45	10:42	14:35	17	Ebb to Flood	12:30	7:12	18:57
30-Sep-15	Sans	11:01	16:25	11:28	16:05	28	Ebb to Flood	13:23	7:14	18:54
01-Oct-15	Map	12:43	18:18	13:05	18:09	28	Ebb to Flood	14:18	7:15	18:52
07-Oct-15	Cow	11:01	17:18	11:31	17:01	27	Ebb to Flood	14:07	7:24	18:40
08-Oct-15	Saan	11:48	18:19	12:37	17:53	19	Ebb to Flood	14:53	7:25	18:38
11-Oct-15	Sans	10:18	14:10	10:49	16:03	29	Ebb to Flood	10:48	7:30	18:32
13-Oct-15	Map	11:23	15:50	11:46	17:37	33	Ebb to Flood	12:07	7:33	18:28
15-Oct-15	Sat	11:46	17:12	12:09	16:45	26	Ebb to Flood	13:26	7:36	18:24
16-Oct-15	Saan	11:43	17:09	12:12	16:48	28	Ebb to Flood	14:08	7:37	18:22
20-Oct-15	Sans	9:08	14:39	9:28	14:17	28	Flood to Ebb	11:06	7:44	18:14
23-Oct-15	Cow	12:21	17:10	12:35	16:51	25	Flood to Ebb	13:59	7:48	18:09

Table 4.2. Overall absolute and proportional mass, counts, and frequency of occurrence of zooplankton groupings identified in 116 vertical 30 m zooplankton tows with a 0.5 m diameter 350 µm ring net over 58 sampling day between 9 July and 23 October at five sites in the Southern Gulf Islands of the Salish Sea. Zooplankton groups were aggregated into analysis categories for spatiotemporal patterns in composition (nMDS, PERMANOVA, SIMPER) and biomass of important juvenile Chinook Salmon prey (generalized additive modelling).

Zooplankton Group	Analysis Category	Composition Analysis	Prey Biomass Analysis	Total Mass (g)	Mass Proportion	Total Count	Frequency of Occurrence
Brachyuran Zoea	Decapod Zoea	Yes	Yes	4.1360	29.48%	7743	97.41%
Calanoid Copepod	Copepod	Yes	No	2.8177	20.08%	8597	97.41%
Caridean Zoea	Decapod Zoea	Yes	Yes	2.7208	19.39%	6710	96.55%
Cyphocaris challengeri	Gammarid	Yes	No	1.0573	7.54%	358	36.21%
Lophopanopeus bellus Megalopa	Decapod Megalopa	Yes	Yes	0.6120	4.36%	479	75.00%
Hyperoche sp.	*Hyperoche sp.*	Yes	Yes	0.6053	4.31%	804	93.10%
Porcellanid Zoea	Decapod Zoea	Yes	Yes	0.5309	3.78%	313	51.72%
Cancrid Megalopa	Decapod Megalopa	Yes	Yes	0.4484	3.20%	121	50.00%
Themisto pacifica	*Themisto sp.*	Yes	No	0.2821	2.01%	555	90.52%
Grapsid Megalopa	Decapod Megalopa	Yes	Yes	0.1510	1.08%	115	35.34%
Polychaete	Polychaete	Yes	No	0.1408	1.00%	438	63.79%
Unidentified Anomuran Zoea	Decapod Zoea	Yes	Yes	0.1072	0.76%	127	44.83%
Euphausiid Larva	Euphausiid	Yes	Yes	0.0865	0.62%	329	64.66%
Unidentified Decapod Zoea	Decapod Zoea	Yes	Yes	0.0852	0.61%	227	3.45%
Pteropod	Pteropod	No	No	0.0697	0.50%	1	0.86%
Insect	Insect	No	No	0.0567	0.40%	38	8.62%
Larval Fish	Larval Fish	Yes	Yes	0.0282	0.20%	45	25.86%
Pagurid Megalopa	Decapod Megalopa	Yes	Yes	0.0211	0.15%	17	11.21%
Majid Megalopa	Decapod Megalopa	Yes	Yes	0.0163	0.12%	17	13.79%
Other	Other	No	No	0.0154	0.11%	9	5.17%
Unidentified Gammarid	Gammarid	No	No	0.0121	0.09%	1	0.86%
Caridean Post Larva	Decapod Post Larvae	No	No	0.0120	0.09%	8	5.17%
Pinnotherid Megalopa	Decapod Megalopa	Yes	Yes	0.0116	0.08%	13	8.62%
Mysid	Other	No	No	0.0014	0.01%	6	4.31%
Hyperia medusarum	*Hyperia medusarum*	No	Yes	0.0013	0.01%	2	1.72%
Caligid Copepod	Copepod	Yes	No	0.0010	0.01%	1	0.86%
Pinnotherid Post Larva	Decapod Post Larvae	No	No	0.0008	0.01%	1	0.86%
Unidentified Amphipod	Unid. or Other Amphipod	No	No	0.0006	0.00%	1	0.86%
Primno sp.	Unid. or Other Amphipod	No	No	0.0004	0.00%	1	0.86%
Gelatinous Zooplankton	Gelatinous Zooplankton	No	No	0.0000	0.00%	39507	100.00%

Table 4.3. (next page) Overall absolute and proportional mass, counts, and frequency of occurrence of prey groups in juvenile Strait of Georgia ocean-type Chinook Salmon with non-empty stomachs (N = 262) between 9 July and 23 October at five sites in the Southern Gulf Islands of the Salish Sea. Prey groups were aggregated into analysis categories to investigate spatiotemporal patterns in diet (nMDS, PERMANOVA, SIMPER).

Prey Group	Analysis Category	Composition Analysis	Total Mass (g)	Mass Proportion	Total Count	Frequency of Occurrence
Clupea pallasi	Herring	Yes	25.7828	25.60%	25	8.40%
Cancridae - Megalopa	Decapod Megalopa	Yes	15.3313	15.22%	5005	69.47%
Teuthida	Cephalopod	Yes	7.1111	7.06%	12	3.82%
Hyperoche medusarum	*Hyperoche sp.*	Yes	6.5841	6.54%	6602	71.76%
Lophopanopeus bellus - Megalopa	Decapod Megalopa	Yes	5.2519	5.21%	5116	52.29%
Brachyura - Zoea	Decapod Zoea	Yes	3.8527	3.82%	2788	55.34%
Embiotocidae	Fish	Yes	3.8287	3.80%	2	0.38%
Osteichthyes - Post Larval	Fish	Yes	3.3198	3.30%	4	1.53%
Octopoda	Cephalopod	Yes	3.2242	3.20%	35	5.73%
Hyperia medusarum	*Hyperia medusarum*	Yes	2.9831	2.96%	294	42.75%
Osteichthyes - Fragments	Fish	Yes	2.6751	2.66%	41	14.50%
Osteichthyes - Larval	Fish	Yes	2.5693	2.55%	94	18.70%
Euphausiidae - Post Larval	Euphausiid	Yes	2.4734	2.46%	114	13.36%
Porcellanidae - Zoea	Decapod Zoea	Yes	1.9897	1.98%	1043	28.24%
Brachyura - Megalopa	Decapod Megalopa	Yes	1.7901	1.78%	2388	48.47%
Engaulis mordax	Fish	Yes	1.2567	1.25%	5	1.15%
Themisto pacifica	Themisto pacifica	Yes	1.2565	1.25%	711	25.57%
Amphipoda	*Unidentified or Other Amphipod*	Yes	1.1205	1.11%	97	27.10%
Myctophidae	Fish	Yes	1.1017	1.09%	1	0.38%
Cephalopoda	Cephalopod	Yes	1.0590	1.05%	5	1.91%
Gammaridae	Gammarid	Yes	0.9125	0.91%	73	13.36%
Syngnathus leptorhynchus	Fish	Yes	0.7952	0.79%	114	7.63%
Insecta	Insect	No	0.6962	0.69%	203	4.96%
Porcellanidae - Megalopa	Decapod Megalopa	Yes	0.6895	0.68%	411	27.86%
Other	Other	No	0.4847	0.48%	53	18.70%
Grapsidae - Megalopa	Decapod Megalopa	Yes	0.3231	0.32%	298	31.30%
Pinnotheridae - Megalopa	Decapod Megalopa	Yes	0.2723	0.27%	260	32.06%
Pinnotheridae - Post Larval	Decapod Post Larvae	No	0.2452	0.24%	14	3.82%
Pleuronectidae - Larval	Fish	Yes	0.2422	0.24%	8	3.05%
Hymenoptera	Insect	No	0.2068	0.21%	22	1.53%
Copepoda	Copepod	Yes	0.2010	0.20%	377	11.45%
Polychaeta	Polychaete	No	0.1520	0.15%	27	6.87%
Calanoidea	Copepod	Yes	0.1373	0.14%	388	20.61%
Cirripedia - Adult Exuviae	Other	No	0.1325	0.13%	102	5.73%
Mysidae	Other	No	0.1105	0.11%	7	1.15%
Cyphocaris challengeri	Gammarid	Yes	0.1052	0.10%	8	0.76%
Majidae - Megalopa	Decapod Megalopa	Yes	0.1012	0.10%	95	16.79%
Digested Material	Other	No	0.0743	0.07%	8	3.05%
Caridea - Post Larval	Decapod Post Larvae	No	0.0673	0.07%	14	4.58%
Decapoda - Megalopa	Decapod Megalopa	Yes	0.0601	0.06%	34	4.20%
Pteropoda	Pteropod	No	0.0414	0.04%	18	4.20%
Decapoda	Other	No	0.0405	0.04%	2	0.76%
Caridea - Zoea	Decapod Zoea	Yes	0.0170	0.02%	19	4.96%
Sebastes sp.	Fish	Yes	0.0148	0.01%	1	0.38%
Paguridae - Megalopa	Decapod Megalopa	Yes	0.0132	0.01%	13	4.20%
Brachyura - Post Larval	Decapod Post Larvae	No	0.0098	0.01%	1	0.38%
Arachnida	Other	No	0.0051	0.01%	1	0.38%
Gastropoda - Larval	Other	No	0.0042	0.00%	4	1.53%
Diptera	Insect	No	0.0029	0.00%	1	0.38%
Caprellidae	Unidentified or Other Amphipod	Yes	0.0023	0.00%	1	0.38%
Caligidae	Copepod	Yes	0.0014	0.00%	1	0.38%
Isopoda	Other	No	0.0010	0.00%	1	0.38%
Monstrilloidea	Copepod	Yes	0.0009	0.00%	2	0.76%
Pycnogonidae	Other	No	0.0008	0.00%	1	0.38%
Euphausiidae - Zoeae	Euphausiid	Yes	0.0004	0.00%	1	0.38%
Cumacea	Other	No	0.0003	0.00%	1	0.38%
Paguridae - Zoea	Decapod Zoea	Yes	0.0002	0.00%	1	0.38%
Euphausiidae - Furcilia	Euphausiid	Yes	0.0002	0.00%	1	0.38%
Cnidaria - Medusae	Gelatinous Zooplankton	No	NA	NA	2	0.38%
Pleurobrachia	Gelatinous Zooplankton	No	NA	NA	1	0.38%
Siphonophora	Gelatinous Zooplankton	No	NA	NA	3	1.15%

Table 4.4. Results of PERMANOVAs comparing biomass density indices for different zooplankton groups and partial fullness indices for different juvenile Chinook Salmon prey groups by site, month/period and the interaction of site and month/period for samples collected between 9 July and 23 October at five sites in the Southern Gulf Islands of the Salish Sea. As the interactions of site and month/period was significant for both zooplankton and diet composition, separate PERMANOVA analyses were run to investigate differences among sites within months/periods. Significant P-values (<0.05) from PERMANOVA are indicated in bold.

Model	Period	Variable	df	Sums of Squares	F	R^2	P
Zooplankton	All Months	Site	4	2.22	6.63	0.22	**0.001**
		Month	3	3.12	12.45	0.31	**0.001**
		Site x Month	12	1.69	1.69	0.17	**0.005**
		Residual	38	3.17		0.31	
	July	Site	4	1.15	3.67	0.65	**0.004**
		Residual	8	0.63		0.35	
	August	Site	4	1.09	4.48	0.56	**0.001**
		Residual	14	0.86		0.44	
	September	Site	4	0.72	1.93	0.39	**0.028**
		Residual	12	1.12		0.61	
	October	Site	4	0.72	1.25	0.56	0.262
		Residual	4	0.58		0.44	
Diet - Fullness Index	All Periods	Site	4	2.11	3.13	0.21	**0.001**
		Period	1	0.94	5.57	0.09	**0.001**
		Site x Month	4	1.09	1.62	0.11	**0.042**
		Residual	34	5.71		0.58	
	July-August	Site	4	1.25	2.41	0.31	**0.001**
		Residual	21	2.73		0.69	
	September-October	Site	4	1.51	1.65	0.34	**0.033**
		Residual	13	2.98		0.66	

Table 4.5. Results of a similarity of percentages (SIMPER) analysis on an index of biomass concentration (units ~ g/m^3) for potential zooplankton prey of juvenile Chinook Salmon sampled with vertical 30 m tows with a 0.5 m diameter 350 µm ring net between 9 July and 23 October at five sites in the Southern Gulf Islands of the Salish Sea (Table 4.1). Results are shown only for months where zooplankton composition differed significantly between sites (PERMANOVA; Table 4.4). Values below the shaded diagonal indicate overall average pairwise dissimilarities between sites. Where zooplankton composition is greater than 50% dissimilar (shaded in bold), letters above the diagonal indicate the zooplankton groups cumulatively contributing at least 70% of the dissimilarity in order of decreasing importance. Abbreviations are decapod zoeae (DZ), gammarid amphipods (Gam), copepods (C), and *Hyperoche sp*. (Hch). Site names are defined in Table 4.1 and mapped in Figure 4.1.

		Cow	Map	Saan	Sans	Sat
July	Cow		DZ, Gam	DZ, C	DZ	DZ
	Map	**0.56**				
	Saan	**0.51**	0.49		C, DZ, Gam	
	Sans	**0.77**	0.44	**0.63**		
	Sat	**0.57**	0.46	0.43	0.49	
August	Cow			C, DZ	DZ, Gam	
	Map	0.33		C, DZ		
	Saan	**0.52**	**0.54**		C, DZ	
	Sans	**0.59**	0.35	**0.58**		
	Sat	0.46	0.45	0.40	0.50	
September	Cow				DZ, Hch, Gam	
	Map	0.40				
	Saan	0.38	0.43		DZ, C, Hch	
	Sans	**0.55**	0.44	**0.56**		DZ, C, Gam
	Sat	0.43	0.47	0.42	**0.56**	

Table 4.6. Regression statistics for a generalized additive mixed effects model (GAMM) relating the log-odds of catching a first ocean year Chinook Salmon to site, hour of the day, day of the year, depth, and stage of the tide. Depth and day of the year are included in the model both as both a global smooth term and site-specific smooth terms. Stage of the tide is included just as site specific smooth terms and hour of the day just as a global smooth term. Site is also included in the model as a parametric fixed effect and fishing event is included in the model as a random effect. Terms which are significant based on approximate P-values are indicated in bold. Plots of all significant smoothers are provided in Figure 4.15.

Type of Term	Variable	Level	Coefficient	Std. Error	z	est. df	Chi.sq	P-value
Parametric Factor								
	Site	Cowichan Bay	0.05	0.13	0.37			0.711
	Site	Maple Bay	0.15	0.12	1.25			0.209
	Site	Saanich Inlet	0.04	0.14	0.25			0.800
	Site	Sansum Narrows	-0.09	0.15	-0.61			0.540
	Site	Satellite Channel	-0.15	0.14	-1.067			0.286
Smooths								
	Hour of Day	Global				1.00	1.794	0.181
	DOY	**Global**				**2.71**	**20.032**	**<0.001**
	DOY	Cowichan Bay				0.06	0.068	0.260
	DOY	Maple Bay				0.00	0.002	0.665
	DOY	**Saanich Inlet**				**3.40**	**24.865**	**<0.001**
	DOY	**Sansum Narrows**				**1.63**	**5.868**	**0.012**
	DOY	Satellite Channel				0.50	0.730	0.199
	Depth	**Global**				**1.89**	**10.616**	**0.003**
	Depth	Cowichan Bay				0.00	0.005	0.321
	Depth	Maple Bay				0.00	0.000	0.828
	Depth	Saanich Inlet				0.00	0.001	0.446
	Depth	**Sansum Narrows**				**1.55**	**9.481**	**0.002**
	Depth	Satellite Channel				0.00	0.001	1.000
	Tide	Cowichan Bay				0.40	0.530	0.276
	Tide	**Maple Bay**				**1.86**	**10.656**	**0.003**
	Tide	Saanich Inlet				0.01	0.003	0.506
	Tide	**Sansum Narrows**				**1.86**	**9.856**	**0.004**
	Tide	Satellite Channel				0.90	1.700	0.162
	Fishing Event (RE)					51.80	55.037	0.059

Table 4.7. Results of a similarity of percentages (SIMPER) analysis on spatial patterns in partial fullness indices (see methods for details) for different prey groups of juvenile Chinook Salmon sampled between 9 July and 23 October at five sites in the Southern Gulf Islands of the Salish Sea (Table 4.1). Values below the shaded diagonal indicate overall average pairwise dissimilarities between sites. Letters above the diagonal indicated the prey groups cumulatively contributing at least 70% of the dissimilarity in order of decreasing importance. Abbreviations are decapod megalopae (DM), decapod zoeae (DZ), Fish (F), Pacific Herring (He), *Hyperoche* sp. (Hch), Euphausiid (Eu) and Cephalopod (Ce).

		Cow	Map	Saan	Sans	Sat
July-August	Cow				DM,He,Ce,F	F,DM,DZ
	Map	0.41			DM,He,Ce,DZ	F,DM,DZ,He
	Saan	0.44	0.39		DM,He,Ce	F,DM,DZ
	Sans	**0.77**	**0.72**	**0.77**		F,DM,He,Ce
	Sat	**0.55**	**0.55**	**0.56**	**0.80**	
September-October	Cow		DM,F,Hch	F,He,Ce	F,Ce,He	F,He,Hch
	Map	**0.83**		DM,He,Hch,DZ	DM,He,Ce,Hch	DM,He,Hch,DZ
	Saan	**0.82**	**0.72**		He,Ce,F,Eu	He,Hch,Ce
	Sans	**0.73**	**0.76**	**0.68**		He,Ce,Hch
	Sat	**0.76**	**0.58**	**0.62**	**0.68**	

4.8 Figures

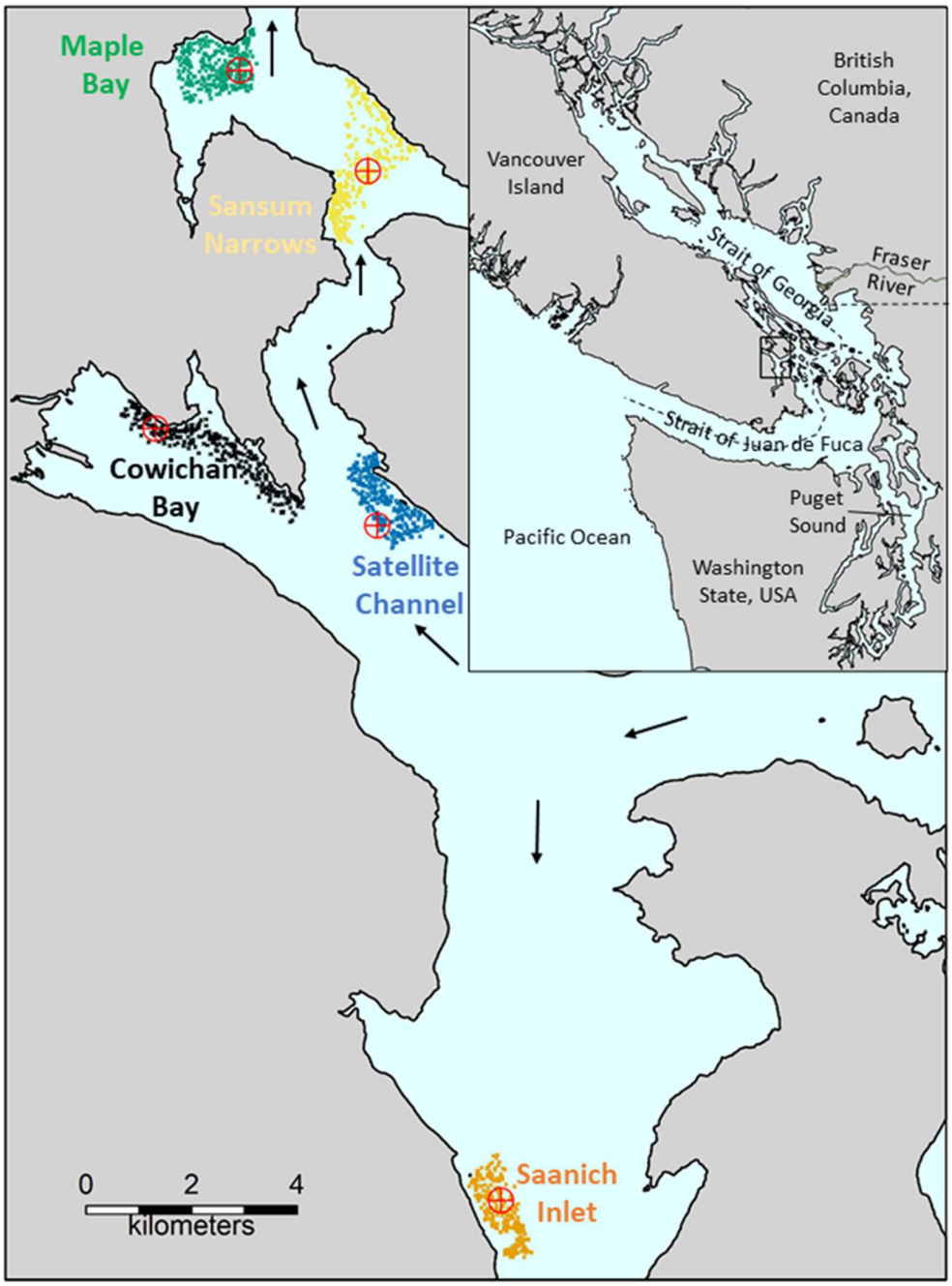

Figure 4.1. Five sites in the Southern Gulf Islands of the Salish Sea (combined waters of the Strait of Georgia, Strait of Juan de Fuca, and Puget Sound) where oceanographic and fish sampling were conducted from 6 July to 23 October 2015; focal region is indicated by the rectangle in the larger scale inset. Coloured crosses indicate the locations of individual fishing events while red quartered-circle symbols indicate the location of the oceanographic station at each site. Arrows indicate the approximate direction of the flood tide current with the ebb tide flowing in the opposite direction.

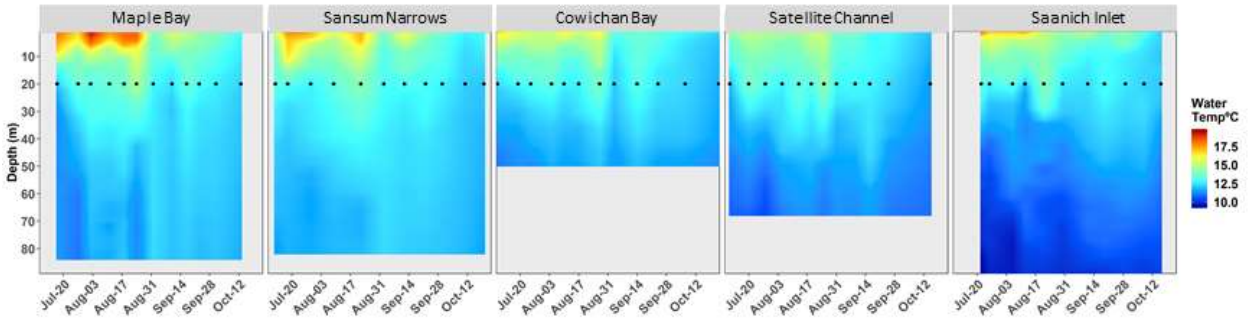

Figure 4.2. Vertical and longitudinal interpolation of water temperature profiles averaged from twice daily (ebb and flood) CTD casts between 9 July and 23 October 2015 at five sites in the Southern Gulf Islands (ordered from North to South; see Figure 4.1 for site locations) of the Salish Sea. Black points indicate sampling dates, only one site was sampled on each date.

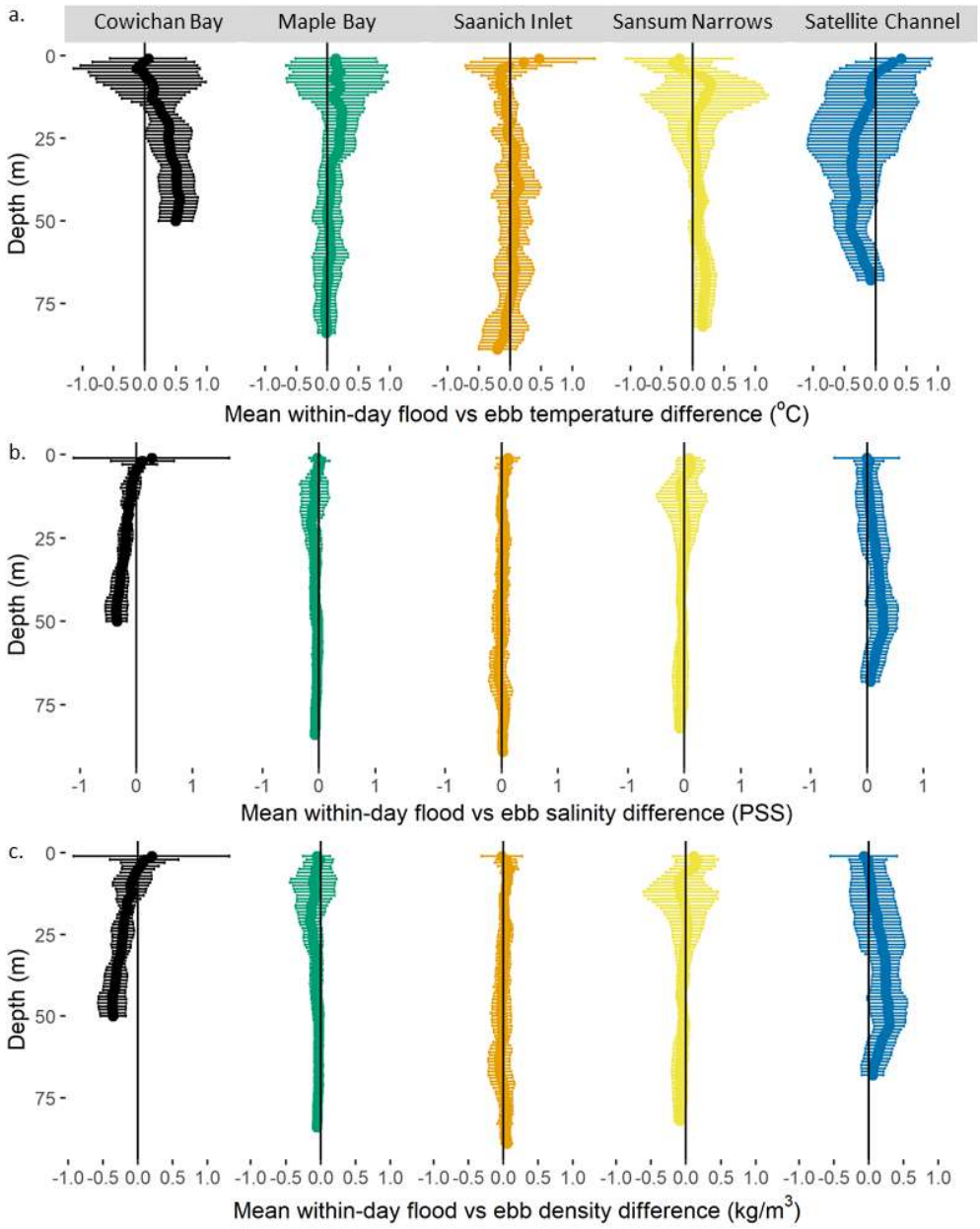

Figure 4.3. Mean within-day difference between flood tide and ebb tide temperature (a), salinity (b), and density (c) for each 1 m of depth between 9 July and 23 October 2015 at five sites in the Southern Gulf Islands of the Salish Sea (see Table 4.1, Figure 4.1 for details). Horizontal error bars indicate standard deviation of the mean.

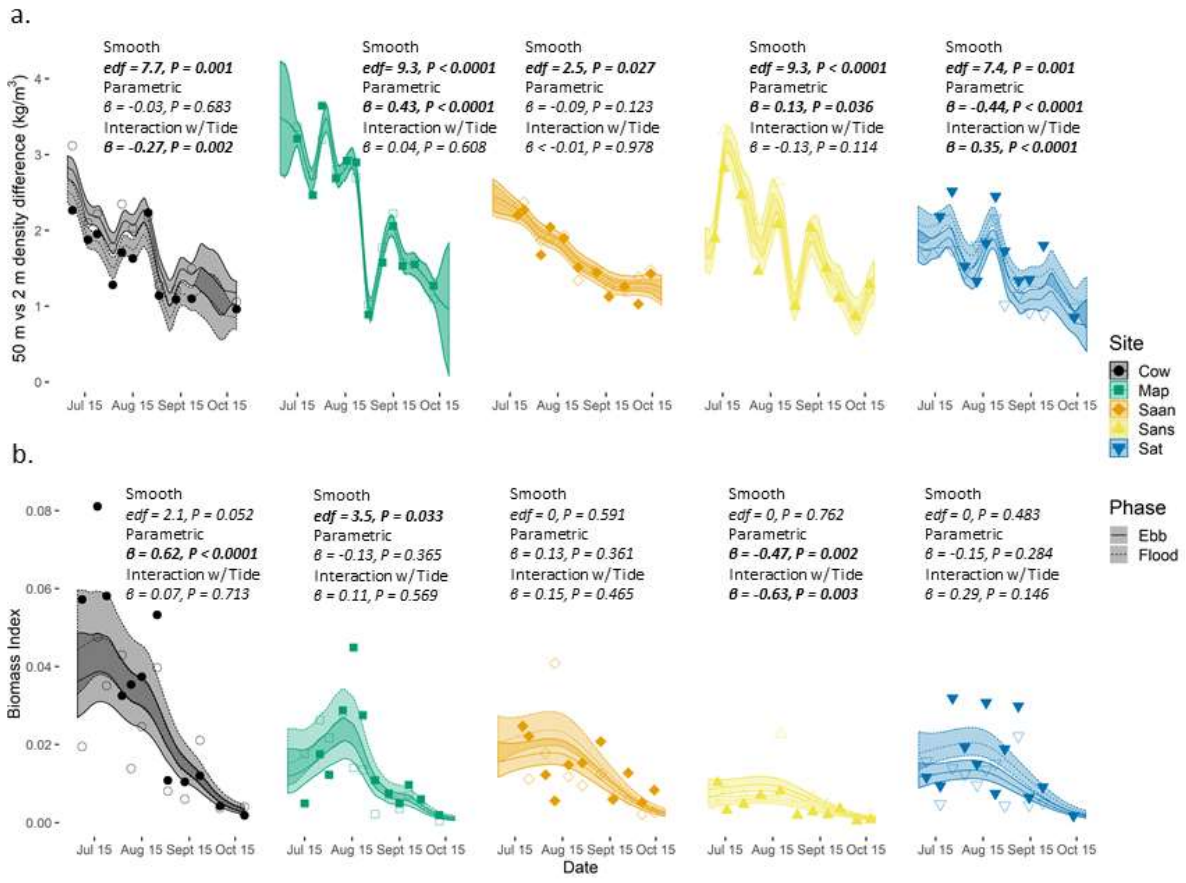

Figure 4.4. Observed values (points) and generalized additive model (GAM) fits for a. an index of stratification (density difference between the 50th and 2nd meter of the water column), and b. an index of aggregate biomass concentration (units ~ g/m^3) for important Chinook Salmon prey groups (contributing to >2% of total diet by mass) sampled with vertical 30 m tows with a 0.5 m diameter 350 µm ring net between 9 July and 23 October 2015 at five sites in the Southern Gulf Islands of the Salish Sea. Filled symbols indicate flood tide samples and open symbols indicate ebb tide samples. Lines indicate fitted values from GAMs relating smoothed terms for day of year and day of year by site and parametric terms for site and phase of the tide (and their interaction) to the density stratification (a) and biomass index (b); shaded ribbons indicate standard error of these predictions. For each site regression statistics are the estimated degrees of freedom (edf) of the smooth term and corresponding approximate P-value, the estimated coefficient (β) for the parametric term for site and corresponding P-value, and the coefficient (β) for the interaction of site and tidal phase and corresponding P-value. A significant global effect of tide was not detected in either GAM. Site names are defined in Table 4.1 and mapped in Figure 4.1.

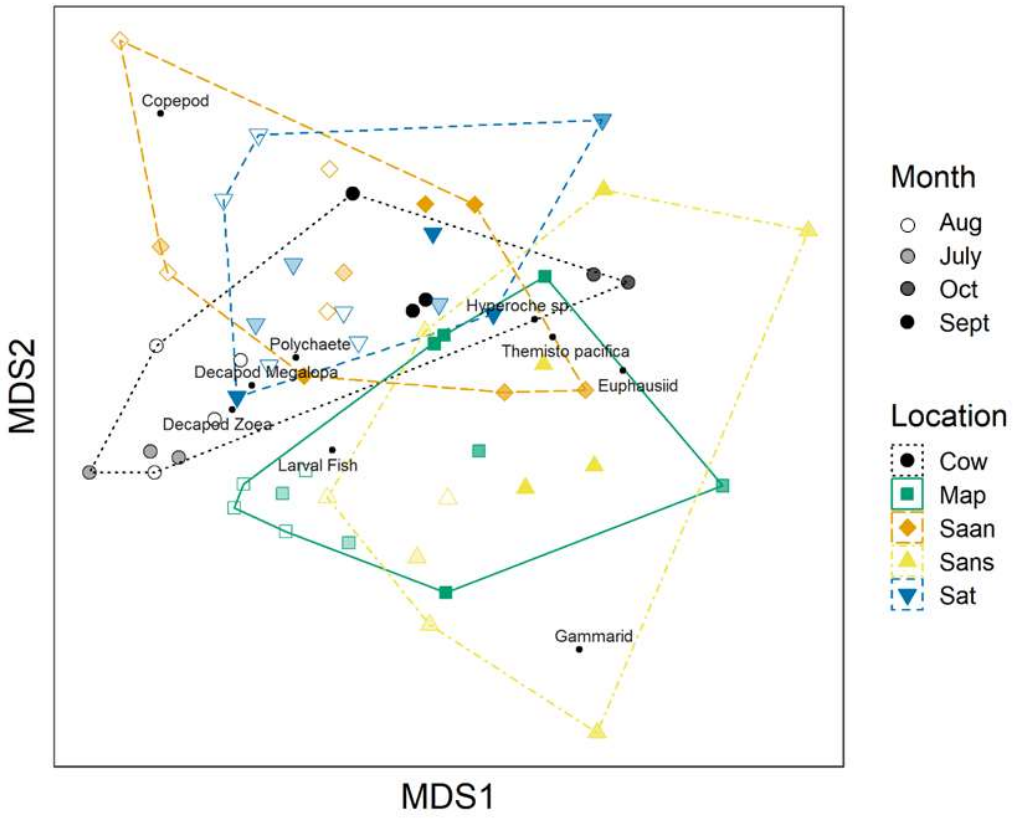

Figure 4.5. Non-metric multidimensional scaling (nMDS) plot (Stress = 0.11) of Bray-Curtis dissimilarity of mean daily zooplankton density indices (~g/m^3, see results for full definition) from vertical 30 m tows with a 0.5 m diameter 350 µm ring net at 5 sites in the Southern Gulf Islands from 6 July to 23 October 2015 (two tows per day). Site names are defined in Table 4.1 and mapped in Figure 4.1.

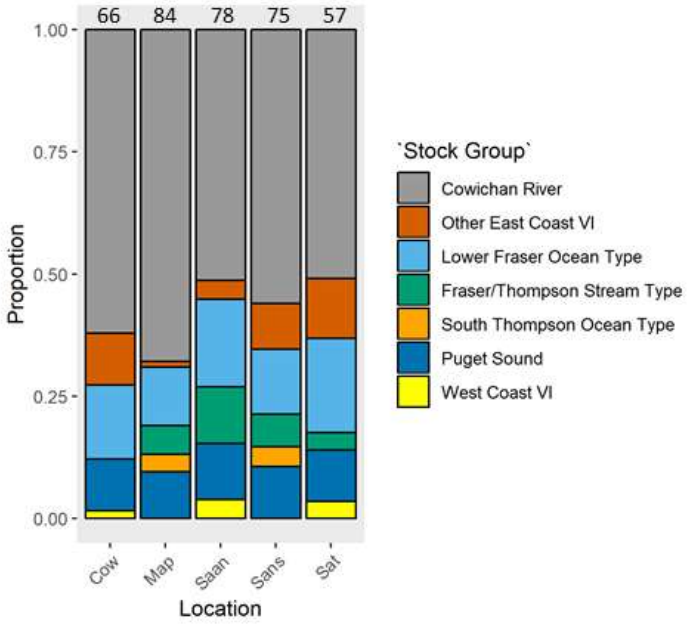

Figure 4.6. Stock group proportions for first ocean year (<300 mm FL) Chinook Salmon captured between 9 July and 23 October 2015 at five sites in the Southern Gulf Islands of the Salish Sea. Sample size is indicated by the numbers above each bar; for individual stocks making up each group see Table 7.1. VI = Vancouver Island. Site names are defined in Table 4.1 and mapped in Figure 4.1.

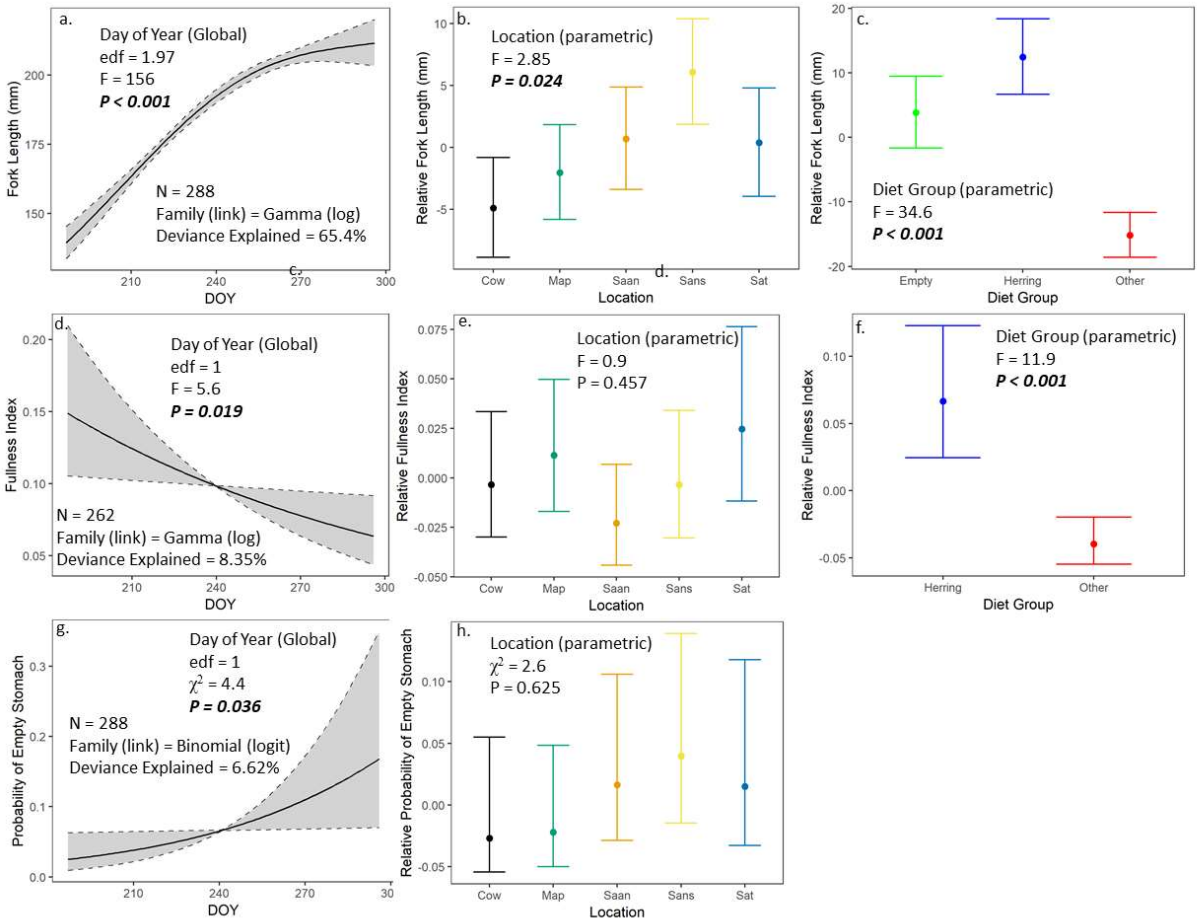

Figure 4.7. Effects plots for generalized additive models relating day of the year (DOY), sampling location, and diet grouping to juvenile Chinook Salmon FL (a-c), stomach fullness index (d-f), and occurrence of empty stomachs (g-h). Regression statistics and the error distribution and link function for each model are reported in the panels; significant terms ($P < 0.05$ are indicated in bold italics. Where effective degrees of freedom (edf) = 1 the relationship between the predictor and response is effectively linear. Site names are defined in Table 4.1 and mapped in Figure 4.1.

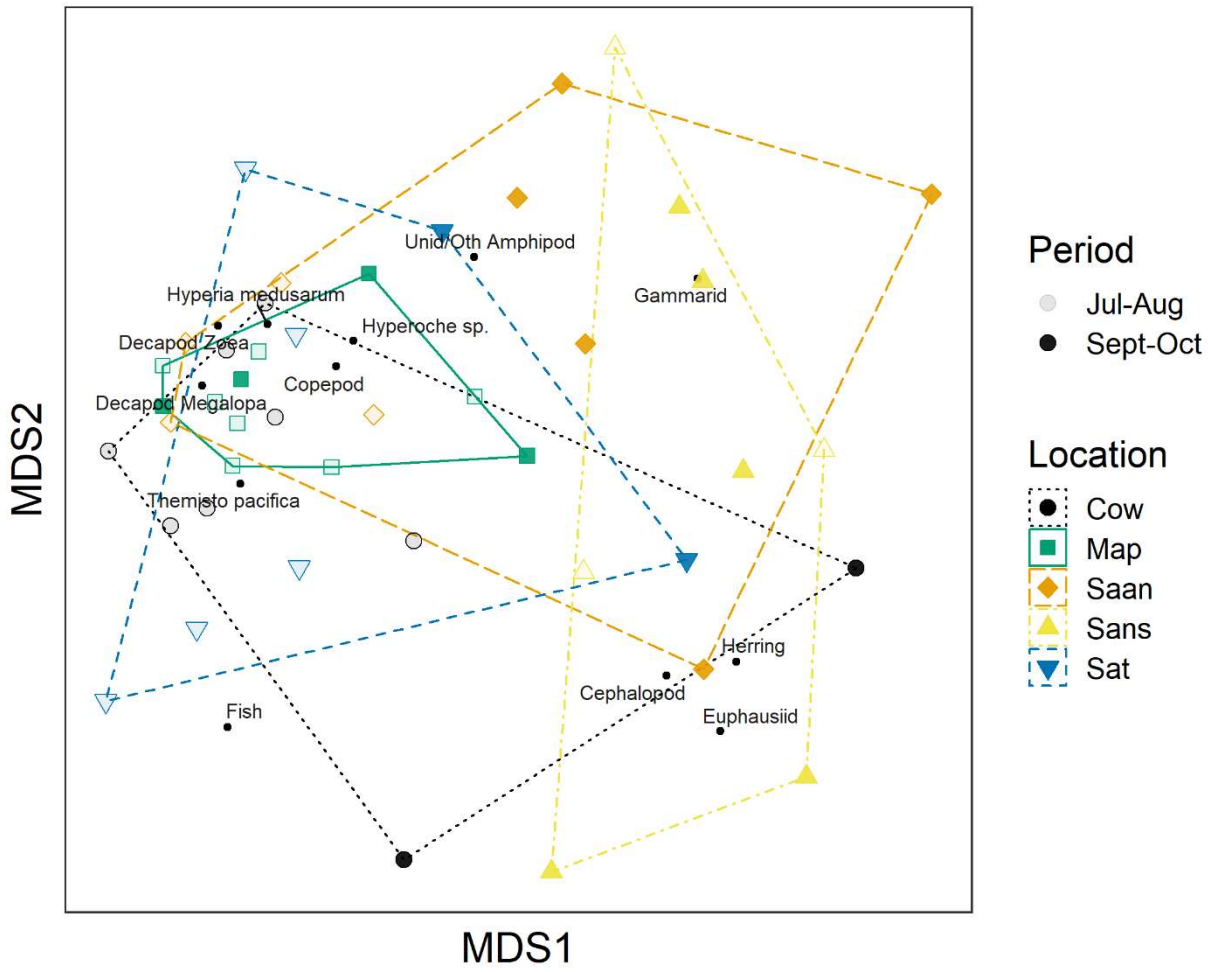

Figure 4.8. Non-metric multidimensional scaling (nMDS) plot (Stress = 0.19) of Bray-Curtis dissimilarity of mean partial fullness values (see methods for full definition) for different prey categories of juvenile ocean-type Chinook Salmon sampled at 5 sites in the Southern Gulf Islands from 6 July to 23 October 2015. Each point represents the mean partial fullness scores for random samples of 5-7 juvenile Chinook Salmon sampled during a specific time stratum at a specific site; time strata were (July-Aug and Sept-Oct). Site names are defined in Table 4.1 and mapped in Figure 4.1.

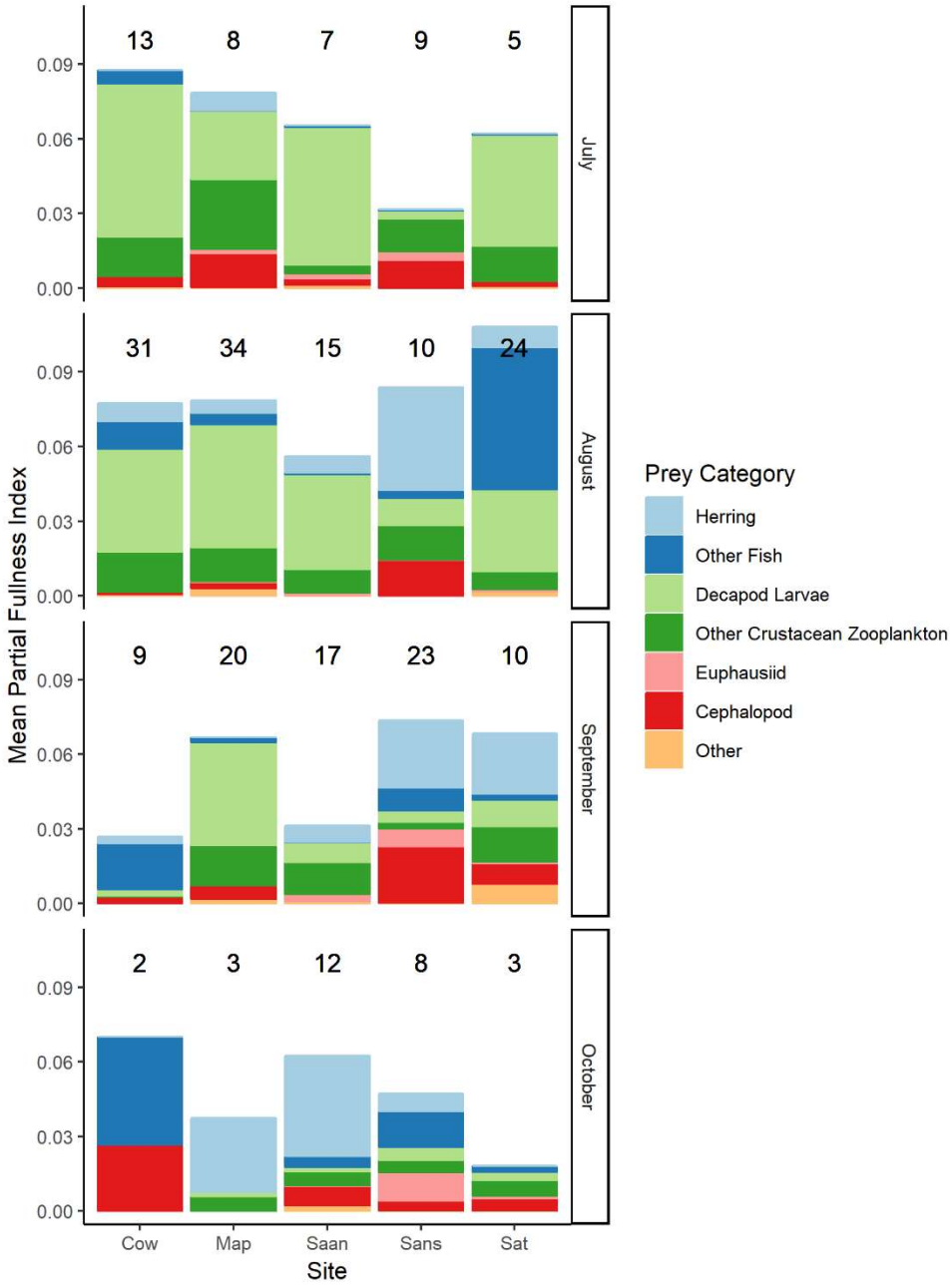

Figure 4.9. Monthly mean partial fullness indices (see text for full definition) for broad taxonomic groupings of the prey of juvenile Chinook Salmon with non-empty stomachs sampled at 5 sites in the Southern Gulf Islands from 6 July to 23 October 2015. Sample sizes are indicated above each bar. The high partial fullness index for "Other Fish" at Satellite Channel in August was driven by an outlier, a 168 mm Chinook Salmon which contained two Shiner Surfperch (*Cymatogaster aggregata*) giving a partial fullness index of 0.80. Site names are defined in Table 4.1 and mapped in Figure 4.1.

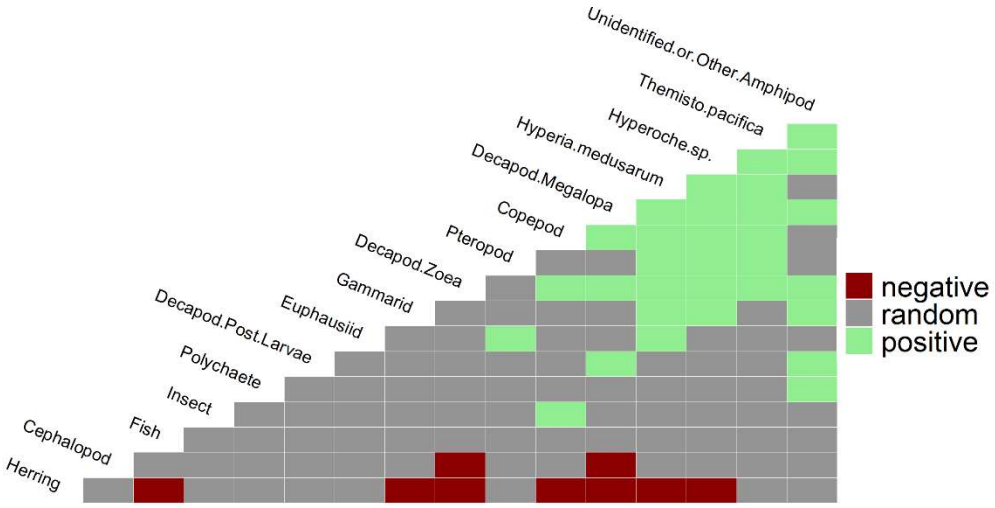

Figure 4.10. Probabilistic analysis of whether pairs of juvenile Chinook Salmon prey categories occurred together in the same fish significantly more (green/lightest) or less (red/darkest) often than expected if prey occurred in Chinook Salmon diets randomly and independently of each other ($\alpha = 0.05$).

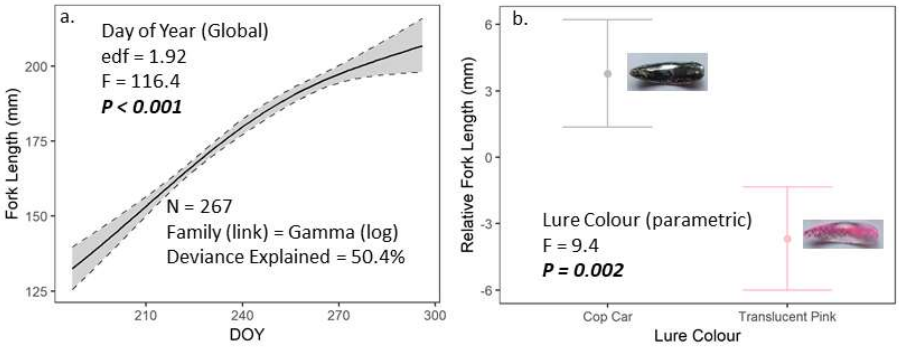

Figure 4.11. Effects plots for a generalized additive model relating FL today of the year (DOY) and lure colour. Regression statistics and the error distribution and link function for the model are reported in the panels; significant terms ($P < 0.05$) are indicated in bold italics.

Figure 4.12. Juvenile Chinook Salmon (FL = 199 mm) and its age-0 Pacific Herring prey (standard length = 80 mm) recovered using gastric lavage. Fish was captured 25 August 2016 in the same region as described in the present study.

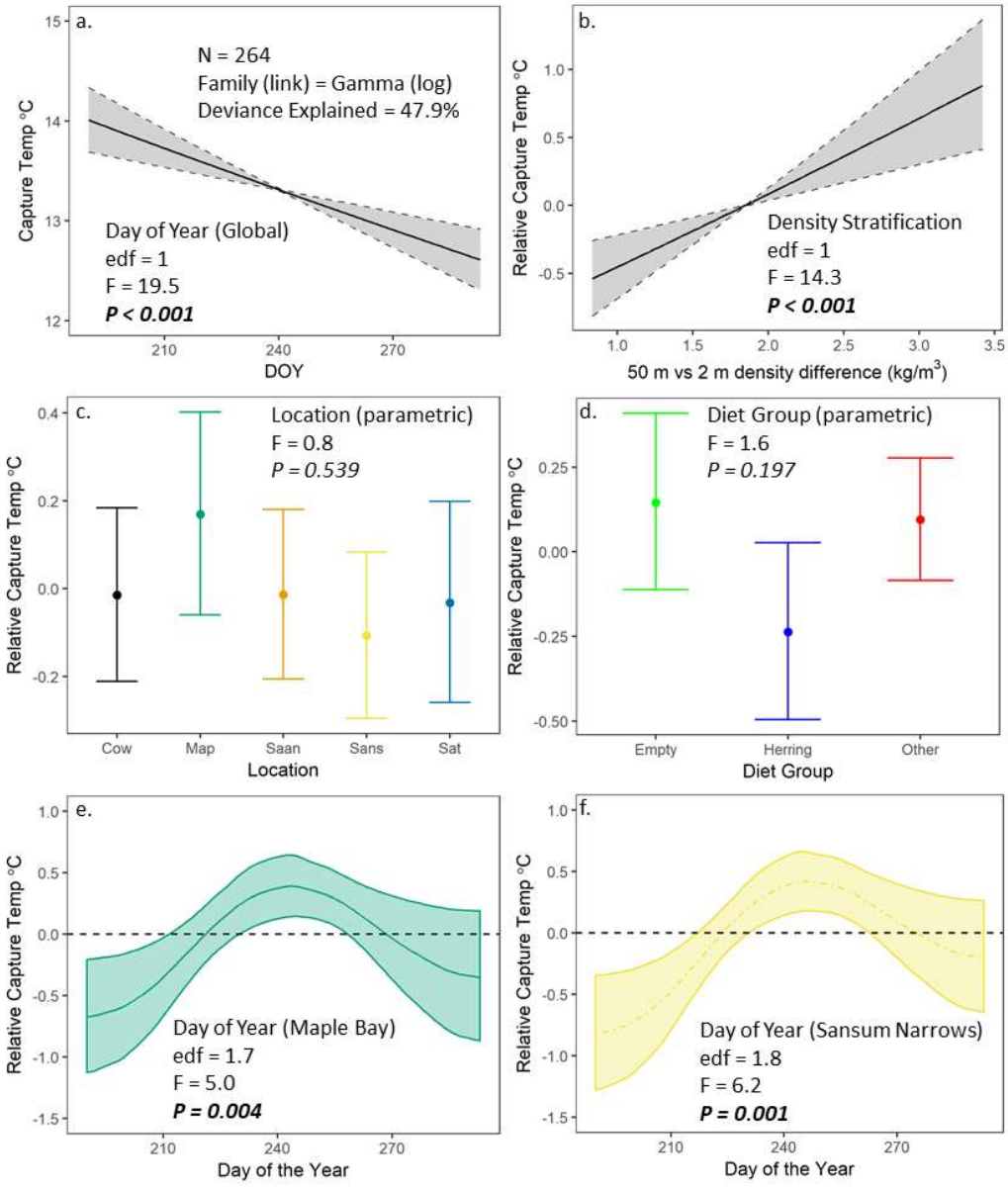

Figure 4.13. Effects plots for a generalized additive model relating (a) day of the year (DOY), (b) density stratification, (c) sampling site, and (d) diet grouping to juvenile Chinook Salmon capture temperature measured by thermistors deployed on leaders during fishing. The relationship between capture temperature and DOY differed significantly from the global linear trend (a) only at Maple Bay (e) and Sansum Narrows (f); non-significant site-specific smoothers are not shown. Regression statistics and the error distribution and link function are reported in the panels; significant terms ($P < 0.05$) are indicated in bold italics. Site names are defined in Table 4.1 and mapped in Figure 4.1.

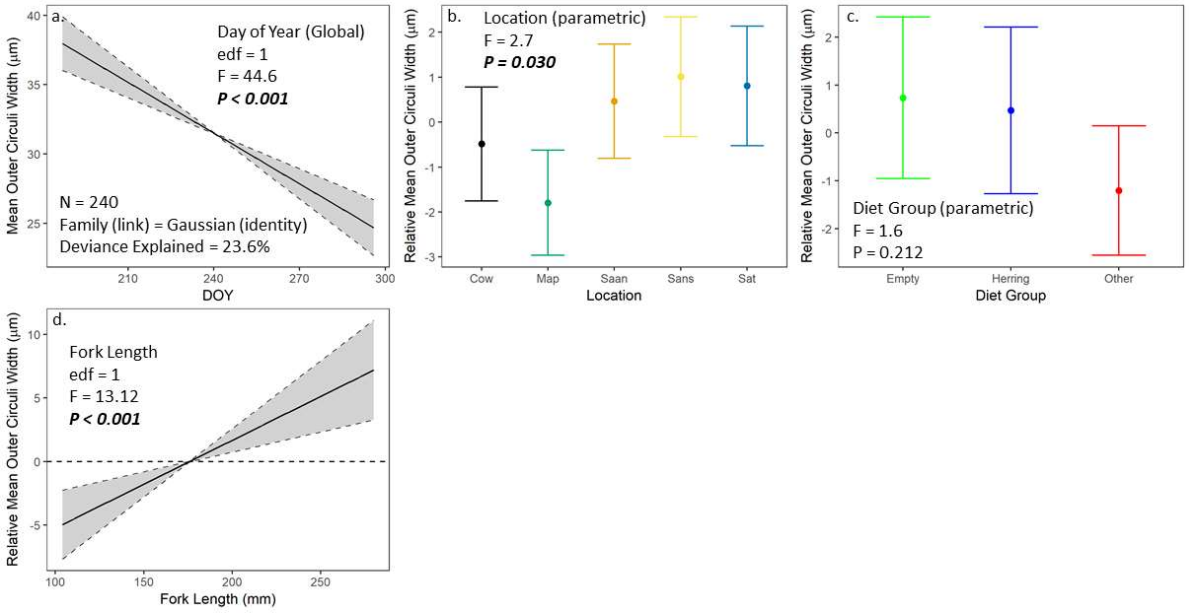

Figure 4.14. Effects plots for a generalized additive model relating day of the year (DOY) (a), sampling site (b), diet grouping (c), and FL (d) to mean spacing of the second and third to outermost scale circuli, an index of recent growth in juvenile Chinook Salmon. Regression statistics and the error distribution and link function are reported in the panels; significant terms ($P < 0.05$) are indicated in bold italics Site names are defined in Table 4.1 and mapped in Figure 4.1.

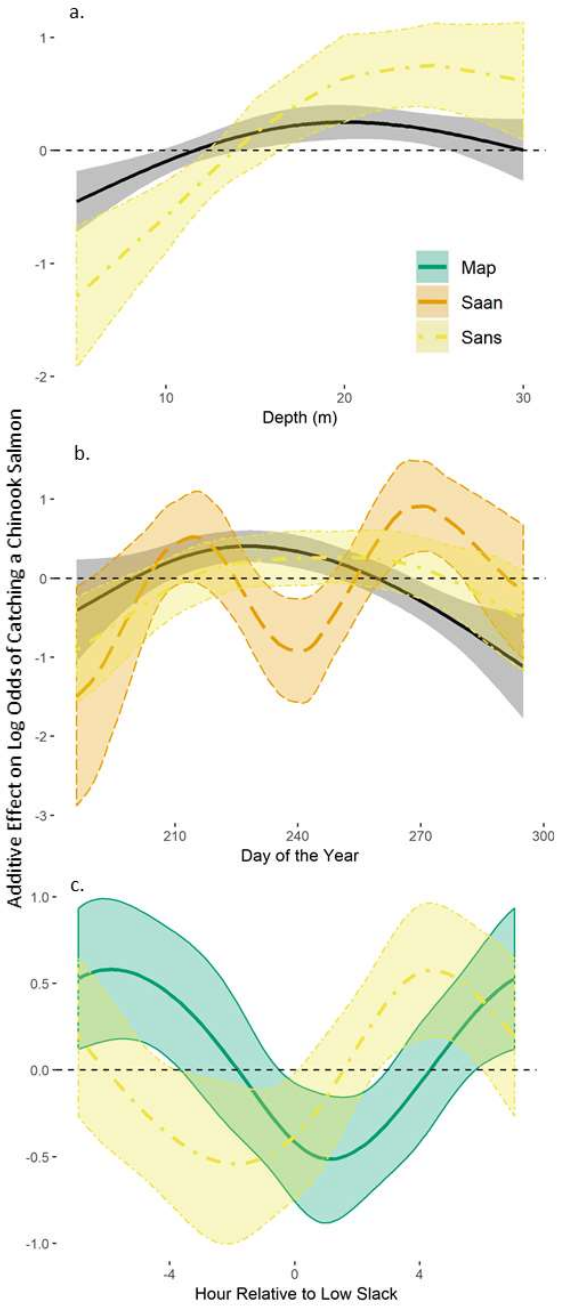

Figure 4.15. Plots for all significant ($p < 0.05$) smooth terms in a generalized additive mixed effects model (GAMM) relating the log-odds of catching a first ocean year Chinook Salmon to site, hour of the day, day of the year, depth, and stage of the tide (see Table 4.6 for all regression statistics). Significant smooth terms were a. global and site-specific (Sansum Narrows) effects of depth, b. global and site-specific (Sansum Narrows and Saanich Inlet) effects of day of the year, and c. site-specific (Sansum Narrows and Maple Bay) effects of stage of the tide. Global smooths are plotted as a solid black line. In the presence of a global smooth, site-specific smooths include the global smooth. Shaded regions indicate 2 x the standard error of the estimated effect, in the case of site-specific smooths, only the error of the site-specific smooth is illustrated. Site names are defined in Table 4.1 and mapped in Figure 4.1.

Chapter 5 - A case study of fine-scale external and intrinsic factors influencing growth potential of juvenile Chinook Salmon at Sea

5.1 Abstract

Pacific Salmon (genus *Oncorhynchus*) undergo complex life histories across heterogeneous freshwater and marine ecosystems. Declines in marine survival for populations of multiple species have focused attention on growth during the first year of marine residence, a period hypothesized to disproportionately regulate survival and subsequent recruitment. Most studies to date have investigated relatively large scale spatial and temporal patterns in early marine growth rates and potential regulating factors. The roles of fine scale habitat variability and the interaction of individual fish behavior and biology with this variability have been largely overlooked. We built on results of an initial, single year study (Chapter 4) which suggested that juvenile ocean-type Chinook Salmon (*Oncorhynchus tshawytscha*) at two closely adjacent sites in the Southern Gulf Islands of the Salish Sea (Sansum Narrows and Maple Bay, approximately 4 km apart) differed in diet, size and growth. We employed a multi-faceted approach to understand if and why the characteristics of juvenile Chinook Salmon differed consistently between these sites. Across two years (2015 and 2016) juvenile ocean-type Chinook Salmon were consistently larger, faster growing, and more piscivorous at Sansum Narrows than Maple Bay. Acoustic tagging of 80 juvenile Chinook Salmon in September 2017 revealed that fish captured at these two sites also exhibited differing distributions. Hydroacoustic surveys and depth-stratified zooplankton sampling in September 2017 confirmed that fish schools (likely juvenile Pacific Herring) were much more abundant at Sansum Narrows while important zooplankton prey (decapod larvae) were more abundant at Maple Bay. Our results were consistent with colocation of piscivorous juvenile Chinook Salmon and juvenile Pacific Herring. Fish schools (detected by hydroacoustics), catch per unit effort of Chinook Salmon, and odds of detecting acoustic tags all increased on the flood tide immediately north of Sansum Narrows. The cause of the greater availability of forage fish prey at Sansum Narrows remains uncertain as we found no evidence for upwelling of zooplankton which has been invoked as a mechanism of forage fish concentration at other tidal narrows. Were piscivorous juvenile Chinook Salmon larger and growing faster because of behaviour which brought them into contact with fish prey or

were they pursuing fish prey because they were larger and faster growing? Consistently faster growth (as indexed by scale circulus spacing) of Cowichan River Chinook Salmon captured at Sansum Narrows during a size range generally spent in freshwater (45-75 mm nose fork length) and during a marine growth period prior to piscivory (114 mm to 173 mm) suggests that growth early in life may be linked both to subsequent growth potential and spatial patterns of marine habitat use. While preliminary surveys did not detect significant spatial structure in harbour seal (*Phoca vitulina*) distribution within our study area, it remains plausible that the interaction of prior growth history, individual behaviour, and heterogeneous prey distribution results in asymmetrical and possibly counterintuitive distribution of predation risk across juvenile Chinook Salmon on different growth trajectories. The potential for such interactions should be considered carefully when interpreting the rapidly growing body of literature on the early marine ecology of juvenile Pacific Salmon.

5.2 Introduction

Dramatic declines in the abundance of many populations of Pacific Salmon (genus *Oncorhynchus*) have been a major concern of fisheries managers and scientists for several decades. Evidence that these declines are largely driven by non-fishery related changes in survival during ocean residence (Beamish and Bouillon 1993, Welch et al. in review) has driven the search for general underlying mechanisms. The "critical period hypothesis" of Hjort (1914) linked recruitment variability of marine fish to the extreme vulnerability of first-feeding larvae to starvation in sub-optimal environmental conditions. While this hypothesis is not applicable to Pacific Salmon, for which first-feeding occurs in freshwater, an alternative suite of "critical period" hypotheses have been invoked to explain recruitment variability of *Oncorhynchus sp*. These hypotheses link size, and hence growth, of juvenile salmon to survival through size-selective predation (Parker 1971, Holtby et al. 1990, Moss et al. 2005) or size-mediated starvation (Beamish and Mahnken 2001, Beamish et al. 2008). These hypotheses have stimulated intensive research into factors affecting growth of juvenile Pacific Salmon during the first year at sea. Given the aforementioned hope of uncovering generalized mechanisms to explain declines in marine survival, many studies have investigated variation in juvenile growth and potential causal factors at large spatial or temporal scales. These studies have included comparisons of feeding ecology, growth, and environmental conditions across years (Duffy and Beauchamp 2011, Tomaro et al. 2012, Graham et al. 2019), broad marine regions (Ferriss et al. 2014, Hertz et al. 2015), and general habitat types (e.g. nearshore vs offshore; Duffy et al. 2010).

Most attempts to infer how and why size and growth of juvenile Pacific Salmon vary at broad spatial and temporal scales, and to link this variation to survival, rely on the assumption that either ecologically meaningful variation does not exist at finer spatial and temporal scales or that studies sample representatively across any fine scale variability. The danger of such assumptions was illustrated by Beacham et al. (2018), who demonstrated that falsely assuming that a sample of juvenile salmon is representative of the entire population can lead to spurious identification of size-selective mortality. Henderson et al. (2019) provided an example of fine scale spatial structure trumping global patterns. These authors employed multivariate spatial analysis of biophysical modelling outputs to demonstrate that complex interactions of spatial

patterns of growth potential off the California Coast, rather than regional growth potential as a whole, predict survival of Central Valley Chinook Salmon (*O. tshawytscha*) . A variety of external and intrinsic processes have the potential to generate fine scale variation in size and growth of juvenile salmon which could overlay and potentially interact with variation at broad spatial and temporal scales.

Marine systems are strongly structured at multiple spatial scales (Stommel 1963) leading to heterogeneity in their capacity to support the growth of fish, including Pacific Salmon. Much of the structure in ocean systems is transient, which may make it challenging to investigate linkages to growth potential. For example, convergent fronts, which can concentrate buoyant or surface oriented planktonic prey (Genin 2004), form, move, and dissipate as a consequence of density, tide, and wind driven currents. This transience was invoked by de Robertis et al. (2005) to explain failure to detect an effect of Columbia River plume fronts on diets of juvenile salmon. Nevertheless, recent work by Sabal et al. (2020) found that stomach fullness of juvenile Chinook Salmon was elevated adjacent to thermal fronts in the California Current. Nearshore, and within coastal basins, the interactions of river inputs, winds, tidal currents, and topography may generate more persistent structure in the capacity of the ocean to support salmon growth. Within the Salish Sea, a juvenile salmon growth index (IGF-1 concentration) varies between sub-basins of the Strait of Georgia (Journey et al. 2020). Persistent differences in diet and growth between sub-basins have also been described for Puget Sound, and it has been hypothesized that access to fish prey may at least in part underpin this variability (Davis et al. 2020, Chamberlin et al. 2017). In coastal waters, persistent variation in pelagic ecosystem structure can also occur at scales of meters to kilometers. In the San Juan Islands of the Salish Sea, Zamon (2000, 2002, 2003) provided a case study of how a tidal jet (San Juan Passage) increased the concentration of zooplankton prey in surface waters, leading to redistribution of forage fish and resulting aggregation of their predators (trophic focusing). Embayments, headlands, and islands can also produce elevated concentrations of zooplankton through the formation of retentive eddies and convergent fronts (Alldredge and Hamner 1980, Wolanski and Hamner 1988, Archambault et al. 1998).

To our knowledge, no work has explicitly investigated the role played by such local-scale oceanographic phenomena in growth potential of juvenile Pacific Salmon in the ocean. This lack of research attention may be due to a general perception of Pacific Salmon as highly migratory species which move quickly through coastal ecosystems. Indeed, acoustic tagging studies suggest that Sockeye Salmon (*O. nerka*) and Steelhead (*O. mykiss*) exhibit directed movements of more than 10 km/day in coastal waters (Welch et al. 2011, Furey et al. 2015). Such rapid movement does not necessarily apply to all Pacific Salmon. Chinook Salmon and Coho Salmon (*O. kisutch*) move more slowly through coastal waters (Welch et al. 2011), may spend at least their first marine summer rearing near their point of ocean entry (Beamish et al. 2000, Beamish et al. 2012a), and in some cases may remain resident within 10s of kilometers of their ocean entry point for their entire lives (Chamberlin and Quinn 2014, Rohde et al. 2014). Acoustic tagging of subadult Chinook Salmon has suggested that resident individuals may also exhibit localized patterns of movement within inshore waters (Arostegui et al. 2017). It remains uncertain whether movement patterns of Pacific Salmon lead individuals to either remain near or repeatedly return to persistent oceanographic features that concentrate food.

In addition to coarse and fine scale environmental effects, intrinsic features of individual juvenile Pacific Salmon also influence size and growth. Growth rate exhibits strong heritable variation in fish (Gjedrem 1983), including salmonids (Vøllestad and Quinn 2003, Debes et al. 2020). Trade-offs exist between growth and survival (Tymchuck et al. 2007), likely maintaining variation in growth rate genotypes. Pacific Salmon also exhibit a diversity of developmental and migratory phenology both between and within species and populations (Quinn 2005). This life history variation can have profound effects on size and growth. Freshwater et al. (2016) demonstrated that within-population latitudinal gradients in size of juvenile Sockeye Salmon off the British Columbia Coast were related to size and timing of ocean entry of individual fish rather than the influence of ocean conditions on growth. Chinook Salmon exhibit variability in early life history with two primary ecotypes: stream-type which rear for a full year in freshwater and ocean-type which enter the ocean within the first year after hatching (Healey 1991). Variation also exists within ecotypes. Ocean-type Chinook Salmon may migrate to the ocean as fry within days to weeks of emergence from the gravel or as parr after one or more months of freshwater rearing (Healey 1991). Recent work has suggested that these strategies represent a

bimodal rather than continuous phenotype, and that both occur ubiquitously where ocean-type Chinook Salmon are present (Apgar et al. 2020). As different Pacific Salmon ecotypes enter the ocean at different times and sizes, and have access to different prey, it follows that they experience different growth potential during early marine residence. Whether a function of environment, intrinsic factors, or their interaction, prior growth of juvenile Pacific Salmon has the potential to influence subsequent growth through positive feedback. Piscivory provides a growth advantage to predatory fish (Juanes and Conover 1994, Juanes et al. 2002) including juvenile Chinook Salmon (Litz et al. 2017, Davis et al. 2020). However, access to fish prey may be limited to individuals that are large enough to consume available forage fish species and age-classes (Chamberlin et al. 2017). Juvenile Chinook Salmon that have experienced rapid early growth may therefore have a greater ability to sustain greater growth rates through access to larger prey.

In 2015 we conducted an investigation of spatial variation in the diet, size and growth of juvenile ocean-type Chinook Salmon in the Southern Gulf Islands (Figure 5.1) of the Salish Sea. An intriguing result of this study was that juvenile Chinook Salmon at two closely adjacent but oceanographically dissimilar sites with similar zooplankton composition (Sansum Narrows and Maple Bay ~ 4 km apart; Figure 5.2) exhibited pronounced differences in diet, size, and growth (Chapter 4). Fish at Sansum Narrows were more piscivorous, larger, and faster growing than those at Maple Bay despite evidence of lower biomass densities of zooplankton prey at the former site. The present investigation is a detailed case study of factors potentially influencing growth of juvenile Chinook Salmon at these two sites. Our overall objective was to determine if environmental variation in conjunction with intrinsic characteristics and behavior could generate fine scale variation in growth potential of juvenile Chinook Salmon. Our first specific objective was to determine if the differences in juvenile Chinook Salmon characteristics between sites that we observed in 2015 were consistent between years. We addressed this by completing a second year of juvenile Chinook Salmon sampling in 2016, and investigated differences in diet, size, and growth of juvenile Chinook Salmon between the sites across the two years. We also sought to determine whether piscivory of juvenile Chinook Salmon at Sansum Narrows was related to a greater availability of forage fish prey at this site, and if so, what mechanism might lead to forage fish aggregation. In September of 2017 we conducted 6 days of acoustic zooplankton fish

profiler (AZFP) surveys (three days at each site) throughout daylight hours to compare abundance of forage fish schools between sites. We coupled these surveys with vertically stratified zooplankton sampling to test whether the tidal jet at Sansum Narrows led to advection of zooplankton from depth as has been described for San Juan Passage (Zamon 2002). We also employed two approaches to assess the role of individual Chinook Salmon characteristics in the diet, size and growth differences observed between sites. We compared a scale circulus spacing-based growth rate index over reconstructed size intervals both before and after ocean entry for juvenile Cowichan River Chinook Salmon captured at Sansum Narrows and Maple Bay in 2015-2016. We also compared spatial and tidal differences in the distribution of 80 juvenile Chinook Salmon captured, tagged, and released at the two sites (41 at Maple Bay and 39 at Sansum Narrows) in September 2017. The present investigation encompasses a breadth of approaches applied to a limited spatial scope. An understanding of the potential of fine scale external and individual scale internal processes to influence growth of juvenile Pacific Salmon is necessary to inform both design and interpretation of larger scale studies investigating links between environment, growth and survival.

5.3 Materials and Methods

5.3.1 *Study Area*

A general description of the Southern Gulf Islands, within which our study sites were located, is provided in Chapter 4 section 4.3.1. Our two study sites, Sansum Narrows and Maple Bay, are located within a north-south oriented, 12 km long channel between Saltspring Island and Vancouver Island that links the strongly tidally mixed waters of Satellite Channel to the more stratified waters of Stuart Channel. Maple Bay covers a surface area of approximately 2.9 km^2 (excluding a shallow southerly extension) on the west side of this channel with a 1.3 km wide mouth opening to the east. The rocky shoreline slopes steeply to a soft bottom that is predominantly 60-90 m deep. Our Sansum Narrows site was immediately north of the narrowest point in the channel (500 m). At its narrowest point this channel is approximately 80 m deep, dropping off to more than 150 m to the north and transitioning to a complex rocky topography with maximum depths of less than 60 m to the south. Maximum flood tide currents through Sansum Narrows are approximately 2 m/s and on strong floods a turbulent tidal jet is visible

extending from the narrowest point in the channel, along the Vancouver Island shore, and northeast into open water (Figure 5.3). The current on the ebb is southerly and is largely laminar north of Sansum Narrows, becoming turbulent to the south. In 2015, the water column at both sites was more stratified than Cowichan Bay and Satellite Channel to the south (Chapter 4). However, depending on the stage of the tide, the Sansum Narrows study site frequently encompasses the interface between tidally mixed water to the south and warmer more stratified water to the north (Figure 5.3).

To generate a spatial visualization of thermal stratification throughout the study area (Figure 5.4) we took advantage of surveys to track acoustic tagged fish to conduct repeated CTD casts to at least 20 m at stations throughout the study area (section 5.3.6).

5.3.2 *Zooplankton Sampling*

5.3.2.1 Sample Collection and Processing

Zooplankton sampling was conducted on 30-31 August and 4-7 September 2017, with the survey site alternating daily between Maple Bay and Sansum Narrows. Zooplankton sampling equipment and methodology followed that described in Chapter 4 section 4.3.2. On each day 8-9 pairs of tows were conducted at a standard sampling station (Figure 5.2) with the first tow from 30 m and the second tow from 60 m. Tows were spread throughout the day to cover as much of the tidal cycle as possible. All tows occurred between 0800 hours and 1900 hours to avoid crepuscular periods where vertical distribution of zooplankton might be influenced by diel vertical migration. Sampling stations were approximately 65 m deep, allowing the majority of the water column to be sampled by the deeper tow. A castaway CTD suspended 3 m below the opening of the net confirmed tow depth and a calibrated TSK flowmeter in the mouth of the net was used to estimate sampled volume. Zooplankton were washed down to the cod end with surface seawater sprayed from the outside of the net and preserved in 10% formalin in seawater.

Lab processing of zooplankton samples followed methodology described in section 4.3.3. with the exception that zooplankton were only counted, not weighed, and no samples required splitting. Levels of taxonomic detail for identification (zooplankton group) and grouping into

categories for analysis are outlined in Table 5.1. Counts for each zooplankton group in each tow were converted to weights based on the mean individual weight for that zooplankton group for all samples analyzed in 2015 and described in Chapter 4. These were in turn converted to biomass densities by dividing by the water volume sampled by the tow. Subsequent analysis was conducted on these biomass densities.

5.3.2.2 Zooplankton Data Analysis

As our objective was to investigate site, depth and tidal differences in availability of zooplankton prey to juvenile Chinook Salmon we focused our analysis primarily on decapod zoeae and megalopae; zooplankton groups that were important in Chinook Salmon diets (see Chapter 4) and abundant in our zooplankton samples. To assess evidence for homogenization of the water column due to tidal mixing we also analyzed spatial and temporal variation in the density of calanoid copepods.

Generalized additive models (GAMs) were employed to test how biomass densities of decapod zoeae, decapod megalopae, and calanoid copepods varied between sites and with depth and stage of the tide. We calculated a continuous variable for stage of the tide relative to low slack as described in section 4.3.5.This tide stage variable was negative during the ebb tide and positive during the flood tide. Generalized additive models included parametric terms for site, tow depth, and day of the year (modelled as a continuous variable), and separate smooth terms for tide for each site and tow depth combination. As minimum values of the variable ‘tide’ approximated high slack, and were therefore theoretically continuous with maximum values, we modelled the relationships between biomass densities and tide using cyclic cubic splines (bs = “cc” in gam model formula) which have matching end points. Due to the positively skewed nature of the biomass density data, models were fit with a gamma distribution and log link. These GAM models (and subsequent GAM and GAMM models employed in this chapter) were fit using maximum likelihood (Wood 2011) and significance of smooth terms was assessed at an alpha level of 0.05 for approximate P-values based on a Wald-type test of the null hypothesis that the smoothing function was equivalent to zero (see Wood 2013 for details).

As not all tows contained decapod megalopae or copepods we employed a hurdle modeling approach where the presence of these taxa in the tow was first modelled with a binomial GAM and biomass density was subsequently modelled using a gamma GAM fit to the subset of tows where the relevant taxa were present. To visualize model predictions we simulated data from the distributions of the fitted models using the 'simulate.gam' function in the package 'mgcViz' in R. Dummy data used for simulations were single tows at each depth (30 m and 60 m) once per hour from 6 hours before low slack to 6 hours after low slack on 3 September. One hundred simulations were run and mean simulated biomass densities and associated confidence intervals were plotted for each site through the tidal cycle. To simulate biomass densities for decapod megalopae and copepods the binomial model was first used to predict the presence of the taxa. Where no aggregations were predicted by the binomial model biomass density was set to 0 and where presence was predicted by the binomial model the gamma model was then used to predict biomass density.

5.3.3 *Acoustic Zooplankton Fish Profiler Surveys*

5.3.3.1 AZFP Surveys

Acoustic surveys were conducted on the same days and at the same sites as zooplankton sampling (see section 5.3.1). Transducers for the four frequency (38 kHz, 67 kHz, 125 kHz and 200 kHz) AZFP were deployed on a boom over the side of the 6.7 m research vessel (Vagle et al. 2017). Between zooplankton tows the vessel ran a series of linear transects (Figure 5.2) at a speed of approximately 2 m/s. Alternating routes (sequences of transects) were followed on every second interval between plankton tows (Supporting Table 7.5) and the transects surveyed were changed slightly between the August and September survey dates. The AZFP produced a 1 ms pulse at each of the four frequencies every 4 seconds. On the August sampling dates the range was set to 250 m, this was reduced to 175 m on the September dates with the vertical sampling resolution set to 0.0373 m in both cases.

5.3.3.2 Oceanographic Parameters

Parameters required for analysis of multifrequency volume backscattering strength were calculated from pressure, temperature and conductivity data collected on down casts by a Castaway CTD deployed below the zooplankton net (see section 5.3.1). Salinity (PSU) and speed of sound (m/s) were calculated using the 'oce' package in R. To calculate the absorption of sound in seawater for each AZFP frequency we used mean temperature (12.4 °C) and salinity (29.3 PSS) values between 30 m and 60 m and the algorithm of Francois and Garrison (1982) as implemented by the UK National Physical Laboratory calculator available at http://resource.npl.co.uk/acoustics/techguides/seaabsorption/.

5.3.3.3 Data Processing and Analysis

Data were downloaded from the AZFP and converted to volume backscattering strengths (S_V; dB re $1m^{-1}$) using Azfplink Software (ASL Environmental Services). Subsequent data processing and analysis were conducted in the R Statistical Environment primarily using the 'raster' package. Data were first subset to linear transects using the start and end time for each transect. Coordinates logged by GPS at the beginning and end of each transect were used to determine transect length and speed based on the assumption of a straight-line course over ground. Data processing and analysis occurred at the level of the individual transect. Within each transect, bottom was conservatively identified as a point 2 m above the largest clump of samples where the greatest raw backscattering value across all four frequencies ≥ -52.5 dB re $1m^{-1}$. Background noise was removed from the raw data (including below-bottom samples) at each frequency following de Robertis and Higginbottom (2007), with the modification that the noise estimate for each pulse was the minimum of all vertically overlapping windows (21 pulses by 10.04 m) centered on each sample within each pulse (for data collected at the 250 m range only the top 175 m were used). The time varied gain adjusted-range (r_{tvg}) for the noise removal algorithm was calculated as $r_{tvg}=r-ct/4$ where r is the unadjusted range, c is the speed of sound, and t is the pulse length in μs. The maximum noise was set to -125 dB and the minimum signal to noise ratio (SNR) was set to 10 dB. All samples below this SNR or with a maximum SV < -80 dB re $1m^{-1}$ across the 38, 125 and 200 kHz frequencies were excluded from subsequent analysis.

Identification of backscatter was based on a modification of the methods of Sato et al. (2015). For identification of fish aggregations, noise-filtered and thresholded data in the linear domain were first smoothed by averaging a 3 pulse by 1 m deep moving window. Fish aggregations were identified in the smoothed 38 kHz data in the logarithmic domain as clumps of adjacent (queen's case) samples at a backscattering threshold of $\geq$ -60 dB re $1m^{-1}$ with a width of at least three pulses and a minimum vertical thickness of 2 m. The footprint of each aggregation was taken to include all samples within each pulse between the top and bottom samples meeting these criteria. Backscattering for all samples not identified as fish aggregations was then classified in the unsmoothed data based on difference between the mean volume backscattering strength for the sample at 200 kHz and 38 kHz ($\Delta MVBS_{200\text{-}38}$) in the logarithmic domain, which is the equivalent of the ratio between backscattering at 200 kHz and 38 kHz in the linear domain. Sato et al. (2015) used trawl gear to validate $\Delta MVBS_{200\text{-}38}$ values in Hood Canal, Puget Sound within the Salish Sea. These authors found that -16 dB < $\Delta MVBS_{200\text{-}38}$ $\leq$ 2 dB indicated fish while 2 dB < $\Delta MVBS_{200\text{-}38}$ $\leq$ 32 dB indicated zooplankton. We used these values to classify samples as dominated by either other fish (distinct from the previously identified fish aggregations) or zooplankton. To assess plausible identities of backscatterers, we calculated $\Delta MVBS_{125\text{-}38}$ and $\Delta MVBS_{200\text{-}38}$ for domains classified as other fish and plankton within each transect and for each fish aggregation within each transect.

Echograms of background noise-filtered data at each frequency and of classified samples (Figure 5.5) were visually examined for impulse noise (vessel noise or echosounder interference), missing data (primarily caused by wave action briefly exposing the transducers), or cases where schools of fish adjacent to the bottom were falsely identified as bottom. Where more than 10% of pulses within a transect were estimated to be affected by these phenomena, the transect was excluded from further analysis.

For each transect retained for analysis we calculated the nautical area backscattering coefficient (S_A) for domains classified as fish aggregations, other fish, and plankton. This coefficient is proportional to the biomass of backscatterers. For fish aggregations and other fish, S_A was calculated from the unsmoothed 38 kHz data while S_A for plankton was calculated from the unsmoothed 200 kHz data. The S_A for each domain was calculated by multiplying the

exponentiated mean $S_V/10$ for the domain by the mean thickness (m) of the domain across all pulses. For comparison to zooplankton tow data we calculated S_A attributable to plankton in bands from 0-30 m and 30-60 m depth. As data from 0-10 m were masked from analysis, we estimated that S_A attributable to plankton in top 30 m was 1.5 times the estimate for 10-30 m.

To test how backscattering attributable to fish aggregations, other fish, and plankton varied between sites and with stage of the tide we employed a generalized additive modelling approach similar to that used to model zooplankton biomass density (section 5.3.1.2). Generalized additive models included parametric terms for site, mean transect water depth, and day of the year (modelled as a continuous variable); site-specific smooth terms for tide; and a random effect for transect (modelled as a penalized smooth term using the coding bs =”re”). This inclusion of transect as a random effect meant models could be effectively considered generalized additive mixed models (GAMMs; Wood 2008). Due to the positively skewed nature of transect-level S_A data, models were fit with a gamma distribution and log link. As not all transects contained aggregations of fish we employed a hurdle modeling approach where the presence of fish aggregations in the transect was first modelled with a binomial GAMM and S_A was subsequently modelled using a gamma GAMM fit to the subset of transects which contained fish aggregations. As for zooplankton biomass densities, we visualized model predictions by simulating data from the distributions of the fitted models. Dummy data used for simulations was the set of all transects once per hour from 6 hours before low slack to 6 hours after low slack on 3 September. Transect depth was set to be the measured mean depth of each transect. One hundred simulations were run and mean simulated S_A and associated confidence intervals were plotted for each site through the tidal cycle. To simulate S_A due to fish aggregations the binomial model was first used to predict the presence of fish aggregations. Where no aggregations were predicted, S_A was set to 0, while where fish aggregations were predicted the gamma model was used to predict S_A.

5.3.4 *Juvenile Chinook Salmon Diet, Size and Growth*

5.3.4.1 Capture and Sampling

Juvenile Chinook Salmon were captured by microtrolling (see Chapter 2) at Sansum Narrows and Maple Bay between July and October in 2015 and August and October in 2016. Details of capture methodology in 2015 are reported in Chapter 4. Microtrolling gear in 2016 was the same as that used in 2015 with the exception that the silver apex lure on one side of the vessel was replaced with a 2.5 cm silver or bronze and silver "dick nite" spoon fished 50 cm behind a 13 cm hot spot flasher. This gear change was made due to the high CPUE experienced by BC Conservation Foundation crews sampling in the same area in 2015. As in 2015 a translucent pink apex lure was fished on the other side of the vessel. To ensure representative sampling through diel and tidal cycles, microtrolling in 2016 occurred in pairs of days at the same site. One day would cover one half of the hours of daylight while the other day covered the balance. Catch processing in 2016 including biological sampling, anaesthesia and passive integrated transponder (PIT) tagging followed methods described for 2015 in Chapter 4.

5.3.4.2 Chinook Salmon genetic stock identification

Chinook Salmon genetic stock identification in 2015 and 2016 followed methods described in Chapter 4. Chinook Salmon samples collected at Maple Bay and Sansum Narrows in 2015 were analyzed together with fish collected at Cowichan Bay, Saanich Inlet, and Satellite Channel as a single mixture using the program cBayes (Neaves et al. 2005). Chinook Salmon samples collected at Sansum Narrows and Maple Bay in 2016 were analyzed as a separate mixture. As described in Chapter 4, analyses of diet and CPUE focused only on ocean-type stocks from systems entering the Strait of Georgia and excepting the South Thompson stock aggregate. Aggregation of individual stocks into region and life history-type groups is outlined in Table 5.2. Analyses of length and growth were focused on Chinook Salmon identified by genetic stock identification as originating from the Cowichan River.

5.3.4.3 Diet Analysis

Diet samples collected by gastric lavage in 2015 were subject to an initial inspection in the field for presence or absence of major taxonomic groupings of prey (corresponding to analysis categories defined in Chapter 4, Table 5.5) and then to detailed quantitative analysis in the laboratory as described in Chapter 4. Diet samples collected in 2016 were also examined in the field for presence or absence of prey groupings. Lab analysis in 2016 was limited to checking all samples identified in the field as containing fish or fish fragments to confirm whether these fragments were from Pacific Herring (*Clupea pallasii*), the primary fish prey of Chinook Salmon as identified in Chapter 4. A comparison of field assessment of presence or absence and quantitative analysis in the laboratory for 2015 samples suggested that the majority of the quantitative diet samples (98.1% of the aggregate diet by mass and a mean of 93% of individual diets by mass) were reflected in field presence/absence assessment (see Appendix 3; section 7.3). The comparison of Maple Bay and Sansum Narrows diets presented here therefore relies on presence/absence data recorded in the field.

Diet analyses focused on ocean-type Chinook Salmon originating from systems draining into the Strait of Georgia (and excepting fish from the South Thompson stock aggregate) as described in Chapter 4. Diet data were grouped by site and into two periods (July-August and September to October). Within these groupings, individual diets were randomly aggregated into units of 5-7 individuals (6 individuals where possible) and presence (1) and absence (0) scores were averaged for each prey category (Platell and Potter 2001). We visualized differences in diet composition by site, year and period using non-metric multidimensional scaling (nMDS) of Bray-Curtis dissimilarities of averaged presence/absence data for random 5-7 fish groupings using the function ‘metaMDS’ in the R package ‘vegan’. The nMDS results were overlaid with ellipses corresponding to the 95% confidence intervals of scores for each site, year and period grouping. To test for significant differences in diet between sites we implemented PERMANOVA on the Bray-Curtis dissimilarity matrix using the ‘adonis’ function in the ‘vegan’ package in R with 999 permutations. An initial PERMANOVA including all three factors (site, period, and year) and their interactions found a significant year by site by period interaction ($P = 0.013$). As our primary interest was in diet differences between sites, we ran separate

PERMANOVAs to test for significant differences between sites for each period within each year with a Bonferroni correction applied to the significance level required to reject the null hypothesis of no difference in diet between sites ($\alpha = 0.013$). As PERMANOVA is sensitive to differences in dispersion among groups we also assessed differences in dispersion between sites for each period within each year using the 'betadisperser' function in 'vegan'.

As a secondary method to compare juvenile Chinook Salmon diets between Sansum Narrows and Maple Bay we categorized diets into three categories: empty, containing Pacific Herring (confirmed by examination of diagnostic hard parts in the laboratory), and those containing other prey (not including Pacific Herring). We employed a Cochran–Mantel–Haenszel test of the null hypothesis of no association between site and diet proportions with year as a stratifying variable. This test is only appropriate if there is no three-way association (interaction) between the year, site, and diet. We tested this null hypothesis (no interaction) using a Woolf test for homogeneity of odds ratios. Where herring were intact, we also measured nose to fork length (FL) to facilitate calculation of predator length to prey length ratios.

5.3.4.4 Chinook Salmon size and growth

Hatchery reared Chinook Salmon experience different early growth conditions than wild Chinook Salmon. The majority of Chinook Salmon produced at Canadian hatcheries within the Salish Sea are not marked with an adipose fin clip, meaning that we could not distinguish which of the fish we sampled were of hatchery origin. The Cowichan River was an exception, as at least 86% of hatchery production in each release year from 2014-2018 was marked with an adipose fin clip (K. Pellett, DFO, pers. comm.). Analysis of fish size and scale-based prior growth trajectories (see below) was therefore focused on Chinook Salmon identified by genetic stock identification as originating from the Cowichan River. These fish represented 67% (605/901; Table 5.2) of juvenile Chinook Salmon sampled at Sansum Narrows and Maple Bay in 2015 and 2016 (530/787 for which usable scale data were available).

To determine if the size of juvenile Cowichan River Chinook Salmon differed by capture site and broad diet category we employed a modification of the GAM approach that was applied to analyze fish length in Chapter 4 (section 4.3.5.2). As the change in FL observed through the

season likely reflected a combination of growth and size selective immigration, emigration and mortality, this approach allowed us to account for change is size through time without imposing parametric assumptions. We included categorical parametric terms in the model for year, capture site, origin (hatchery or wild), and coarse diet grouping (empty stomachs, containing Pacific Herring, or containing other prey); a global smooth term for day of the year; and year-, capture site-, and origin-specific smooth terms for day of the year. To prevent over-smoothing, all smooth terms were constrained to a maximum of three knots. As discussed in Chapter 4, where both a global smooth and site specific smooths were included in the model (DOY), a first derivative penalty was applied to the site-specific smoothers, effectively facilitating comparison to the global smooth (Pedersen et al. 2019). Application of a first derivative penalty also allows these smooth terms to be effectively penalized out of the model (reduced to a line with 0 slope) when non-significant. As residuals of preliminary GAMs fit with a Gaussian distribution and either identity- or log- link exhibited positive skew and heteroscedacity, we fit the model with a gamma distribution and log link. To visualize model results we plotted predicted values and associated standard errors generated using the 'predict.gam' function in 'mgcv' for a hypothetical wild Chinook Salmon captured at each site on each day between 14 July and 22 October 2015.

Processing and measurement of scales from juvenile Chinook Salmon followed methods described in Chapter 4 section 4.3.4.5. Cowichan River Chinook Salmon scale measurements from 2015 and 2016 were pooled for quality control. Where residuals from linear regressions of scale diameter on FL and circulus count exceeded 200 µm, scales were excluded from analysis. Scales with a measured radius of the origin of < 40 µm or > 110 µm were also excluded. In 2015 multiple scales were measured for most fish, and circulus width for each circulus number was averaged across measured scales for each fish. In 2016 a single scale was measured for each fish.

Circulus width varies positively with both growth rate and fish size (Chapter 3, Chapter 4, Bilton and Robins 1971, Fisher and Pearcy 1990) therefore we adopted an analytical framework which compared growth rates of fish within common size bins. This necessitated reconstructing FLs of individual Chinook Salmon at each circulus interval. Other workers (e.g. Weitkamp et al. 2011, Davis et al. 2020) have recently employed the Fraser-Lee method to back

calculate Chinook Salmon lengths from scale measurements. This method assumes proportionality between scale radius and body length, with the ratio of scale radius to body length at capture used to account for variation in slope of this relationship for individual fish. The relationship between scale radius and body length is anchored by an intercept that represents the theoretical body length at zero scale radius, with this intercept typically being determined as the intercept of a regression of body length on scale radius for a sample of the population. Campana (1990) described how the Fraser-Lee method applied to otoliths can produced biased estimates of previous body length if the fish to otolith size ratio varies with growth rate. It is uncertain whether the scale radius to fish length ratio could also vary with growth rate, but the biological intercept modification of the Fraser-Lee method proposed by Campana (1990) should provide better reconstructed length estimates if such an effect does occur.

The proportionality of scale size and body length may also break down for Chinook Salmon at small sizes. Welander (1940) investigated the histology of scale development in juvenile Chinook Salmon and described the initial formation of the scale as occurring rapidly, with the initial plate of the scale filling the entire scale papilla at one time. If the origin of the scale forms suddenly it is incorrect to conceptualize a FL corresponding to zero scale radius, as this FL will also correspond to the radius of the scale origin. We reconstructed NFLs of juvenile Chinook Salmon using the biological intercept model of Campana (1990) with the initiation of proportional scale and body growth (the biological intercept) set as the mean diameter of the scale origin for our measured scales (70.4 μm) and a FL of 45 mm. This model is:

$$L_n = L_c + (S_n - S_c)\,(L_c - L_i)\,(S_c - S_i)^{-1}$$

Where L_n is the reconstructed for length at circulus n, L_c is FL at capture, S_n is scale radius at circulus n, S_c is scale radius at capture, L_i is FL at the biological intercept (45 mm), and S_i is scale radius at the biological intercept (70.4 μm). Selection of 45 mm as the FL at the biological intercept was based on the results of Welander (1940) who reported that scales first form near the lateral line in Chinook Salmon at 40-50 mm standard length and Rich (1920) who reported that many Chinook Salmon fry sampled in the lower Columbia River had scales by 40 mm FL with almost all having scales by 45 mm FL.

For each fish we employed the biological intercept model to reconstruct FL at each circulus. We then calculated the mean circulus width for each fish within length bins of 45 mm to 70 mm, 70 mm to 114 mm, 114 mm to 173 mm and 173 mm to 187 mm. In each case the upper limit of the length bin was included within the bin. These length bins were selected to represent periods prior to the mean size at ocean entry (45 mm to 70 mm) based on otolith and PIT tag-based ocean entry lengths for Cowichan River Chinook Salmon reported in Atkinson (2019); between ocean entry and the smallest sizes captured by microtrolling (70 mm to 114 mm); between becoming vulnerable to microtrolling and the smallest size which had consumed Pacific Herring (114 mm to 173 mm); and between the smallest size consuming Pacific Herring and the mean size captured by microtrolling (173 mm to 187 mm). For each size bin we used generalized linear models to evaluate how an index of growth rate (mean circulus width) within that bin was related to origin (hatchery vs wild), year, and site of capture. For each length bin, analysis was limited to fish that were longer at capture than the upper limit of the bin. This ensured that mean circulus spacing for each fish in each length bin covered the entire length bin. Generalized linear models were fit using the function 'glm' in the R statistical language with a gamma distribution and log link to accommodate the positively skewed nature of the circulus spacing data. In each case we first assessed whether plausible interactions between predictor variables were present by fitting models with all three terms (year, origin, and capture site) in addition to the interactions of year and origin and year and site both together and individually. Where interactions were not significant ($P > 0.05$) they were not included in a final model. Given that growth rate models were run for four separate size intervals we applied a Bonferroni correction to the critical P value required to reject the null hypothesis of no difference in growth rates between years, origins and capture sites ($P = 0.0125$). To visualize trends in growth rate by size we also plotted the mean and standard error of circulus spacing averaged within 10 mm bins from 45 mm to 185 mm for juvenile Cowichan River Chinook Salmon of hatchery and wild origin at Sansum Narrows and Maple Bay in each year.

5.3.5 *Analysis of catch per unit effort*

Analysis of catch per unit effort (CPUE) of first ocean year, ocean-type Chinook Salmon originating from Strait of Georgia systems followed a GAMM framework similar to that

described in Chapter 4 for CPUE data in 2015. Each hook where a Chinook Salmon was captured was scored as a 1 while all other hooks were scored as 0s. To investigate how CPUE varied across sites, years, depths, time of day, DOY, and stage of the tide we specified a binomial GAM on the basis of *a priori* hypotheses. Specifically, we hypothesized that Chinook Salmon CPUE would differ between sites and years and would vary globally and non-linearly by depth, DOY, and hour of the day. We also hypothesized that site and year-specific non-linear relationships might exist between CPUE and depth, DOY, and stage of the tide. Our binomial GAM included parametric terms for site and year; global smooth terms for hour of the day, depth, and DOY; and site and year-specific smooth terms for DOY, depth, and tide. As speed through water was not found to have a significant effect on CPUE in 2015 (see Chapter 4) and as this variable was not available for all fishing events, we excluded it from the analysis. As for other analyses we modelled stage of the tide as a continuous variable using cyclic cubic splines. Where both global and site- and year-specific smoothers were present in the model a second derivative penalty was applied to the non-global smoothers. To prevent over-fitting we limited the maximum degrees of freedom (knots) to 5 for smoothers of DOY, tide, and hour of the day, and to 3 for depth. We included fishing event as a random effect in our model to account for non-independence of hooks within a fishing event, thereby generating a generalized additive mixed model (GAMM). We fit the GAMM using the function 'bam' in the package 'mgcv' in R which is optimized for efficient computation with large sample sizes (Wood et al. 2015).

5.3.6 *Spatiotemporal patterns of habitat occupation by acoustic tagged juvenile Chinook Salmon and surface distribution of harbour seals*

As part of a study of the migration timing and survival of Cowichan River Chinook Salmon we tagged 80 juvenile Chinook Salmon with VEMCO V9-6L acoustic tags (69 kHz, 9 x 20 mm, 2.9 g in air) between 12 September and 15 September 2017. A secondary objective of this acoustic tagging was to investigate fine-scale movement of juvenile Chinook Salmon within the vicinity of Maple Bay and Sansum Narrows. Specifically, we aimed to assess whether fish captured at Maple Bay and Sansum Narrows exhibited patterns of habitat use that would be consistent with the differences in size and growth we observed between these sites in 2015 and 2016 (Chapter 4 and the present chapter). Tags transmitted at random intervals every 30-60

seconds for the first two weeks after activation to accommodate mobile surveys (see below), and then transitioned to 30-90 second intervals to prolong battery life. Movements and fates of tagged fish were monitored with local arrays of 69 kHz receivers deployed between North Reef and the Saanich Peninsula (Figure 5.6) combined with 10 days of intensive mobile tracking (see below). Receivers were deployed in four linear arrays to census fish moving out of the study area to the north and south, with additional groups of receivers deployed at two seal haul-outs (Burial Island and North Reef) and single receivers deployed adjacent to tagging and release sites at Sansum Narrows and Maple Bay to investigate site fidelity. Details of fish capture, sampling and tagging; and receiver array design, deployment and recovery are provided in Rechisky et al. (2019).

Mobile tracking was conducted within the inner set of passive receiver arrays on ten days during the two weeks following tagging (Sept 16, 18-24, 26-27). On each day the tracking vessel occupied 60 stations (1-2 visits per day) of which 51 were alongshore stations spaced approximately 600 m apart and 200 m offshore (mean = 189 m based on field validation with rangefinder) and 9 were mid-channel stations located approximately equidistant between shoreline stations within and adjacent to Maple Bay (Figure 5.6). At each station the vessel motor and sonar were switched off and tags were detected using a Vemco VHTx-69k omnidirectional hydrophone on 12 m of cable connected to a VR-100 deck box receiver. As a secondary detection method, a VR2 receiver was also deployed on an 18 m line weighted with a 0.75 kg weight at stations where water depth permitted. The initial listening time at each station was 135 seconds (the mean time required for a tag to transmit three times) and was extended by 60 seconds (up to a maximum of 255 seconds) for each tag collision heard or interference due to passing vessel noise. The order of stations surveyed was varied as much as possible between successive days but was not systematically randomized due to the need to respond to weather conditions and avoid vessels which would interfere with tag detections.

As a preliminary assessment of the overlap in habitat occupancy of seals and juvenile Chinook Salmon we conducted an instantaneous 360 º scan (Altmann 1974) around the vessel prior to departing each station. The presence or absence of seals within an estimated 200 m

radius 360 degrees around the vessel was recorded. We qualitatively examined the shoreline for the presence of hauled-out seals throughout mobile tracking surveys.

The fates (date of emigration from study area or death within study area) of tagged juvenile Chinook Salmon were assigned based on a combination of detections on passive receivers and detections during mobile tracking (for details see Rechisky et al. 2019). The relationship between the number of surviving juvenile Chinook Salmon and time suggested that elevated mortality occurred immediately after tagging, possibly due to the cumulative stress of handling and tagging. A break-point analysis was employed to separate this putative tagging-related mortality from subsequent mortality. Based on this analysis, mortality occurring within 2.6 days of tagging was assigned as tagging-related (Rechisky et al. 2019).

We analyzed spatiotemporal patterns of occupancy of the study area during the mobile tracking phase of the study (Sept 16-Sept 27) using a binomial generalized additive model. For every occupation of a mobile tracking station we generated a data point for each fish which was theoretically available to be detected within the study area. Fish were defined as available to be detected if 48 hours had passed since they were released, they did not belong to the group which experienced tagging-related mortality, they had not yet been assigned as having died or emigrated from the study area (defined as the area within the outer receiver arrays in Stuart Channel and between Saltspring Island and the Saanich Peninsula), and they were detected at least once during mobile tracking. Each point in this data set where an individual tag was not detected in an individual listening event was scored as 0 while each point where a fish was detected during the listening event by either the VR100 or VR2 was scored as a 1.

The log-odds of detecting a given juvenile Chinook Salmon at a given station on a given listening event was modelled as a product of independent two dimensional smooths of geographic coordinates in meters (UTM) for each release group (Maple Bay and Sansum Narrows). Listening stations were also assigned to groups (North of Sansum Narrows, South of Sansum Narrows, and Maple Bay Area; Figure 5.6), and the effect of stage of the tide on log-odds of detection was included as an independent smooth predictor for each receiver group and release group combination. Parametric terms were included in the model for both release site and

station group. To account for non-independence of observations, tag, station, and date were included in the model as random effects. To visualize detection probabilities in space and through the tidal cycle for fish tagged at Sansum Narrows and Maple Bay we calculated and mapped model predictions for a hypothetical data set. This data set included a single listening event at each station on 22 September (the midpoint of mobile tracking) at low slack, mid ebb, high slack and mid flood (tidal stage variable values of -6, -3, 0 and 3 respectively). Two tags, one from Sansum Narrows and one from Maple Bay, were included in this data set as levels of the random tag effect. Selection of representative Maple Bay and Sansum Narrows tags for dummy data was based on similar, near-zero coefficients. Model predictions were converted from log-odds to probability for plotting.

As a secondary method to visualize patterns of habitat use during and after the mobile tracking phase we aggregated valid detections (detections were valid if occurring at least 48 hours after tagging, not belonging to the group which experienced tagging-related mortality, and not being attributed to a stationary tag) at each receiver array by week for the 6 weeks post-tagging beginning on 16 September 2017. For receiver arrays adjacent to Maple Bay and Sansum Narrows (Sansum S., Burial Island, Sansum Narrows tagging site dock, Maple Bay tagging site buoy, and Sansum N.; Figure 5.6) we plotted the proportions (and associated standard errors) that Sansum Narrows-origin tags represented of the weekly total unique tags and total detections at each array.

To investigate spatial patterns of seal presence in the vicinity of Maple Bay and Sansum Narrows we employed a simplified version of the binomial GAM model applied to acoustic tag detections. Presence or absence of seals at each station occupation was modeled as a two dimensional smooth of geographic coordinates in meters (UTM). The seal occurrence data had too few positive events to allow fitting more complex models including random effects.

5.4 Results

5.4.1 *Zooplankton Sampling*

A total of 100 vertical zooplankton tows were conducted across six sampling days at Maple Bay and Sansum Narrows with tows split evenly between sites and depths (30 m and 60

m). A CTD deployed 3 m below the mouth of the net recorded maximum depth reached for 98 of these tows; in all cases the net began sampling within 3 m of the target depth. The volume sampled averaged 5.5 m^3 (SD = 0.4 m^3) for 30 m tows and 10.6 m^3 (SD = 0.5 m^3) for 60 m tows (net mouth area = 0.2 m^2; flowmeter calibrated at 6.57 revolutions/m). Mean sample volume values were assigned for the two tows where the flow meter failed. Retrieval times averaged 53.4 s (SD = 3.5 s) for 30 m tows and 105.9 s (SD = 7.6 s) for 60 m tows.

Calanoid copepods and decapod larval forms were the dominant organisms in zooplankton tows (Table 5.1) collectively making up 91% of the estimated sampled biomass (excluding gelatinous zooplankton for which estimated weights were not available). Of the zooplankton groups that individually represented more than 2% of juvenile Chinook Salmon diets in 2015, and were included in modelling of spatial and temporal patterns of biomass density in Chapter 4, decapod zoeae and megalopae collectively represented 99.5% of the estimated biomass sampled in 2017 zooplankton tows.

The density of calanoid copepods was far greater in 60 m than 30 m tows (Table 5.3, Figure 5.7). While the presence of copepods was not significantly related to tow depth, biomass densities were significantly higher in 60 m tows (see Table 5.3 for regression statistics). We did not detect an overall significant difference in copepod densities between sites, but the smooth term for stage of the tide was significant for 60 m tows conducted at Maple Bay (Table 5.3). Copepod densities in 60 m tows at Maple Bay were lowest near high slack and were elevated either side of low slack when they were also higher than densities in 60 m tows at Sansum Narrows (Figure 5.7). We did not detect a significant relationship between copepod densities and date.

No significant effects of site, date, tow depth, or site- and depth specific-stage of the tide were detected for the log-odds of encountering decapod megalopae. However, biomass densities of megalopae were significantly lower at Sansum Narrows and in deep (60 m) tows and declined with sampling date (Table 5.3). A significant non-linear relationship between biomass density of megalopae and stage of the tide was detected only for 60 m tows at Sansum Narrows where densities were elevated on either side of high slack. Biomass densities of decapod zoeae were

significantly lower at Sansum Narrows and declined with date, but no overall differences were detected between 30 m and 60 m tows. Significant non-linear relationships between zoeal densities and stage of the tide were detected for 30 m tows at Sansum Narrows and tows at both depths at Maple Bay (Table 5.3). At Sansum Narrows, zoeal biomass densities in 30 m tows were elevated on the ebb and depressed on the flood, while densities at 60 m at Maple Bay followed the opposite pattern (Figure 5.7). In 30 m tows at Maple Bay, biomass densities of decapod zoea increased through the ebb and declined in the second half of the flood.

5.4.2 *Acoustic Zooplankton Fish Profiler Surveys*

We conducted 231 AZFP transects, 211 of which met data quality standards for analysis (103 at Maple Bay and 108 at Sansum Narrows). The mean of mean transect water column depths was greater at Sansum Narrows (101 m; SD = 42 m) than Maple Bay (71 m; SD = 23 m).

Aggregations of fish, other backscatter attributable to fish, and backscatter attributable to plankton were all more evident in echograms at Sansum Narrows than at Maple Bay. At Maple Bay 19 of 103 transects contained no fish aggregations as compared to 1 of 108 transects at Sansum Narrows. At Sansum Narrows, fish aggregations were dramatically larger and more abundant on the flood tide (Figure 5.5). Backscatter attributed to fish aggregations, other fish, and plankton were primarily located in the top 50 m of the water column at both sites.

The distribution of transect mean (calculated in the linear domain) $\Delta MVBS_{200\text{-}38}$ and $\Delta MVBS_{125\text{-}38}$ for fish aggregations was broader at Maple Bay than at Sansum Narrows (Figure 5.8). At Maple Bay, 25 of 84 transects containing fish aggregations had $\Delta MVBS_{200\text{-}38}$ above the 2 dB threshold used by Sato et al. (2015) to separate fish and plankton while at Sansum Narrows it was 22 of 107. For other fish targets the peak of the distributions of $\Delta MVBS_{200\text{-}38}$ (-4 dB) and $\Delta MVBS_{125\text{-}38}$ (-1 dB) were the same at both sites while the distribution of ΔMVBS values for plankton were shifted slightly higher at Maple Bay for both frequency pairs (Figure 5.8).

Generalized additive mixed models indicated that the occurrence of fish aggregations and nautical area backscattering coefficients attributable to fish aggregations, other fish, and plankton were significantly higher at Sansum Narrows than Maple Bay (Table 5.4, Figure 5.9). The

presence or absence of fish aggregations was not significantly related to transect depth or day of the year and did not vary significantly with the stage of the tide at either site. However, S_A attributable to fish aggregations did vary with stage of the tide at both sites, decreasing through the first part of the ebb and increasing to a peak during the middle of the flood tide (Figure 5.9). This change in fish aggregations with stage of the tide was dramatically more pronounced at Sansum Narrows than Maple Bay. Backscatter attributed to other fish and plankton in the top 30 m and 30-60 m strata were also significantly greater at Sansum Narrows than Maple Bay (Table 5.4). For all site-category combinations, with the exception of plankton in the 30-60 m stratum at Sansum Narrows, a significant u-shaped relationship was detected with stage of the tide, with backscatter greatest near high slack and decreasing to a minimum near low slack (Figure 5.9). Significant negative relationships with day of the year were detected for other fish and plankton in the top 30 m, while a significant positive relationship to transect depth was detected only for other fish (Table 5.4).

5.4.3 Juvenile Chinook Salmon Diet, Size and Growth

We captured 921 first ocean summer (< 300 mm FL) Chinook Salmon at Sansum Narrows and Maple Bay on 23 days between 12 July and 20 August 2015 (N =160) and 28 days between 8 August and 12 October 2016 (N = 761). Stock of origin was successfully determined by GSI for 901 of these fish. Of these fish, 605 (67%) were from the Cowichan River, 105 (12%) were ocean-type fish from the lower Fraser River, 55 (6%) were from other East Coast Vancouver Island Rivers, and the balance were from a variety of other stock groups (Table 5.2). During microtrolling in 2016, crews frequently stayed overnight at a floating aquaculture facility in Sansum Narrows to facilitate sampling before and after sunset. During hours of darkness, abundant age-0 Pacific Herring were visible and audible feeding on the surface.

5.4.3.1 Diet

We analyzed the diet of 765 ocean-type Chinook Salmon originating from systems draining into the Strait of Georgia. Sample sizes were 68 at Maple Bay and 59 at Sansum Narrows in 2015 and 323 at Maple Bay and 315 at Sansum Narrows in 2016. Of these fish, 710 individuals contained food from at least one of the taxonomic analysis categories (Table 5.5) and

were included in multivariate analyses. Non-metric multidimensional scaling suggested a clear separation of diets between Sansum Narrows and Maple Bay (Figure 5.10) with Sansum Narrows diets shifted more towards the presence of fish, gammarids, and euphausiids while Maple Bay diets were shifted towards the presence of copepods, decapods, and hyperiids (Figure 5.10; Table 5.5). Significant differences in diet between sites were also detected for each diet period within each year by PERMANOVA (Table 5.6) with the exception of September-October diets in 2015 which were marginally non-significant ($P = 0.021$) given the Bonferonni corrected critical P value (0.013). Significant differences in dispersion were also detected for both periods in 2016, suggesting that significant PERMANOVA results could be at least in part due to differences in group dispersion. Nevertheless, NMDS results for 2016 suggest that diet compositions were also different between sites in 2016.

The frequency of occurrence of Pacific Herring and empty stomachs were both 3-4 times higher at Sansum Narrows than Maple Bay in 2015 and 2016 (Figure 5.11). A Woolf test failed to detect a three-way interaction between year, site, and the proportions of juvenile Chinook Salmon in the categories empty stomachs, containing Pacific Herring, and not containing Pacific Herring ($\chi^2 = 0.10$, $P = 0.75$). This result suggested that a Cochran–Mantel–Haenszel test was appropriate to test for an association between site and diet. This test was highly significant ($M^2 = 62.22$, $P < 0.001$) confirming that proportions of coarse diet groupings differed between Sansum Narrows and Maple Bay.

As in 2015 (see Chapter 4) only larger juvenile ocean-type Chinook Salmon sampled in 2016 contained Pacific Herring (mean = 211 mm FL, range = 173 mm – 255 mm FL; see section 5.4.3.2). Very few Pacific Herring in stomachs were intact enough to measure and FLs were obtained for only 11 individuals (Mean = 90.4 mm, range = 78 mm to 100 mm). Of these, 7 Pacific Herring were found in juvenile Chinook Salmon from a stock which was included in diet analyses (Cowichan River), 4 were from Puget Sound Chinook Salmon, and one was from an upper Fraser Stream Type Chinook Salmon. The mean prey length to predator length ratio for Cowichan River Chinook Salmon was 0.42 with a range of 0.38 to 0.44; for other stocks the mean ratio was 0.41 with a range of 0.36 to 0.45.

5.4.3.2 Cowichan Chinook Salmon Size and Growth

Cowichan River-origin Chinook Salmon increased in size during the summer and early fall (Figure 5.12). We did not detect differences in the shape of the relationship between FL and day of the year for different origin (hatchery versus wild), years, or capture locations (P values for smooth terms all ≥ 0.08). We also detected no overall difference in size between years or origins ($P = 0.18$ and $P = 0.51$ respectively). The differences in size between capture sites and coarse diet groupings were both highly significant ($P < 0.001$). Juvenile Cowichan Chinook Salmon captured at Sansum Narrrows were about 8 mm longer in mid-July and 11 mm longer in mid-October than those captured at Maple Bay. Fish which contained juvenile Pacific Herring were the largest of the three coarse diet groupings, with the difference in predicted length relative to fish with other diets increasing from approximately 15 mm in July to 22 mm in October. Predicted lengths of fish with empty stomachs were very close to those of fish containing Pacific Herring (Figure 5.12).

Interactions between year and status (hatchery or wild origin) and year and site were not significant whether included together or independently in models relating an index of growth (scale circulus spacing) over four size intervals to year, capture site, and status ($P \geq 0.12$ in all cases). These interactions were therefore omitted from the models. Juvenile Cowichan River Chinook Salmon captured at Sansum Narrows in 2015 and 2016 exhibited significantly faster growth than those captured at Maple Bay over the size ranges corresponding to primarily freshwater growth (45 mm to 70 mm), microtroll sampling prior to consumption of Pacific Herring (114 mm to 173 mm), and microtroll sampling after the onset of consumption of Pacific Herring (173 mm to 187 mm). Growth rate did not vary significantly between 2015 and 2016 for any growth stanza. Growth rate was significantly faster for wild fish than hatchery fish for the first two periods of growth (45 mm to 70 mm and 70 mm to 114 mm). For both hatchery- and wild-origin fish at both sites and in both years growth rate declined from soon after the onset of scale formation to a minimum between 60 mm and 90 mm FL before increasing again and leveling off at a size corresponding to the smallest fish captured by microtrolling (~ 114 mm FL). Binning scale circulus spacing into 10 mm intervals of FL suggested that in 2016 both hatchery and wild Cowichan River Chinook salmon captured at Maple Bay had experienced a

minimum growth rate at a smaller size (65 mm to 75 mm) than those captured at Sansum Narrows (75 mm to 85 mm; Figure 5.13). While growth rate did not differ significantly between fish captured at Maple Bay and those captured at Sansum Narrows for the growth interval from 70 mm to 114 mm, a pattern was evident for wild fish when growth rate was binned by 10 cm FL intervals (Figure 5.13). Specifically, the general pattern of growth rate by site was reversed, with faster growth between 95 mm and 115 mm for fish captured at Maple Bay.

5.4.4 *Analysis of Catch Per Unit Effort*

Our generalized additive mixed model explained 14% of the deviance in juvenile ocean-type Chinook Salmon CPUE across 14013 individual hook deployments at Sansum Narrows and Maple Bay in 2015 and 2016. The log-odds of catching a Chinook Salmon was significantly greater in 2016 than 2015 but did not differ globally between Sansum Narrows and Maple Bay (Table 5.8) We detected significant effects of stage of the tide on Chinook Salmon CPUE at Sansum Narrows in both years and at Maple Bay in 2015 (Table 5.8, Figure 5.14 a-c). At Maple Bay in 2015, CPUE was elevated from the late flood tide through most of the ebb but declined to a minimum in the two hours after low slack. At Sansum Narrows CPUE was elevated during the middle of the flood tide and reached a minimum during the late ebb in both years, although the magnitude of the effect was lower in 2016. The marginally non-significant ($P = 0.077$; Table 5.8) global relationship between day of the year and CPUE consisted of a slight increase over the first part of the sampling period with a plateau after mid-August (Figure 5.14). Relative to this global pattern, site- and year-specific smooths were significant at Maple Bay in 2015 (higher prior to September and lower after September), Maple Bay in 2016 (lower during September), and Sansum Narrows in 2016 (higher after September). Globally, Chinook Salmon CPUE was significantly lower at 5-10 m and significantly elevated from 15 m to 25 m. Significant differences from this global pattern were detected at Sansum Narrows in 2015 (relative increase in catch with depth) and Maple Bay in 2016 (relative decrease in catch with depth).

5.4.5 *Spatiotemporal patterns of habitat occupation by acoustic tagged juvenile Chinook Salmon and surface distribution of harbour seals*

Juvenile Chinook Salmon were captured, tagged and released at Maple Bay (N = 41) on 12-13 September and Sansum Narrows (N = 39) on 14-15 September 2017. Genetic stock identification indicated that 70 of these fish were of Cowichan River origin with the balance being ocean-type stocks from the British Columbia South Coast or East Coast Vancouver Island. Genetic samples for four fish failed to amplify. Nineteen of the juvenile Chinook Salmon had an adipose clip, 58 were unclipped, and adipose status was not recorded for two fish. Mean FL of juvenile Chinook Salmon tagged at Maple Bay and Sansum Narrows was 172 mm (SD = 20 mm) and 178 mm (SD = 25 mm) respectively. Further details are provided in Rechisky et al. (2019).

Movement patterns and duration of residence of juvenile Chinook Salmon in the study area was highly variable. Some individuals left immediately, while one was detected alive on the day receivers were removed in late March 2018. Median emigration date from the study area was 19 days after tagging (see Rechisky et al. 2019). Animations of the movements of tagged fish, including their detections on static receivers and during mobile tracking, and their final detection location are available from the Kintama Research Services website at http://kintama.com/animator/dep/Cowichan2017_mobile/.

Break point analysis suggested that 12 fish likely experienced tagging related mortality (Rechisky et al. 2019) and these individuals were removed from subsequent analysis. We conducted a total of 608 listening events at 60 stations over 10 days between 16 September and 27 September 2017. After censoring fish which were never detected by mobile tracking or were only detected within the first 48 hours after tagging, 52 juvenile Chinook Salmon met the criteria for inclusion in the analysis of these mobile tracking data (23 from Sansum Narrows and 29 from Maple Bay). This resulted in a total data set of 27,058 potential detections where one of these 52 tags was estimated to be alive and within the study area during a listening event. In 777 cases a juvenile Chinook was detected during an individual listening event.

We detected no significant effects of tagging location or listening station group on probability of detection of juvenile Chinook Salmon during mobile tracking (Table 5.9). Two dimensional spatial smooths of detection probability for fish tagged at Maple Bay and Sansum Narrows were highly significant, as were cyclic smooths of detection probability by stage of the tide for fish from both release sites at station groups north and south of Sansum Narrows but not around Maple Bay (Table 5.9, Figure 5.15). The effect size of stage of the tide was much larger for fish tagged at Sansum Narrows than Maple Bay (Figure 5.15, Figure 5.16). Fish tagged at Sansum Narrows had a higher probability of being detected north and south of Sansum Narrows, while those tagged at Maple Bay had a higher probability of being detected in the vicinity of Maple Bay. Probability of detecting tags from both sites was elevated south of Sansum Narrows at low slack and north of Sansum Narrows on the flood. At high slack, probability of detecting Maple Bay tags was elevated north of Sansum Narrows and probability of detecting Sansum Narrows tags was elevated on both sides of the narrows. Some degree of spatial autocorrelation in mobile tracking data was likely, but spatial autocorrelation is difficult to address with binomial data in a GAMM framework. This spatial autocorrelation may have led to underestimation of P-values which should be treated with caution. Nevertheless, the overall differences in spatial patterns of detection probability by release site and tidal effects for fish tagged at Sansum Narrows were substantial.

Detections of juvenile Chinook Salmon tagged at Maple Bay and Sansum Narrows on passive receivers generally corroborated patterns observed during mobile tracking. At the Maple Bay tagging site and the nearest passive array (Sansum North) the proportion of unique tags that were of Sansum Narrows origin was lower than at the Sansum Narrows tagging site, Burial Island, and the Sansum South array for the first two weeks after tagging (Figure 5.17). This pattern broke down after two weeks; however, the proportion of total tag detections that were attributable to Sansum Narrows fish remained between 20% and 40% at the two sites closest to Maple Bay through six weeks after tagging, while at the other arrays this proportion was generally between 50% and 100%. The only exception to this general pattern was in week five where the proportion of total detections attributable to Sansum Narrows tags was higher at the Maple Bay tagging site than at the Sansum South array.

We observed seals within 200 m of the vessel on 57 of 625 station occupations during mobile tracking of acoustic tags. Seals were most frequently encountered on the surface at stations adjacent to and south of Sansum Narrows (Figure 5.18). A GAMM relating log-odds of observing seals to a two-dimensional spatial smooth found a marginally non-significant spatial pattern in seal occurrence (P =0.070). Seals were observed routinely on the haul-out at Burial Island and hauled out on the shoreline at a number of locations in the vicinity of Sansum Narrows (Figure 5.18).

5.5 Discussion

We conducted a multifaceted case study of factors influencing the growth potential of juvenile ocean-type Chinook Salmon at two closely adjacent sites (~ 4 km apart) in the Southern Gulf Islands of the Salish Sea. We confirmed that juvenile salmon differed consistently in size, diet and growth between these sites across two years (2015 and 2016). Hydroacoustic and zooplankton abundance data collected in a third year (2017) confirmed that forage fish were more abundant and zooplankton less abundant at Sansum Narrows, the site where captured Chinook Salmon were larger, faster growing and more piscivorous. Acoustic tagging, also conducted in 2017, confirmed that the distribution within the study area of fish tagged and released at Sansum Narrows was different from that of those tagged and released at Maple Bay, providing a potential basis for size and growth rate differences. Occurrence of forage fish schools, CPUE of juvenile Chinook Salmon, and detection probability of acoustic tagged Chinook Salmon followed similar tidal patterns at Sansum Narrows, suggesting co-location of piscivorous Chinook Salmon and their prey. Scale circulus spacing-based growth rates of Cowichan River-origin Chinook Salmon captured at Sansum Narrows were greater not only over reconstructed sizes corresponding to summer marine growth, but also for the size interval corresponding to freshwater or very early marine growth (45-70 mm FL). Our results suggest that individual growth history interacts with behaviour and fine-scale spatial structure within the marine environment to regulate growth potential of juvenile Chinook Salmon.

5.5.1 *Consistent differences in juvenile Chinook Salmon diet, size, and growth between sites*

Diet differences between juvenile ocean-type Chinook Salmon captured at Maple Bay and Sansum Narrows were consistent in 2015 and 2016. In both years fish captured at Sansum Narrows consumed more fish and euphausiids and less small crustacean zooplankton (primarily decapod larvae) than those at Maple Bay. The occurrence of both Pacific Herring and empty stomachs was also higher at Sansum Narrows. As discussed in Chapter 4, fish which had made the transition to feeding on Pacific Herring were likely over-represented among those with empty stomachs on capture. Our analysis of Cowichan River-origin Chinook Salmon lengths expanded and corroborated results for ocean-type Chinook Salmon in 2015 (Chapter 4). Juvenile Cowichan River Chinook Salmon were significantly larger at Sansum Narrows than Maple Bay, and those with Pacific Herring in their diet or with empty stomachs were larger than those which had fed on other diet items. It is uncertain what proportion of juvenile Chinook Salmon captured with prey other than Pacific Herring in their stomachs had also transitioned to including Pacific Herring in their diet. It is also uncertain whether capture by micotrolling biased estimates of diet composition. Quantitative diet analysis in 2015 (Chapter 4) indicated that Chinook Salmon containing Pacific Herring had greater stomach fullness. It is possible that this could make piscivorous salmon less vulnerable to hook and line sampling if fish with fuller stomachs are less likely to feed. Conversely, the relationship between juvenile Chinook Salmon size and lure colour described in Chapter 4 suggests that the use of terminal gear imitating small fish (spoons) could bias catches towards piscivorous salmon. Diet comparisons of fish captured simultaneously by microtrolling and seining or trawling would be necessary to resolve these issues. Nevertheless, as microtrolling was conducted using identical methods throughout the study area we are confident that the relative differences that we observed in size and diet of Chinook Salmon at Sansum Narrows and Maple Bay reflect genuine differences in the ecology of fish captured at these sites.

Surprisingly, we detected no effect of either year or origin (hatchery vs wild) on size of juvenile Chinook Salmon. This contrasts with Beamish et al. (2012a) who reported that hatchery origin Cowichan River Chinook Salmon were considerably larger than wild individuals through summer and fall of 2008 in the Southern Gulf Islands. Chinook Salmon are reared on

groundwater at the Cowichan River hatchery and therefore experience higher rearing temperatures during winter and lower rearing temperatures during spring than their wild counterparts. Typically, these hatchery fish are 5-10 mm longer at release (between April and May) than wild Chinook Salmon at the equivalent time (Kevin Pellett DFO pers. comm.). The winter and spring of both 2015 and 2016 were unusually warm in the eastern North Pacific and Chinook and Coho Salmon captured in annual Strait of Georgia trawl surveys were larger than average (Neville 2017). It is possible that warmer than average incubating and rearing conditions for juvenile wild Cowichan River Chinook Salmon reduced the size difference with hatchery fish reared on constant temperature ground water. We also found that scale circulus spacing-based indices of growth rate were significantly higher for wild than hatchery Cowichan River Chinook Salmon over the 45-70 mm and 70 - 114 mm reconstructed size ranges. This growth rate difference likely also contributed to closing the size gap between hatchery and wild individuals prior to them becoming vulnerable to microtrolling.

Scale circulus width-based growth rate of juvenile Cowichan River Chinook Salmon which had reached a size to potentially feed on Pacific Herring (173-187 mm FL) was greater at Sansum Narrows than Maple Bay. Given the growth advantage of piscivory to predatory fish (Juanes and Conover 1994, Juanes et al. 2002, Litz et al. 2017, Davis et al. 2020), it is likely that at least part of this difference in growth rate was related to the different diets of fish captured at the two sites. However, given that growth rates during two earlier size intervals (45-70 mm and 114-173 mm) were also greater for fish captured at Sansum Narrows, consumption of Pacific Herring is unlikely to be the only factor underlying spatial differences in size and growth (discussed further in section 5.5.3).

5.5.2 *External factors influencing growth potential*

Zooplankton sampling in 2015 suggested that biomass densities (henceforward ‘densities’) of crustacean zooplankton prey of juvenile Chinook Salmon in the top 30 m of the water column were the lowest at Sansum Narrows of five sites sampled in the Southern Gulf Islands and were significantly lower on the flood than the ebb (Chapter 4). This result was confirmed by zooplankton sampling conducted in September 2017, with densities of decapod

zoea and megalopae in both the top 30 m and top 60 m lower at Sansum Narrows than Maple Bay. Sampling stations at the two sites were at different locations in 2015 and 2017 (Figure 5.2), increasing probability that the lower density of zooplankton detected at Sansum Narrows was not a station effect. While densities of decapod megalopae in the top 30 m were not significantly related to stage of the tide, densities of decapod zoeae, which represented several times the biomass density of decapod megalopae, were lower on the flood relative to the ebb tide at Sansum Narrows. This result was consistent with lower densities of zooplankton on the flood reported for Sansum Narrows in 2015 (Chapter 4). While many crustacean zooplankton taxa exhibit diel vertical migration, descending to deep water during the day and rising close to the surface at night, others may remain associated with chlorophyll maxima throughout the day (Harris 1988). Disruption of such vertical structure in zooplankton distribution by turbulent tidal mixing was one hypothesis to explain the lower density of crustacean zooplankton in the top 30 m observed at Sansum Narrows relative to all other sites in 2015 (see Chapter 4). Our results were not consistent with this hypothesis. While densities of decapod megalopae were significantly lower in 60 m tows than in 30 m tows, the difference was modest relative to differences between sites. We also detected no evidence that densities of either decapod zoeae or megalopae at Sansum Narrows were greater in 60 m tows when they were lower in 30 m tows which would be expected if a high density layer in the top 30 m was being distributed through the water column. Vertical structure in copepod abundance also provided strong evidence that homogenization of the water column by tidal mixing was not responsible for lower zooplankton abundance in the top 30 m at Sansum Narrows. At both sites, copepods were almost absent from the top 30 m of the water column throughout the tidal cycle but were consistently abundant in 60 m tows. Zamon (2002) reported that advection from depth resulted in elevated densities of copepods in the top 25 m of the water column on the flood tide at San Juan Passage. Aggregations of forage fish (juvenile Pacific Herring and Pacific Sandlance *Ammodytes hexapterus*) and their predators on the flood tide at this site (Zamon 2000, 2002) were in turn attributed to this zooplankton subsidy. Our zooplankton sampling results suggest that such a mechanism is not operating at Sansum Narrows.

Detection of backscatter attributed to zooplankton ($2\ dB < \Delta MVBS_{200\text{-}38} \leq 32\ dB$) in acoustic fish profiler (AZFP) surveys was inconsistent with results from zooplankton net

sampling. Area backscattering coefficient values attributed to zooplankton were considerably higher at Sansum Narrows than Maple Bay in both the 0-30 m (expanded from 10-30 m values) and 30-60 m strata. Backscatter attributed to zooplankton in the top 30 m at Sansum Narrows also exhibited a strong tidal pattern with values depressed during the ebb tide and elevated during the flood tide, mirroring patterns for fish aggregations (see below). Zooplankton nets do a poor job of capturing highly motile zooplankton taxa, for example euphausiids (Brodeur et al. 2011). Euphausiids were more prevalent in juvenile Chinook Salmon diets at Sansum Narrows than Maple Bay; but it seems unlikely that euphausiids could explain the difference in acoustic backscatter between the sites, particularly as they were entirely absent from zooplankton samples at Sansum Narrows in 2017 (juvenile euphausiids were encountered only in a few 60 m tows at Maple Bay). It is also possible that the range of $\Delta MVBS_{200-38}$ values that we used to classify fish was not broad enough. These values were based on trawl validation of $\Delta MVBS_{200-38}$ values by Sato et al. (2015) in Puget Sound. Trawl catches considered representative of fish targets by Sato et al. (2015) included Pacific Herring with mean FLs from 14.7 cm to 17.5 cm and Pacific Hake (*Merluccius productus*) with mean FLs from 19.0 cm to 20.6 cm. These fish were considerably larger that the age-0 Pacific Herring which were frequently observed in Chinook Salmon diets and on the surface at Sansum Narrows. Other small schooling fish which were observed in the study area were Threespine Stickleback (*Gasterosteus aculeatus*) and Shiner Surfperch (*Cymatogaster aggregata*). While zooplankton generally span the size transition from Rayleigh backscatter to geometric backscatter for acoustic frequencies used in fisheries oceanography, fish with gas filled swim bladders produce exclusively geometric backscatter, limiting the usefulness of differences in backscatter between frequencies to differentiate fish size or species (De Robertis et al. 2010). Nevertheless, ΔMVBS values have been used successfully to differentiate species (e.g. Sato et al 2015) and size (Rousseau et al. 2020) of fish within aggregations, with the latter authors demonstrating a positive relationship between length and $\Delta MVBS_{67-38}$ for juvenile Pacific Salmon in the Discovery Islands. We suspect that some of the acoustic backscatter attributed to zooplankton may in fact have been produced by fish smaller, or with different acoustic properties, than those sampled during ΔMVBS validation by Sato et al. (2015). It is notable that approximately one quarter of fish aggregations at both sites (see below) also had mean $\Delta MVBS_{200-38}$ above the range used by Sato et al. (2015) to identify fish, and both

$\Delta MVBS_{200\text{-}38}$ and $\Delta MVBS_{120\text{-}38}$ attributed to plankton in transects at Sansum Narrows were shifter to lower values than at Maple Bay. Fraser et al. (2017) used a broader range of -10 dB < $\Delta MVBS_{200\text{-}38}$ < 10 dB to identify fish schools at a tidal power site in the North Sea. Without validation of organisms present in the water column (for example by trawling) we cannot rule out that a zooplankton taxon that was not sampled by our nets exhibits high abundance with strong tidal patterns at Sansum Narrows, but it appears unlikely.

While AZFP results for zooplankton were equivocal, elevated abundance of fish aggregations, with abundance higher on the flood than on the ebb, was fairly definitive. These 2017 results corroborated qualitative observations using the vessel sonar in 2015 and 2016. One possible confounding factor in acoustic data at Sansum Narrows, particularly on the flood, was the potential of strong turbulence to generate acoustic backscatter (Fraser et al. 2017). Turbulent flows can generate backscatter through entrainment of air bubbles (Plueddemann et al. 1996) or steep density gradients (Lavery et al. 2003). Backscatter associated with turbulence in tidal passages is often strongest near the surface, with backscattering features often continuous with the surface (Fraser et al. 2017). To limit the potential of bubbles and other turbulence-associated backscatter to influence results we filtered a conservative 10 m band below the surface from analysis. While we did not also filter out all putative fish aggregations continuous with the bottom of this band, examination of classified echograms revealed that the bulk of classified fish aggregations were discontinuous with the surface 10 m, with many centered on approximately 30 m depth. As discussed in the previous paragraph, approximately one quarter of all fish aggregations had $\Delta MVBS_{200\text{-}38}$ above the threshold used by Sato et al. (2015) to separate fish and plankton. Nevertheless, for the reasons provided above we do not feel that this means that these aggregations were not fish. We believe that the bulk of fish aggregations that we observed were age-0 Pacific Herring. In pelagic trawl surveys conducted in the Strait of Georgia in July between 1998 and 2009, Pacific Herring represented 91.6% of the catch numerically (Beamish et al. 2012b). Age-0 Pacific Herring were also the dominant post-larval fish observed in juvenile Chinook Salmon diets in both 2015 and 2016 and were periodically observed at the surface in the study area, particularly at night.

The strong tidal patterns that we observed in area backscattering coefficient attributable to fish aggregations at Sansum Narrows suggest that schools of age-0 Pacific Herring move into this area on the flood tide and depart on the ebb. Given the current direction and lack of increase in fish aggregations in Maple Bay on the ebb (the tidal pattern at Maple Bay was actually similar to that at Sansum Narrows with a modest increase in fish aggregations on the flood) it seems likely that these schools move back south through Sansum Narrows on the ebb. This movement pattern would keep herring schools constantly downstream from the narrowest part of Sansum Narrows in an area of turbulent rather than laminar flow. Future acoustic or net based sampling programs at Sansum Narrows or similar tidal narrows conducted both upstream and downstream of the narrows on both flood and ebb tides could determine if such a pattern does occur. If aggregations of age-0 Pacific Herring do indeed move back and forth through the narrows with the tide this could simply be a function of passive transport coupled to with active swimming to resist dislocation, as suggested for seamount micronekton by Wilson and Boehlert (2004). Alternatively, staying 'downstream' of the tidal narrows could provide a foraging or survival advantage to Pacific Herring. As previously mentioned, our zooplankton sampling results do not suggest that advection of zooplankton from depth by tidal currents is providing a feeding opportunity for forage fish at Sansum Narrows as was suggested by Zamon (2002) for San Juan Passage. Nevertheless, maintaining position downstream of Sansum Narrows could still provide potential advantages to age-0 Pacific Herring. Occupying slower currents in the lee of topographic relief while taking advantage of a flux of particles in adjacent faster moving flows could provide an energetic advantage (the feed-rest hypothesis; reviewed by Genin 2004). Turbulence could also disrupt the ability of crustacean prey to detect predators (Clarke et al. 2005, Gilbert and Buskey 2005), facilitating efficient predation by juvenile Pacific Herring. Given a lack of evidence that lower densities of zooplankton prey of juvenile Chinook Salmon in the top 30 m at Sansum Narrows relative to other sites in the area (Chapter 4) are a consequence of homogenization of the water column by tidal mixing, it remains possible that zooplankton densities are locally reduced by Pacific Herring foraging. A similar mechanism has been suggested to explain reduced zooplankton densities downstream of seamounts (Genin et al. 1988, Dower and Mackas 1996). If the same mass of water passes repeatedly back and forth through

the narrows over several tidal cycles it is possible that a depletion of zooplankton due to locally abundant forage fish could be amplified.

Embayments can concentrate zooplankton both through retention and local production of meroplankton (Archambault et al. 1998), and such mechanisms could be operating at Maple Bay. As we did not sample further north into Stuart Channel it is not clear whether the crustacean zooplankton densities observed in Maple Bay were elevated or typical of this larger sub-basin. Zooplankton densities at this site were the second highest of the four sites investigated in 2015 (Chapter 4) but all sampling occurred to the South and only one station at each of 5 sites was monitored. Given this uncertainty, we do not make any assumptions in interpreting our data as to whether Maple Bay is a particularly high zooplankton abundance site, or indeed whether Sansum Narrows is a particularly low zooplankton and high forage fish abundance site. Rather we conclude that forage fish, likely age-0 Pacific Herring, are relatively more abundant at Sansum Narrow than Maple Bay, and that crustacean zooplankton prey of Juvenile Chinook Salmon are more abundant at Maple Bay than Sansum Narrows.

5.5.3 *Intrinsic factors influencing growth potential*

The differences in size and growth of Cowichan River Chinook Salmon captured at Sansum Narrows and Maple Bay suggested that fish encountered at these two sites were using marine habitat in different ways. One possibility was that fish captured at Maple Bay were primarily local residents, while those captured at Sansum Narrows included more migratory individuals passing through the area. An alternative hypothesis was that many individuals at both sites occupied only small local ranges. Our acoustic tagging results did not provide support for either of these extreme cases. Forty-eight hours after tagging, 58% of fish tagged at Sansum Narrows and 71% of fish tagged at Maple Bay were still alive within the study area, and two individuals from each tag group were still being detected on local arrays into early 2018, at least four months after tagging. Fish tagged at both sites moved throughout the study area, and fish tagged at one site were frequently detected at the other site. This mixing was unsurprising given a minimum median travel rate for these acoustic tagged fish of 1.2 body lengths per second (Rechisky et al. 2019). This travel rate estimate is conservative as it assumes straight line

movements and adjusts for detection range of the tags. Given this estimate, direct travel times between the Maple Bay and Sansum Narrows tagging sites would range from 4.6 to 7.6 hours for the largest and smallest tagged fish respectively. While mixing between the two tag groups did occur, fish tagged at Maple Bay and Sansum Narrows exhibited different patterns of utilization of the study area. Modeling of detections during mobile tracking suggested that fish tagged at Sansum Narrows were more likely to be detected adjacent to the narrows and tended to move back and forth through Sansum Narrows with tidal currents. This pattern was consistent with patterns of CPUE to the North of Sansum Narrows in both years and with the hypothesized movement of age-0 Pacific Herring schools. Elevated detections of Sansum Narrows tags south of the narrows at high slack were inconsistent with this pattern. It is possible that fish tagged at Sansum Narrows which had moved south into Satellite Channel tended to get drawn north into this region by the flooding tide. Fish tagged at Maple Bay were detected with greater frequency in and to the north of Maple Bay.

As mobile tracking only occurred during the two weeks following tagging it could be argued that the differences in distribution of fish tagged at the two sites were due to passive dispersal rather than distinct patterns of habitat utilization. However, the ratio of tag detections from the two tag groups at receiver arrays adjacent to the two tagging sites suggests that divergent patterns of habitat use persisted for at least 6 weeks after tagging, albeit for much smaller numbers of fish.

Taken together, acoustic tagging results and characteristics of fish captured at Sansum Narrows and Maple Bay are consistent with individual juvenile Chinook Salmon exhibiting different habitat use depending on their size and diet. Larger, more piscivorous fish appear to be collocating with age-0 Pacific Herring schools while smaller fish are occupying regions where zooplankton are more abundant. As smaller fish may also be unable to consume age-0 Pacific Herring (Chamberlin et al. 2017; Chapter 4), and as piscivory provides a growth advantage (Juanes and Conover 1994, Juanes et al. 2002, Litz et al. 2017, Davis et al. 2020), size and individual behaviour of juvenile Chinook Salmon appear to be interacting to regulate growth potential. Our acoustic tagging occurred in mid-September, coincident with the period where we documented marked declines in the availability of zooplankton prey in 2015 (Chapter 4). Many

juvenile Chinook Salmon are believed to emigrate out of the Salish Sea in fall (Neville et al. 2015) and most individuals that we tagged in 2017 had indeed left the Southern Gulf Islands by the end of October (35 of 39 emigrants; Rechisky et al. 2019). Given that our study of distribution occurred during a period where feeding on zooplankton may be becoming progressively less profitable, we may also have failed to fully capture differences in habitat use related to different foraging strategies.

While piscivory likely facilitates more rapid growth of juvenile Chinook Salmon (Litz et al. 2017, Davis et al. 2020), our results suggest that this strategy was only available to large individuals. The prey length to predator length ratios that we measured (~ 0.4) for juvenile Chinook Salmon consuming age-0 Pacific Herring were close to the maximum ratios reported by Brodeur (1991) for juvenile Chinook Salmon and their prey in the California Current. Consumption of Pacific Herring was also strongly related to juvenile Chinook Salmon length. Size dependence in the transition to piscivory has also been inferred for juvenile Chinook Salmon in Puget Sound (Chamberlin et al. 2017). It is possible that the larger, piscivorous Chinook Salmon that we encountered had transitioned to piscivory soon after ocean entry, and that the resulting growth advantage had allowed them to keep pace with the cohort of age-0 Pacific Herring that was available to them. However, while consumption of Pacific Herring soon after ocean entry was documented in historical studies within the Southern Gulf Islands (Healey 1980, Argue et al. 1986), we found that Pacific Herring did not become important in diets until August in 2015 (Chapter 4). Scale circulus spacing-based growth rates of juvenile Cowichan River Chinook Salmon captured at Sansum Narrows were higher over reconstructed size intervals of 45-70 mm, corresponding to the period prior to mean size at ocean entry (Atkinson 2019); and 114-173 mm, corresponding to microtrolling-sampled fish smaller than the minimum size at which consumption of Pacific Herring was observed. These results suggest that growth rate well prior to the onset of piscivory, and perhaps prior to ocean entry, may be related to size, diet and growth in late summer.

While most recent studies on marine growth and survival of juvenile salmon focus on the influence of environmental factors (e.g. Hertz et al. 2015, Journey et al. 2020, Henderson et al. 2019) it is important to remember that growth rate in salmonids is also under genetic control and

may be linked to other traits (Vøllestad and Quinn 2003, Hard et al. 2008, Debes et al. 2020, Monnet et al. 2020). Our results suggest that even at very small sizes (45-55 mm FL) fish that would subsequently be captured at Sansum Narrows were growing faster than those that would subsequently be captured at Maple Bay. It is possible that these individuals were expressing a rapid growth genotype throughout their early life. If this is the case, the transition to piscivory associated with this genotype would represent a form of positive feedback, where genetically controlled growth potential mediated environmentally controlled growth potential. Alternatively, it is possible that external factors during early growth in freshwater, for example lotic microhabitat occupation, provided an initial growth advantage that was then maintained through ontogeny. Evidence against this hypothesis is that early growth was greater for hatchery origin Cowichan River Chinook Salmon captured at Sansum Narrows than for those captured at Maple Bay, although these differences were less than those for wild fish. It is also possible that late summer diet, size and growth was linked to ocean entry phenology of juvenile Chinook Salmon. Ocean-type Chinook Salmon exhibit a bimodal ocean entry strategy throughout their range (Apgar et al. 2020) including in the Cowichan River (Atkinson 2019). It is intriguing that the growth rate of Chinook Salmon captured at Sansum Narrows was not significantly greater than those captured at Maple Bay over a size interval of 75-114 mm, corresponding to a period shortly after ocean entry. In fact, with the exception of hatchery-origin fish in 2015, juvenile Cowichan River Chinook Salmon which were captured at Maple Bay had a growth advantage over those captured at Sansum Narrows for at least part of this size interval. Examination of Figure 5.13 also suggests that at least in 2016, fish captured at Maple Bay experienced minimum scale circulus spacing at a smaller size than those captured at Sansum Narrows. A minimum in circulus spacing followed by wider circuli has been interpreted as a marker for changes in growth rate at ocean entry (Koo 1967; Reimers 1971; Tovey 1999). Ocean-type Chinook Salmon which migrate to the ocean as fry were originally considered to be surplus to the freshwater carrying capacity and not contribute to stock productivity (Healey 1991). While fry migrants are now known to contribute to adult returns (Atkinson 2019), the proportion of individuals migrating as fry is density dependent (Apgar et al. 2020), suggesting the intraspecific competition is involved in inducing migration. It is possible that juvenile Chinook Salmon which experienced poor initial growth in freshwater and migrated to sea earlier to avoid intraspecific

competition were more common in catches at Maple Bay relative to Sansum Narrows. If this was the case, it implies that individuals which experienced faster growth in freshwater entered the ocean later, and that for a period their growth rates may have fallen behind their initially slower growing, earlier migrating compatriots. The initial growth rate advantage was subsequently reestablished, with initially faster growing fish extending a size advantage through late summer, potentially facilitating a transition to piscivory. This hypothesis relating initial freshwater growth rate to ocean entry timing and subsequent early marine growth is speculative but would be testable using a combination of otolith microchemistry and microstructure (e.g. Freshwater et al. 2016).

Disentangling the role of genetic and environmental influences acting at different ontogenetic stages on variation in late summer size and growth of juvenile Chinook Salmon is beyond the scope of the present study. Nevertheless, our results suggest that growth potential of these fish is not simply a product of environmental variability across which they are passively distributed. Rather, individual prior growth histories and movement behaviors interact with fine scale spatial variation in prey availability to regulate growth.

A growing body of research has suggested that pinniped predation may play a role in declining Pacific Salmon productivity (Chasco et al. 2017, Thomas et al. 2017, Nelson et al. 2019). Within our study area, harbour seal scat collected at the Burial Island haul-out (Figure 5.6) during the summer of 2017 contained Chinook Salmon remains (S. Majewski, C. Nordstrom and W. Duguid, unpublished data). Also, PIT tags applied to Chinook Salmon as part of the larger Cowichan River survival study (Pellett et al. in prep), including some applied by microtrolling between August and October, were detected on Burial Island and other haul-outs in the Southern Gulf Islands (K. Pellett and W. Duguid, unpublished data). While spatial patterns in the occurrence of harbour seals on the surface during mobile tracking were marginally non-significant, the different patterns of distribution that we observed for juvenile Chinook Salmon tagged at Maple Bay and Sansum Narrows suggest potential for differential predation exposure. Pacific Herring are a primary prey of harbour seals (Thomas et al. 2017), and if larger, faster growing juvenile Chinook Salmon collocate with age-0 Pacific Herring they may expose themselves to greater predation risk. If growth during the first marine summer increases survival,

and growth is accelerated by piscivory, a survival trade-of may occur if piscivory increases predation risk (Tymchuck et al. 2007).

5.5.4 *Conclusion*

Given the cultural, economic and ecological importance of Pacific Salmon, population level recruitment trends and variability will continue to be a key research focus around the Pacific Rim. Evidence that early marine survival plays a key role in regulating recruitment is compelling (Beamish and Bouillon 1993, Welch et al. in review). While a reductionist approach to the complexity of ecological systems is appealing, the results we present here a reminder that large-scale environmental factors do not influence the physiology of organisms in a vacuum. For juvenile Pacific Salmon, both local scale environmental variability and individual characteristics influence growth. These factors likely interact with large spatial and temporal scale environmental variability to regulate survival and recruitment.

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5.7 Tables

Table 5.1. Individual counts of for zooplankton groups in 30 m and 60 m vertical tows with a 50 cm diameter 350 µm ring net at Maple Bay and Sansum Narrows on 6 days between 30 August and 7 September 2017. Analysis category corresponds to the aggregation of these groups for analysis in Chapter 4. The estimated individual mass is based on mean individual mass calculated for each zooplankton group in 2015.

		Maple Bay Count		Sansum Narrows Count			
Zooplankton Group	Analysis Category	30 m	60 m	30 m	60 m	Total Count	Individual Mass (g)
Calanoid Copepod	Copepod	67	10077	123	2392	12659	0.00033
Caridean Zoea	Decapod Zoea	974	2842	458	749	5023	0.00041
Brachyuran Zoea	Decapod Zoea	1579	1613	676	914	4782	0.00053
Gelatinous Zooplankton	Gelatinous Zooplankton	273	553	611	976	2413	NA
Themisto sp.	Themisto sp.	32	297	36	225	590	0.00051
Other	Other	44	163	73	111	391	NA
Porcellanid Zoea	Decapod Zoea	120	137	61	63	381	0.00170
Grapsid Megalopa	Decapod Megalopa	32	49	34	42	157	0.00131
Cancrid Megalopa	Decapod Megalopa	32	55	10	10	107	0.00371
Cyphocaris challengeri	Gammarid	7	52	6	41	106	0.00295
Xanthid Megalopa	Decapod Megalopa	19	35	12	23	89	0.00128
Pagurid Zoea	Other	22	27	15	22	86	0.00084
Euphausiid	Euphausiid	0	57	0	0	57	0.00026
Polychaete	Polychaete	3	20	9	7	39	0.00032
Insect	Insect	3	1	13	2	19	0.00149
Larval Fish	Larval Fish	7	4	3	4	18	0.00063
Pagurid Megalopa	Decapod Megalopa	0	1	1	5	7	0.00124
Majid Megalopa	Decapod Megalopa	0	1	0	5	6	0.00096
Caridean Post Larva	Decapod Post Larvae	0	0	4	1	5	0.00150
Unid. or Other Amphipod	Unid. or Other Amphipod	5	0	0	0	5	0.00060
Hyperia medusarum	Hyperia medusarum	0	4	0	1	5	0.00065
Hyperoche sp.	Hyperoche sp.	1	1	1	1	4	0.00075
Gammarid Amphipod	Gammarid	0	0	3	0	3	0.01210
Pinnotherid Megalopa	Decapod Megalopa	0	2	0	1	3	0.00089
Caligid Copepod	Copepod	0	0	1	1	2	0.00100
Pteropod	Pteropod	0	0	0	1	1	0.06970
Unid. Decapod Megalopa	Decapod Megalopa	1	0	0	0	1	0.00128
Monstrilloidid Copepod	Copepod	0	0	0	1	1	NA

Table 5.2. Number of Chinook Salmon less than 300 mm in FL captured at Maple Bay and Sansum Narrows in 2015 and 2016 by Pacific Biological Station molecular genetics laboratory Chinook Salmon stock codes and region and/or life history type groupings. Four hybrid Chinook/Coho Salmon (as identified by genetics) were also captured at these sites in each of 2015 and 2016 (Araujo et al. in prep).

		2015		2016	
DFO Stock Codes	Stock Grouping	Maple Bay	Sansum Narrows	Maple Bay	Sansum Narrows
Cowichan	Cowichan River	57	42	267	239
Bessette	Fraser/Thompson Stream Type			5	
Bowron	Fraser/Thompson Stream Type			1	2
Chilko	Fraser/Thompson Stream Type			1	3
Clearwater	Fraser/Thompson Stream Type	2		3	1
Elkin_R	Fraser/Thompson Stream Type	1			
Goat	Fraser/Thompson Stream Type				1
McGregor	Fraser/Thompson Stream Type	2	4		
Morkill	Fraser/Thompson Stream Type				2
N_Thom@Main	Fraser/Thompson Stream Type			1	1
Nazko	Fraser/Thompson Stream Type				3
Nechako	Fraser/Thompson Stream Type			2	2
U_Coldwat_SP	Fraser/Thompson Stream Type		1	2	1
Chilliwack_F	Lower Fraser Ocean Type	6	4	25	31
Harrison	Lower Fraser Ocean Type	4	6	14	15
Elwha_F	Other				1
Chemainus	Other East Coast VI		1		
Nanaimo_F	Other East Coast VI			3	5
Nanaimo_SU	Other East Coast VI		1	4	6
Puntledge_F	Other East Coast VI	1	5	10	19
Green@Kendal_F	Puget Sound		1	5	18
Nooksack_SP@Ke	Puget Sound		1	2	4
Snohomish_R	Puget Sound	4	3		1
Soos_Cr_H	Puget Sound	4	3	5	13
L_Adams	South Thompson Ocean Type			7	3
L_Shuswap	South Thompson Ocean Type	3	3		
L_Thompson	South Thompson Ocean Type			3	8
Maria_Slough	South Thompson Ocean Type			1	
Gold_R	West Coast VI			1	1
Totals		84	75	362	380

Table 5.3. Regression statistics for generalized additive models (GAMs) relating the log-odds of presence and biomass density (g/m^3) of three different zooplankton groups to site, day of the year, tow depth (30 or 60 m), and stage of the tide (see methods for details of model specification) for 100 zooplankton tows at Sansum Narrows and Maple Bay over 6 days from 30 August to 7 September 2017 (25 tows at each depth at each site). Site and tow depth were included in the model as parametric fixed effects and day of the year was included as parametric continuous variable. Models include site- and tow depth-specific smooth terms relating response variables to a continuous variable for stage of the tide. Terms which were significant ($\alpha = 0.05$) based on approximate P-values are indicated in bold. Note that parametric test statistics were z for the binomial models and t for the gamma models while test statistics for smooth terms were Chi squared for the binomial models and F for the gamma models.

GAM Response (Distribution: Link)	Type of Term	Variable	Level	Coeff.	Std. Error	z or t	est. df	Chi.sq or F	P-value	Deviance Explained
Decapod Zoea g/m3										69.8%
(Gamma: Log)	Parametric Factor	Site	Sansum Narrows	**-0.723**	**0.074**	**-9.72**			**<0.001**	
	Parametric Factor	Tow Depth	60 m	-0.063	0.073	-0.86			0.390	
	Parametric Continuous	DOY		**-0.128**	**0.013**	**-9.70**			**<0.001**	
	Smooth	Stage of Tide	Maple Bay 30 m				**2.09**	**5.59**	**<0.001**	
	Smooth	Stage of Tide	Sansum Narrows 30 m				**1.92**	**3.82**	**0.002**	
	Smooth	Stage of Tide	Maple Bay 60 m				**1.60**	**2.08**	**0.019**	
	Smooth	Stage of Tide	Sansum Narrows 60 m				<0.01	<0.01	0.387	
Decapod Megalopa Presence										40.8%
(Binomial: Logit)	Parametric Factor	Site	Sansum Narrows	-1.673	1.155	-1.45			0.148	
	Parametric Factor	Tow Depth	60 m	1.425	1.031	1.38			0.167	
	Parametric Continuous	DOY		-0.363	0.208	-1.75			0.081	
	Smooth	Stage of Tide	Maple Bay 30 m				0.01	0.01	0.345	
	Smooth	Stage of Tide	Sansum Narrows 30 m				1.53	3.93	0.068	
	Smooth	Stage of Tide	Maple Bay 60 m				<0.01	0.00	1.000	
	Smooth	Stage of Tide	Sansum Narrows 60 m				1.20	2.65	0.103	
Decapod Megalopa g/m3										51.7%
(Gamma: Log)	Parametric Factor	Site	Sansum Narrows	**-0.665**	**0.115**	**-5.78**			**<0.001**	
	Parametric Factor	Tow Depth	60 m	**-0.253**	**0.114**	**-2.21**			**0.030**	
	Parametric Continuous	DOY		**-0.099**	**0.020**	**-4.97**			**<0.001**	
	Smooth	Stage of Tide	Maple Bay 30 m				0.92	0.47	0.215	
	Smooth	Stage of Tide	Sansum Narrows 30 m				<0.01	0.00	0.457	
	Smooth	Stage of Tide	Maple Bay 60 m				<0.01	0.00	0.499	
	Smooth	Stage of Tide	Sansum Narrows 60 m				**2.67**	**5.56**	**0.001**	
Copepod Presence										36.9%
(Binomial: Logit)	Parametric Factor	Site	Sansum Narrows	-0.089	0.704	-0.13			0.899	
	Parametric Factor	Tow Depth	60 m	34.440	>999	0.00			1.000	
	Parametric Continuous	DOY		-0.001	0.121	-0.01			0.993	
	Smooth	Stage of Tide	Maple Bay 30 m				0.57	0.80	0.243	
	Smooth	Stage of Tide	Sansum Narrows 30 m				**1.58**	**5.03**	**0.035**	
	Smooth	Stage of Tide	Maple Bay 60 m				<0.01	0.00	1.000	
	Smooth	Stage of Tide	Sansum Narrows 60 m				<0.01	0.00	1.000	
Copepod g/m3										74.6%
(Gamma: Log)	Parametric Factor	Site	Sansum Narrows	-0.218	0.196	-1.11			0.270	
	Parametric Factor	Tow Depth	60 m	**3.457**	**0.195**	**17.74**			**<0.001**	
	Parametric Continuous	DOY		-0.045	0.035	-1.28			0.205	
	Smooth	Stage of Tide	Maple Bay 30 m				1.22	0.72	0.169	
	Smooth	Stage of Tide	Sansum Narrows 30 m				<0.01	0.00	0.375	
	Smooth	Stage of Tide	Maple Bay 60 m				**1.73**	**2.33**	**0.016**	
	Smooth	Stage of Tide	Sansum Narrows 60 m				1.23	0.72	0.174	

Table 5.4. Regression statistics for generalized additive mixed effects models (GAMMs) relating the log-odds of fish aggregation presence and the nautical area backscattering coefficient (S_A) attributable to fish aggregations, other fish, and plankton to site, day of the year, mean water depth, and stage of the tide. The S_A attributable to plankton was modelled separately for 0-30 m and 30-60 m depth strata to facilitate comparison with zooplankton tows. Site was included in the model as a parametric fixed effect and day of the year and mean water depth were included as parametric continuous variables. Transect was included in the model as a random effect. Terms which were significant ($\alpha = 0.05$) based on approximate P-values are indicated in bold. Note that parametric test statistics were z for the binomial model and t for the gamma models while test statistics for smooth terms were Chi squared for the binomial model and F for the gamma models.

GAMM Response (Distribution: Link)	Type of Term	Variable	Level	Coeff.	Std. Error	z or t	est. df	Chi.sq or F	P-value	Deviance Explained
Presence of Fish Aggregations										21.1%
(Binomial: Logit)	Parametric Factor	Site	Sansum Narrows	**3.451**	**1.124**	**3.07**			**0.002**	
	Parametric Continuous	DOY		-0.170	0.116	-1.47			0.142	
	Parametric Continuous	Mean Depth		-0.003	0.010	-0.31			0.754	
	Smooth	Stage of Tide	Sansum Narrows				0.06	0.068	0.342	
	Smooth	Stage of Tide	Maple Bay				0.79	1.400	0.165	
	Smooth (Random Effect)	Transect					0.00	0.000	0.727	
38 kHz Fish Aggregation S_A m^2 nmi^{-2}										44.6%
(Gamma: Log)	Parametric Factor	Site	Sansum Narrows	**1.720**	**0.176**	**9.78**			**<0.001**	
	Parametric Continuous	DOY		-0.011	0.033	-0.33			0.161	
	Parametric Continuous	Mean Depth		-0.003	0.002	-1.41			0.744	
	Smooth	Stage of Tide	Sansum Narrows				**2.40**	**12.076**	**<0.001**	
	Smooth	Stage of Tide	Maple Bay				**1.89**	**3.203**	**0.004**	
	Smooth (Random Effect)	Transect					0.00	0.000	0.825	
38 kHz Other Fish S_A m^2 nmi^{-2}										60.3%
(Gamma: Log)	Parametric Factor	Site	Sansum Narrows	**1.165**	**0.119**	**9.81**			**<0.001**	
	Parametric Continuous	DOY		**-0.055**	**0.018**	**-3.03**			**0.003**	
	Parametric Continuous	Mean Depth		**0.004**	**0.002**	**2.68**			**0.008**	
	Smooth	Stage of Tide	Sansum Narrows				**2.00**	**4.340**	**0.001**	
	Smooth	Stage of Tide	Maple Bay				**2.29**	**6.660**	**<0.001**	
	Smooth (Random Effect)	Transect					4.59	0.462	0.075	
200 kHz 0-30 m Plankton S_A m^2 nmi^{-2}										38.5%
(Gamma: Log)	Parametric Factor	Site	Sansum Narrows	**1.444**	**0.187**	**7.707**			**<0.001**	
	Parametric Continuous	DOY		**-0.129**	**0.034**	**-3.73**			**<0.001**	
	Parametric Continuous	Mean Depth		-0.004	0.002	-1.72			0.088	
	Smooth	Stage of Tide	Sansum Narrows				**2.44**	**10.967**	**<0.001**	
	Smooth	Stage of Tide	Maple Bay				**1.82**	**2.358**	**0.016**	
	Smooth (Random Effect)	Transect					0.00	0.000	0.986	
200 kHz 30-60 m Plankton S_A m^2 nmi^{-2}										31.1%
(Gamma: Log)	Parametric Factor	Site	Sansum Narrows	**1.121**	**0.131**	**8.573**			**<0.001**	
	Parametric Continuous	DOY		-0.030	0.023	-1.328			0.186	
	Parametric Continuous	Mean Depth		-0.001	0.002	-0.309			0.757	
	Smooth	Stage of Tide	Sansum Narrows				0.00	0.000	0.877	
	Smooth	Stage of Tide	Maple Bay				**2.25**	**6.806**	**<0.001**	
	Smooth (Random Effect)	Transect					0.00	0.000	0.782	

Table 5.5 Sample size (N) and frequency of occurrence of different prey categories in the diets of juvenile ocean type Chinook Salmon at Sansum Narrows and Maple Bay in 2015 and 2016.

	Maple Bay		Sansum Narrows	
	2015	2016	2015	2016
N	68	323	59	315
Cephalopod	0.07	0.06	0.14	0.03
Copepod	0.41	0.53	0.14	0.27
Decapod	0.90	0.89	0.51	0.65
Euphausiid	0.06	0.07	0.17	0.15
Fish	0.32	0.39	0.39	0.48
Gammarid	0.06	0.01	0.07	0.03
Hyperiid	0.88	0.80	0.58	0.46
Insect	0.09	0.08	0.00	0.07
Polychaete	0.01	0.18	0.00	0.10
Pteropod	0.06	0.03	0.03	0.04

Table 5.6. Results of PERMANOVAs comparing presence and absence of different juvenile Chinook Salmon prey groups by site for samples collected between July and October 2015 and 2016 at Maple Bay and Sansum Narrows. Diet samples were aggregated into groups of 5-7 (target 6 where possible) and presence (1) and absence (0) scores for each prey category were averaged prior to analysis. Below each PERMANOVA result is a corresponding result of a test of homogeneity of dispersion between sites. Significant results at a Bonnferoni-corrected critical P value of 0.0125 are indicated in bold.

Year	Period	Test	Variable	df	Sums of Squares	F	R^2	P
2015	July-August	PERMANOVA	Site	**1**	**0.12**	**5.59**	**0.41**	**0.012**
			Residual	8	0.17			
		Homogeneity of Dispersion	Site	1	0.01	3.35		0.116
	September-October	PERMANOVA	Site	1	0.2	5.12	0.42	0.021
			Residual	7	0.27			
		Homogeneity of Dispersion	Site	1	0.01	1.28		0.318
2016	July-August	PERMANOVA	Site	**1**	**0.28**	**13.36**	**0.28**	**0.001**
			Residual	35	0.74			
		Homogeneity of Dispersion	Site	**1**	**0.04**	**13.11**		**0.002**
	September-October	PERMANOVA	Site	**1**	**0.76**	**19.24**	**0.24**	**0.001**
			Residual	61	2.42			
		Homogeneity of Dispersion	Site	**1**	**0.09**	**27.91**		**0.001**

Table 5.7. Regression statistics for generalized linear models (gamma distribution, log link) relating the an index of growth rate (mean circulus spacing) to capture site, year, and origin (hatchery or wild) for Cowichan River Chinook Salmon during four periods of growth during their first year of life. Bold text indicates where the indicated level of a term was significantly different from the base level (not shown); the Bonferonni-corrected critical P-value for rejecting the null hypothesis was 0.0125.

GLM Response (df)	Variable	Level	Coeff.	Std. Error	t	P-value
Growth Index 45 mm to 70 mm (526)						
	Site	**Sansum Narrows**	**0.061**	**0.015**	**4.069**	**<0.001**
	Year	2016	-0.038	0.021	-1.789	0.074
	Origin (Hatch/Wild)	**Wild**	**0.073**	**0.019**	**3.827**	**<0.001**
Growth Index 70 mm to 114 mm (525)						
	Site	Sansum Narrows	-0.012	0.009	-1.275	0.203
	Year	2016	-0.014	0.013	-1.026	0.305
	Origin (Hatch/Wild)	**Wild**	**0.124**	**0.012**	**10.427**	**<0.001**
Growth Index 114 mm to 173 mm (376)						
	Site	**Sansum Narrows**	**0.061**	**0.015**	**4.045**	**<0.001**
	Year	2016	-0.061	0.038	-1.607	0.109
	Origin (Hatch/Wild)	Wild	0.047	0.041	1.155	0.248
Growth Index 173 mm to 187 mm (248)						
	Site	**Sansum Narrows**	**0.065**	**0.022**	**2.959**	**0.003**
	Year	2016	0.054	0.041	1.329	0.185
	Origin (Hatch/Wild)	Wild	0.005	0.027	0.179	0.858

Table 5.8. Regression statistics for a generalized additive mixed effects model (GAMM) relating the log-odds of catching a first ocean year Chinook Salmon to site, year, hour of the day, day of the year, depth, and stage of the tide. Both global and year and site specific smooth terms are included in the model for day of year and depth while only year and site specific smooth terms are included for tide and only a global smooth term is included for hour of the day. Site and year are also included in the model as parametric fixed effects and fishing event is included in the model as a random effect. Terms which are significant based on approximate P-values are indicated in bold. Plots of all significant smooths are provided in Figure 5.14.

Type of Term	Variable	Level	Coefficient	Std. Error	z	est. df	Chi.sq	P-value
Parametric Factor								
	Site	Sansum Narrows	-0.17	0.09689	-1.716			0.09
	Year	**2016**	**1.61**	**0.12349**	**13.076**			**<0.001**
Smooths								
	Tide	**Maple Bay 2015**				**1.79**	**9.709**	**0.005**
	Tide	**Sansum Narrows 2015**				**1.77**	**8.148**	**0.011**
	Tide	Maple Bay 2016				1.13	3.048	0.124
	Tide	**Sansum Narrows 2016**				**1.49**	**7.288**	**0.024**
	Hour of Day	Global				1.00	0.024	0.877
	Day of Year	**Maple Bay 2015**				**2.20**	**11.382**	**0.001**
	Day of Year	Sansum Narrows 2015				0.00	0.002	0.377
	Day of Year	**Maple Bay 2016**				**2.51**	**13.387**	**0.002**
	Day of Year	**Sansum Narrows 2016**				**1.13**	**2.901**	**0.048**
	Day of Year	Global				1.72	4.929	0.077
	Depth	**Global**				**1.97**	**37.888**	**<0.001**
	Depth	Maple Bay 2015				0.00	0.000	0.839
	Depth	**Sansum Narrows 2015**				**1.51**	**10.064**	**0.001**
	Depth	**Maple Bay 2016**				**1.22**	**4.744**	**0.021**
	Depth	Sansum Narrows 2016				0.00	0.000	1.000
	Fishing Event (RE)					157.20	199.816	<0.001

Table 5.9. Regression statistics for a generalized additive mixed effects model (GAMM) relating the log-odds of detecting acoustic tagged Chinook Salmon at individual monitoring stations in the vicinity of Sansum Narrows and Maple Bay (Figure 5.6) to the site at which tags were applied, the receiver group (colours in Figure 5.6); two dimensional smooths of UTM coordinates for each release group; smoothed effect of stage of the tide for each release group at each receiver group; and random effects of tag, monitoring station and date. * for smooth terms the degrees of freedom reported are effective degrees of freedom. Terms which are significant based on approximate P-values are indicated in bold. Plots of all significant one-dimensional smooths are provided in Figure 5.15.

Type of Term	Variable	Level	df*	Chi.sq	P-value
Parametric Factor					
	Tagging Site		1	2.254	0.13
	Receiver Group		2	1.598	0.45
Smooths					
	Easting X Northing	**Maple Bay Releases**	**11.33**	**45.736**	**<0.001**
	Easting X Northing	**Sansum Narrows Releases**	**13.99**	**66.026**	**<0.001**
	Tide	Maple Bay Tags X Maple Bay Area	0.64	0.993	0.240
	Tide	**Maple Bay Tags X North of Sansum**	**1.40**	**5.490**	**0.027**
	Tide	**Maple Bay Tags X South of Sansum**	**1.97**	**10.702**	**0.004**
	Tide	Sansum Narrows Tags X Maple Bay Area	0.19	0.215	0.327
	Tide	**Sansum Narrows Tags X North of Sansum**	**2.24**	**42.023**	**<0.001**
	Tide	**Sansum Narrows Tags X South of Sansum**	**2.86**	**39.931**	**<0.001**
	Tag (RE)		**42.51**	**358.480**	**<0.001**
	Waypoint (RE)		0.08	0.062	0.780
	Date (RE)		**6.27**	**20.502**	**0.001**

5.8 Figures

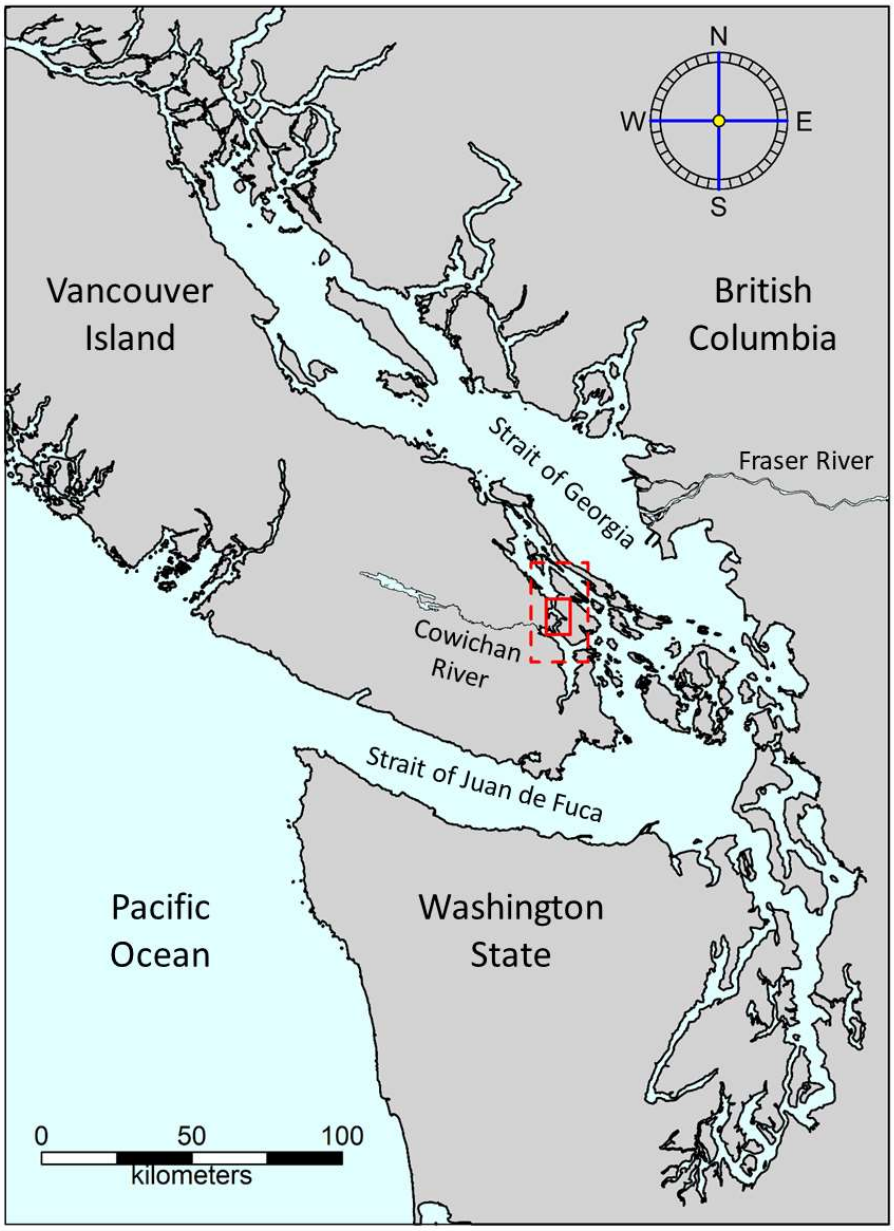


Figure 5.1. Overview map of the study region. The red solid rectangle indicates the extent of the region of oceanographic and juvenile Chinook Salmon sampling (Figure 5.2) while the red dashed rectangle indicates the study area for acoustic tagging investigations of juvenile Chinook Salmon movements (Figure 5.6).

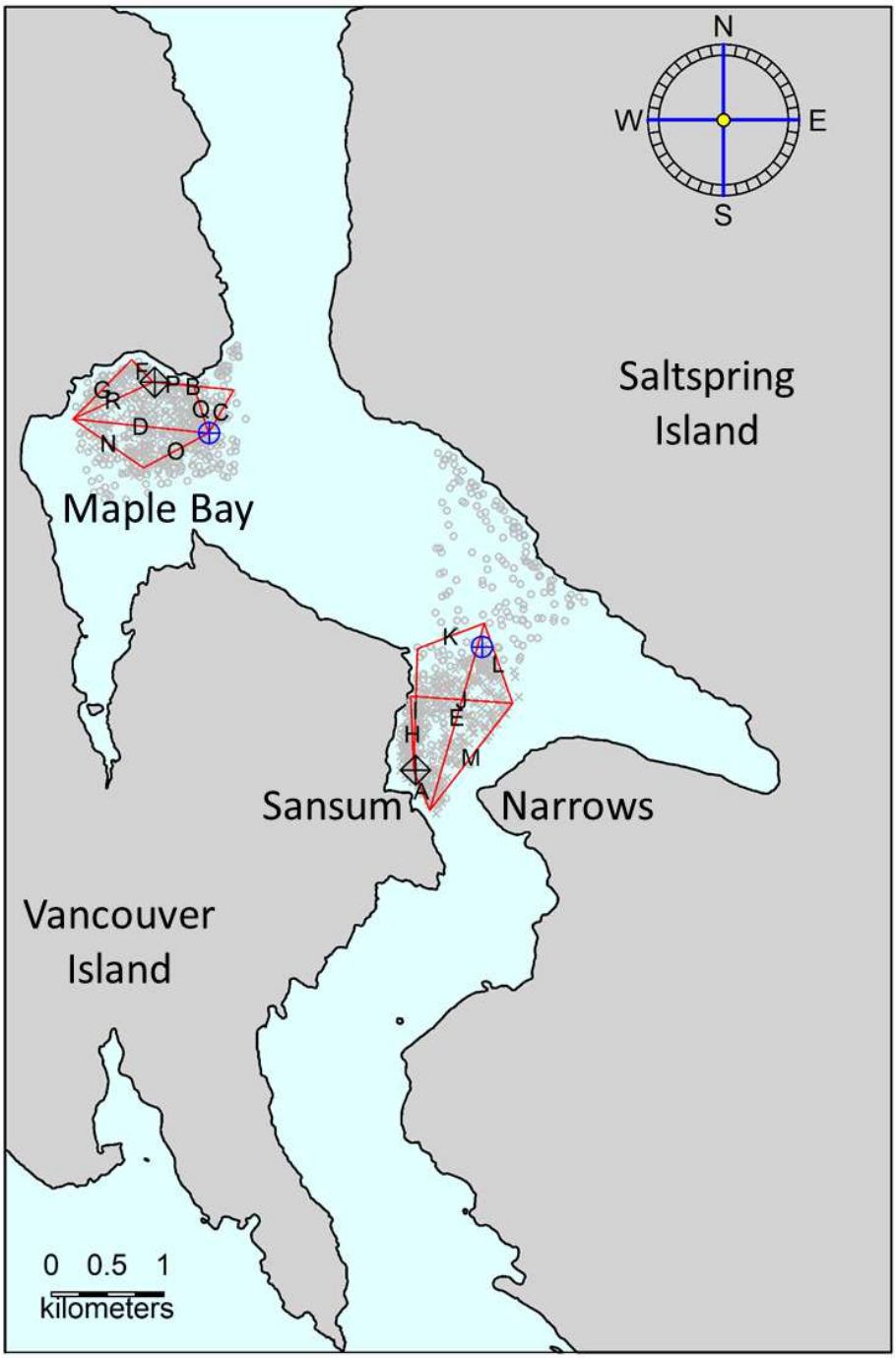


Figure 5.2. Map of Maple Bay and Sansum Narrows. Acoustic zooplankton fish profiler (AZFP) transects are indicated with red lines and black letters (details in Table 7.5). Blue crossed circles and black crossed diamonds indicate oceanographic stations where zooplankton tows were conducted in 2015 and 2017 respectively. Small grey circles and xs indicate locations of fish sampling events in 2015 and 2016 respectively.

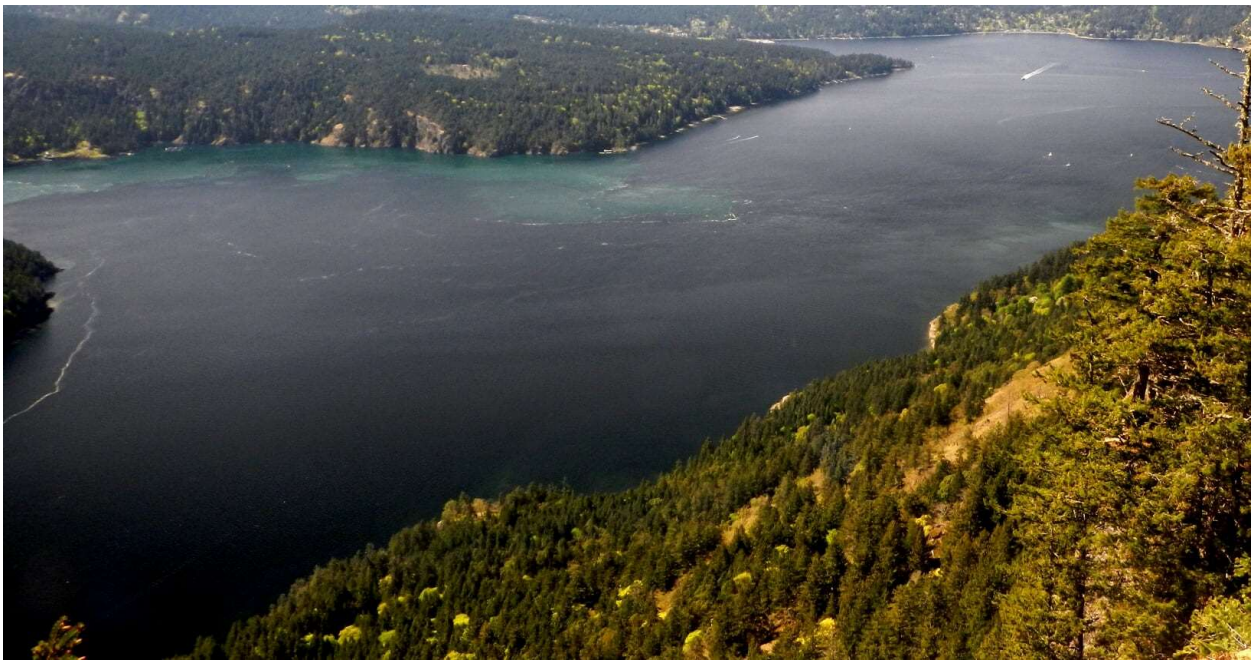


Figure 5.3. Study area viewed looking west from the top of Mount Maxwell on Saltspring Island on a large flood tide. The narrowest point of Sansum Narrows is just out of the image to the left. The flood tide jet can be seen as lighter coloured water moving along the Vancouver Island shore and out into open water. Maple Bay is in the top right of the image. The image was taken through a polarizing lens and has been colour enhanced.

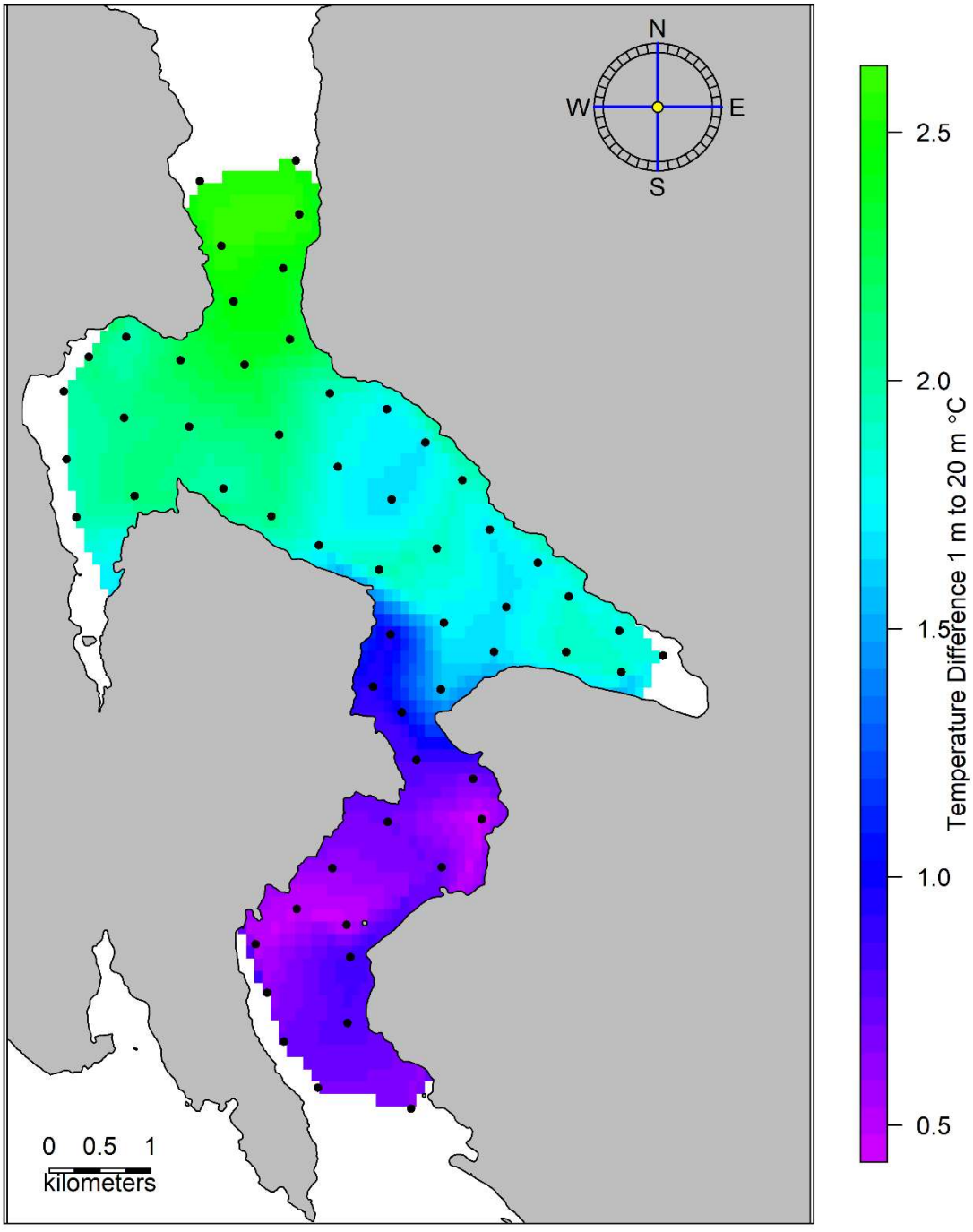
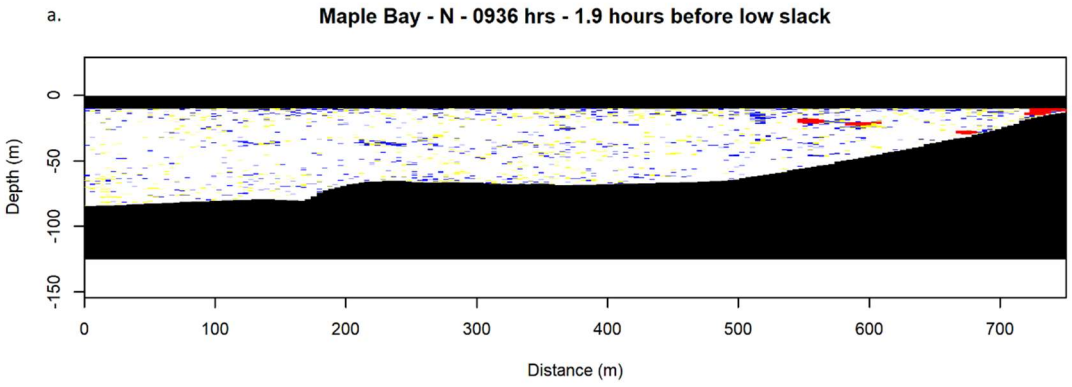
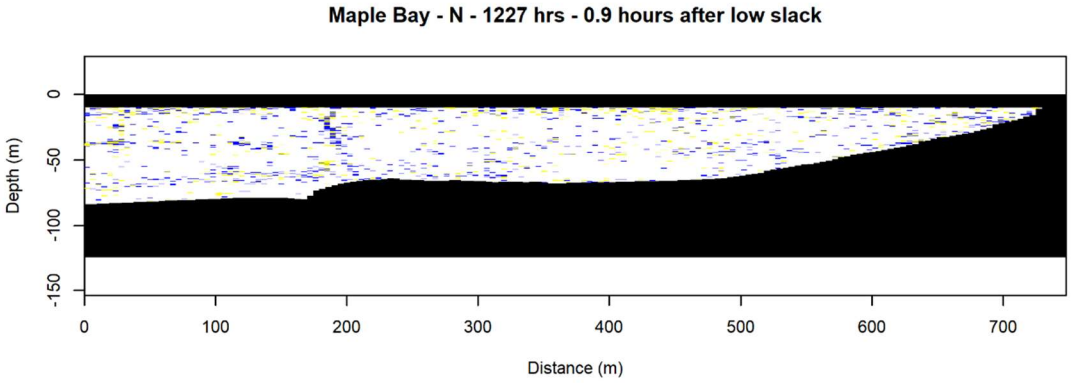
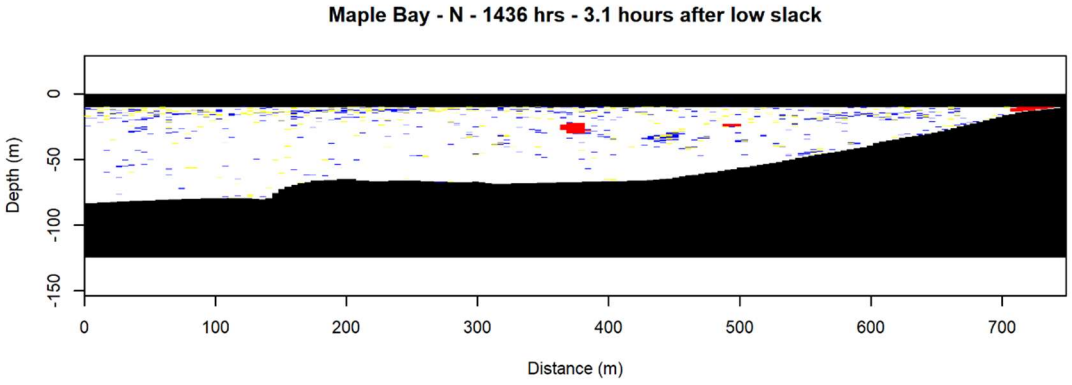


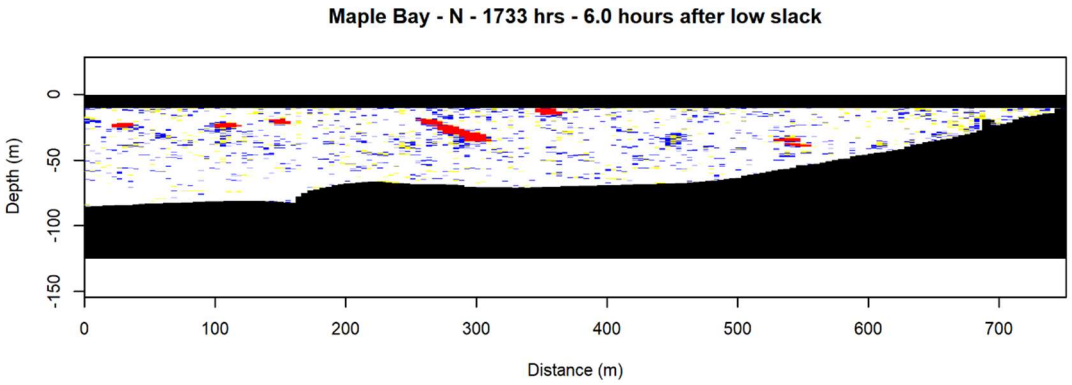
Figure 5.4. Linear interpolation of mean temperature difference between 1 m and 20 m for 575 CTD casts across 60 stations (black points) in the Sansum Narrows and Maple Bay area on 10 days between 16 September and 27 September 2017.

a.

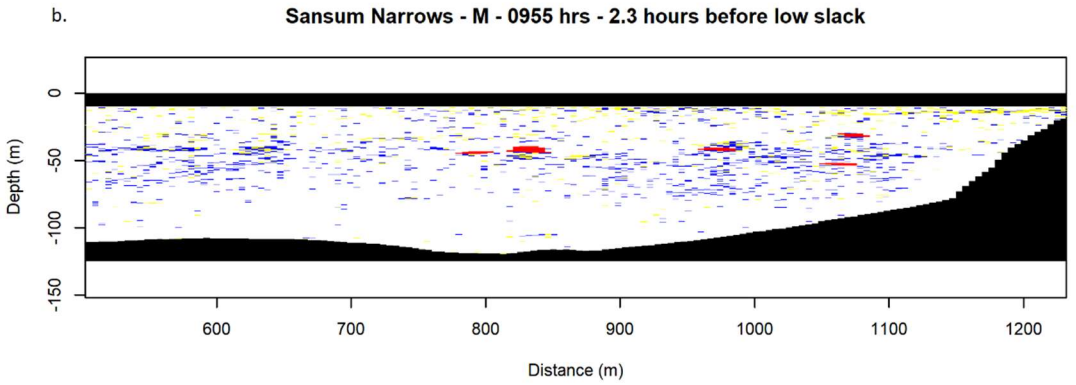

Maple Bay - N - 0936 hrs - 1.9 hours before low slack
Depth (m)
0
-50
-100
-150
0
100
200
300
400
500
600
700
Distance (m)

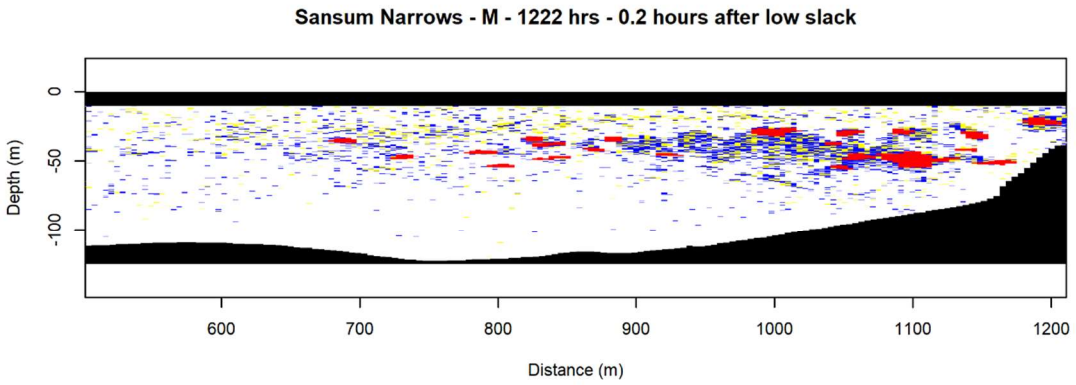

Maple Bay - N - 1227 hrs - 0.9 hours after low slack
Depth (m)
0
-50
-100
-150
0
100
200
300
400
500
600
700
Distance (m)

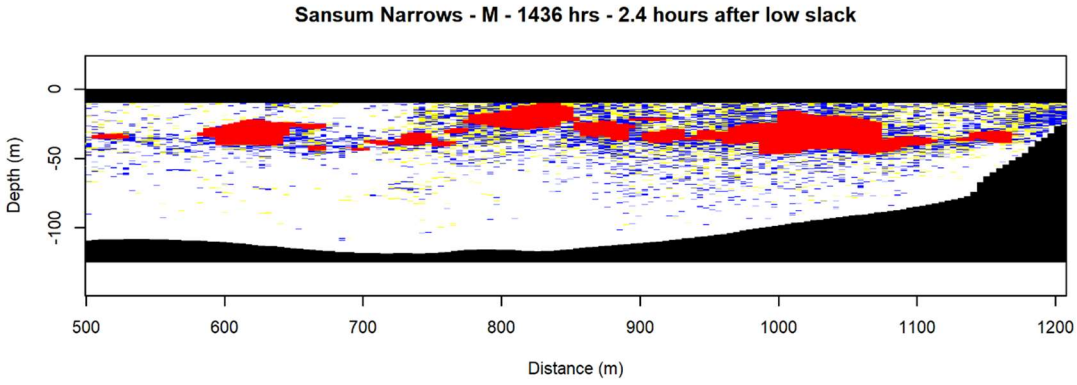

Maple Bay - N - 1436 hrs - 3.1 hours after low slack
Depth (m)
0
-50
-100
-150
0
100
200
300
400
500
600
700
Distance (m)


Maple Bay - N - 1733 hrs - 6.0 hours after low slack
Depth (m)
0
-50
-100
-150
0
100
200
300
400
500
600
700
Distance (m)

b.


Sansum Narrows - M - 0955 hrs - 2.3 hours before low slack
Depth (m)
0
-50
-100
-150
600
700
800
900
1000
1100
1200
Distance (m)


Sansum Narrows - M - 1222 hrs - 0.2 hours after low slack
Depth (m)
0
-50
-100
600
700
800
900
1000
1100
1200
Distance (m)


Sansum Narrows - M - 1436 hrs - 2.4 hours after low slack
Depth (m)
0
-50
-100
500
600
700
800
900
1000
1100
1200
Distance (m)

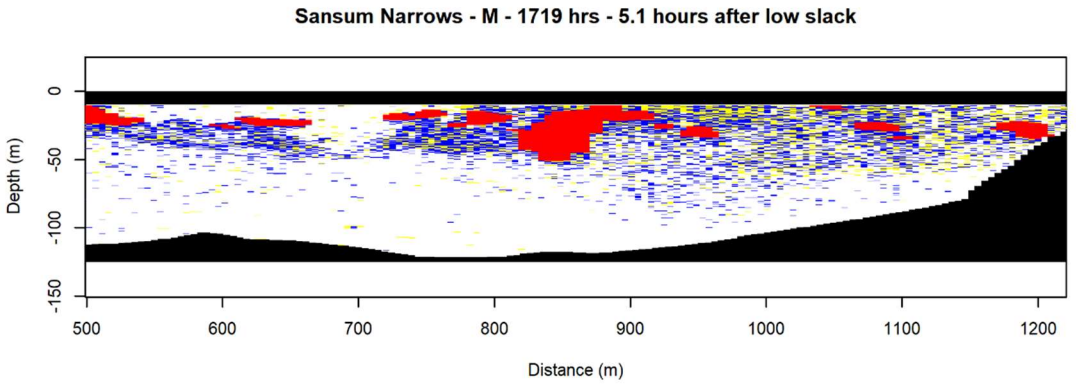

Sansum Narrows - M - 1719 hrs - 5.1 hours after low slack
Depth (m)
0
-50
-100
-150
500
600
700
800
900
1000
1100
1200
Distance (m)

Figure 5.5. (previous two pages) Echograms of a. transect N at Maple Bay and b. transect M in Sansum Narrows from late ebb to late flood on 6 and 7 September 2017 respectively. Noise-filtered S_v data exceeding a threshold of -80 dB re $1m^{-1}$ at one of three frequencies (38, 125 or 200 kHz) have been classified as fish aggregations (red), other fish (blue), plankton (yellow) or other (grey). Classification methodology is described in the text and transect locations are provided in Figure 5.2. Only the shoreward end of transect M is shown.

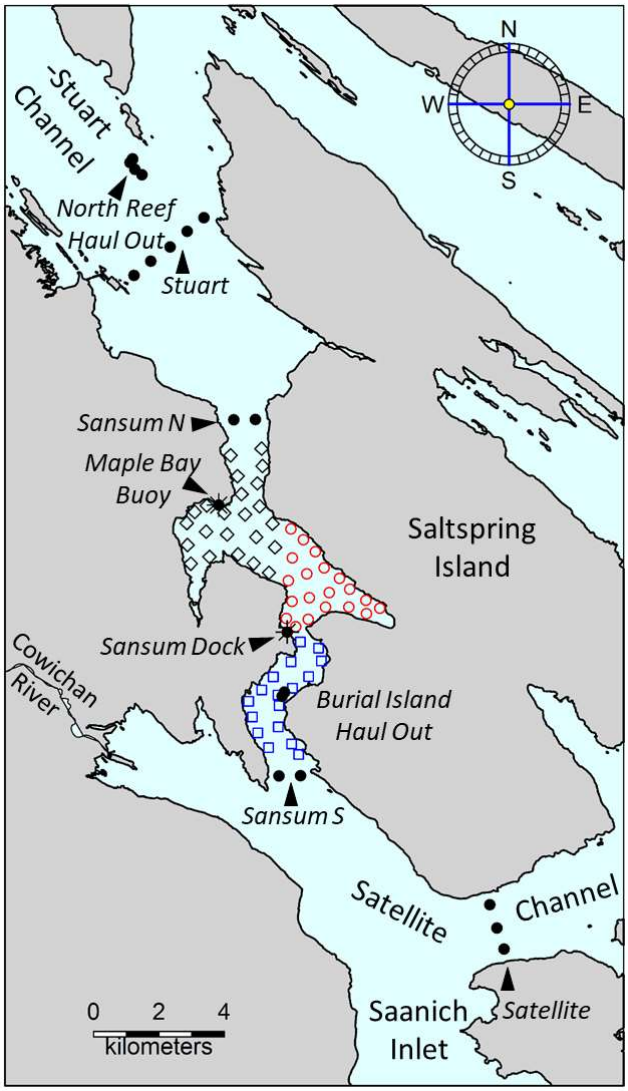


Figure 5.6. Map of monitoring efforts for acoustic tagged juvenile Chinook Salmon in 2017. Fish were captured and released adjacent to two tagging sites at Maple Bay and Sansum Narrows (black stars). Receivers (69 kHz) were deployed at these sites and in arrays indicated by filled black circles with array designations indicated with italic text and black arrows. Open symbols indicate the 60 listening stations that were occupied daily during 10 days of intensive mobile tracking during the 2 weeks following tagging. The colors and shapes indicate grouping of these listening stations for analysis of tidal patterns of fish movement as South of Sansum Narrows (blue squares), North of Sansum Narrows (red circles) and Maple Bay Area (black diamonds).

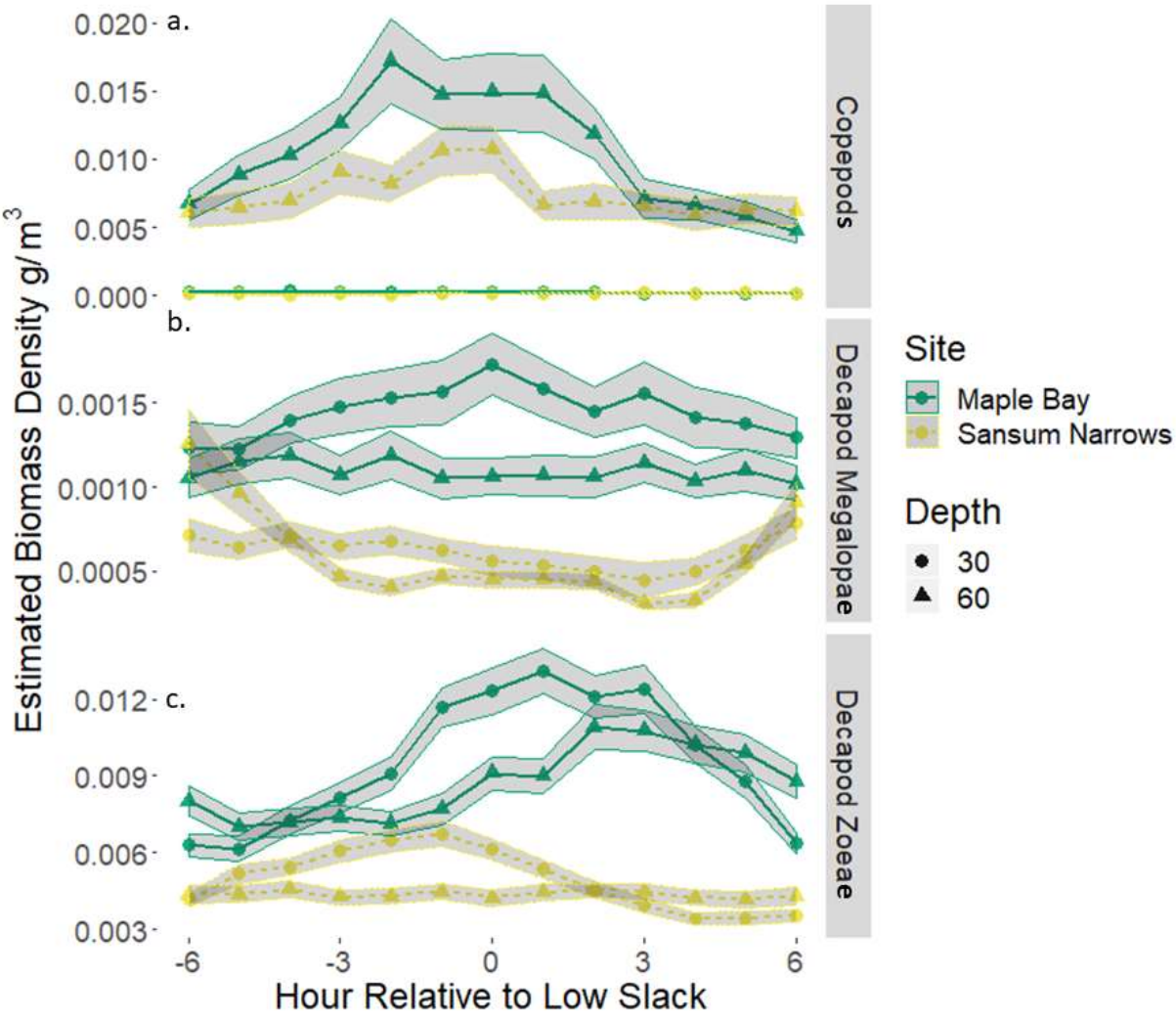


Figure 5.7. Simulated biomass densities (g/m^3) of a. copepods, b. decapod megalopae and c. decapod zoeae in 0-30 m and 0-60 m vertical plankton tows throughout the tidal cycle at Sansum Narrows and Maple Bay. Lines and ribbons indicate the mean and 95% confidence intervals for 100 simulations from the posterior distributions of the models detailed in Table 5.3. Details of the simulation procedure are described in the methods.

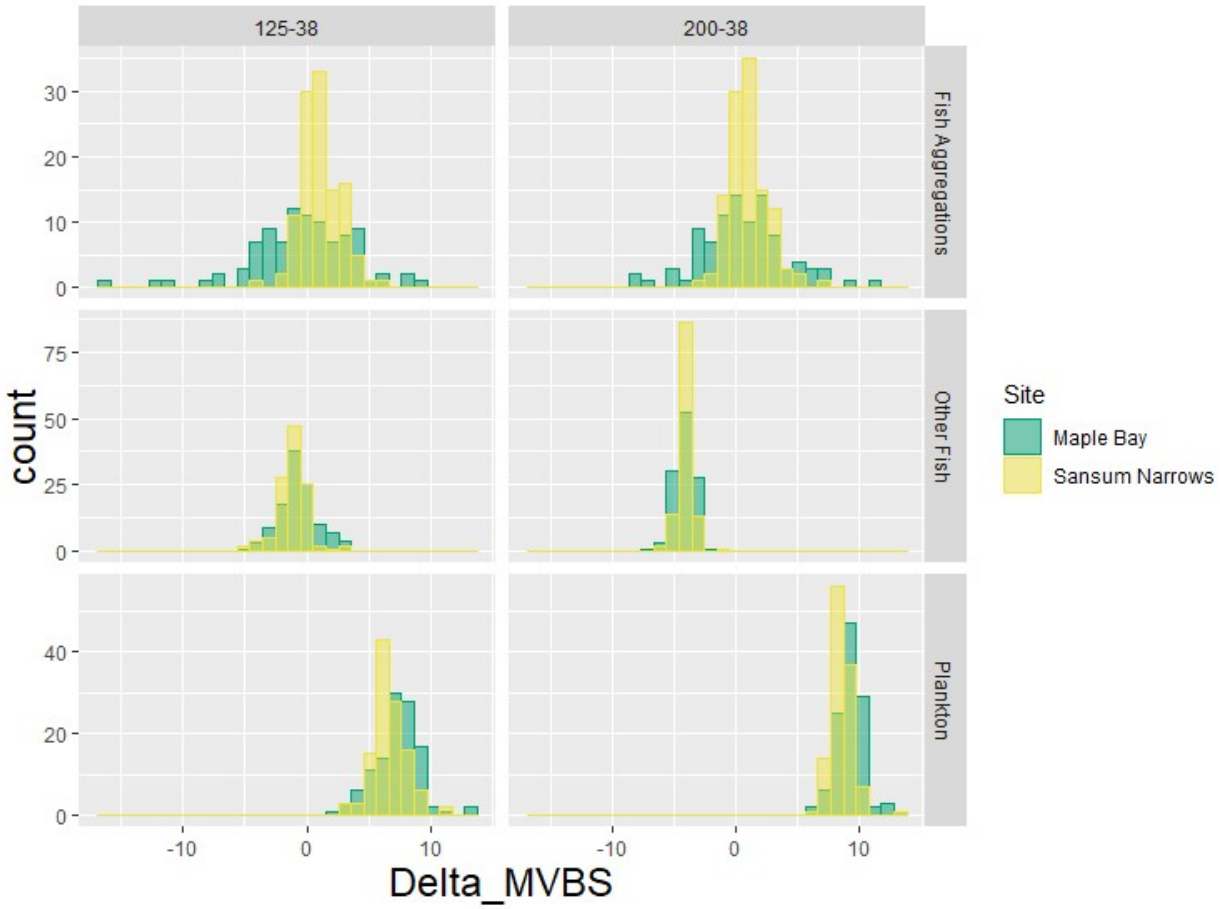


Figure 5.8. Histograms of transect mean values of $\Delta MVBS_{125\text{-}38}$ (left panels) and $\Delta MVBS_{200\text{-}38}$ (right panels) for fish aggregations (top), other fish (middle) and plankton (bottom).

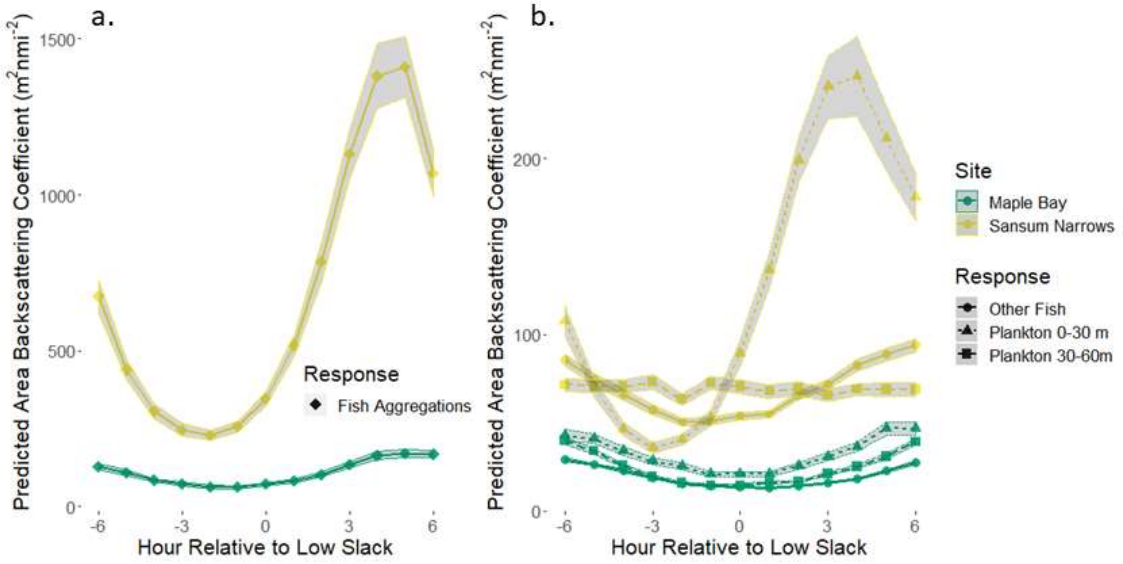


Figure 5.9. Simulated nautical area backscattering coefficients (S_A) attributable to a. fish aggregations (38 kHz) and b. zooplankton (200 kHz) in the 0-30 m and 30-60 m depth strata and other fish (38 kHz) throughout the water column at Sansum Narrows and Maple Bay. Lines and ribbons indicate the mean and 95% confidence intervals for 100 simulations from the posterior distributions of the models detailed in Table 5.4. Details of the simulation procedure are described in the methods.

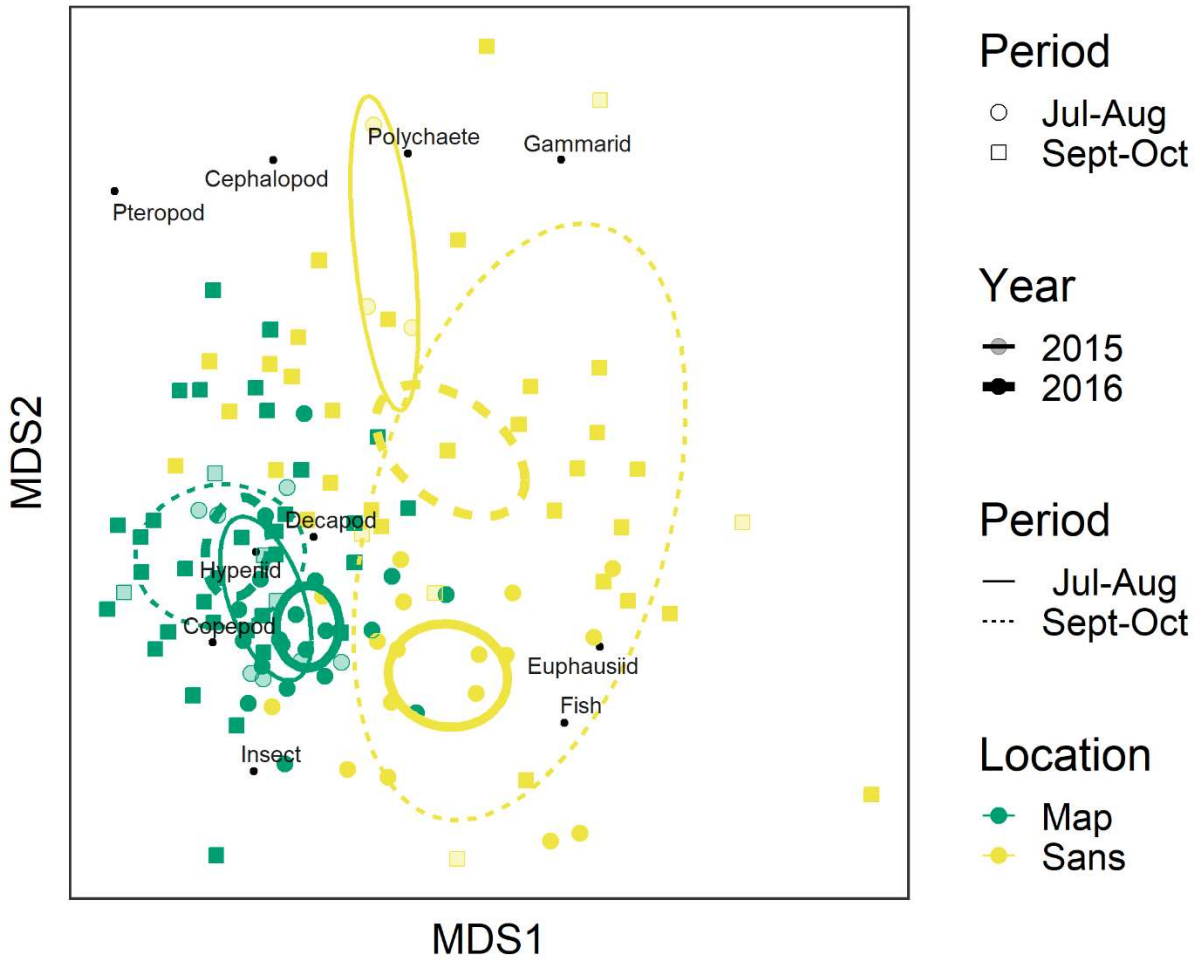


Figure 5.10. Non-metric multidimensional scaling (nMDS) plot (Stress = 0.22) of Bray-Curtis dissimilarity of mean presence or absence of prey categories (see methods for full definition) for juvenile ocean-type Chinook Salmon sampled at Sansum Narrows (Sans) and Maple Bay (Map) from July to October 2015 and 2016. Each point represents the mean presence (1) and absence (0) scores for random samples of 5-7 juvenile Chinook Salmon sampled during a specific time stratum at a specific site; time strata were (July-Aug and Sept-Oct). Ellipses indicate 95% confidence intervals of the mean location for each group of points.

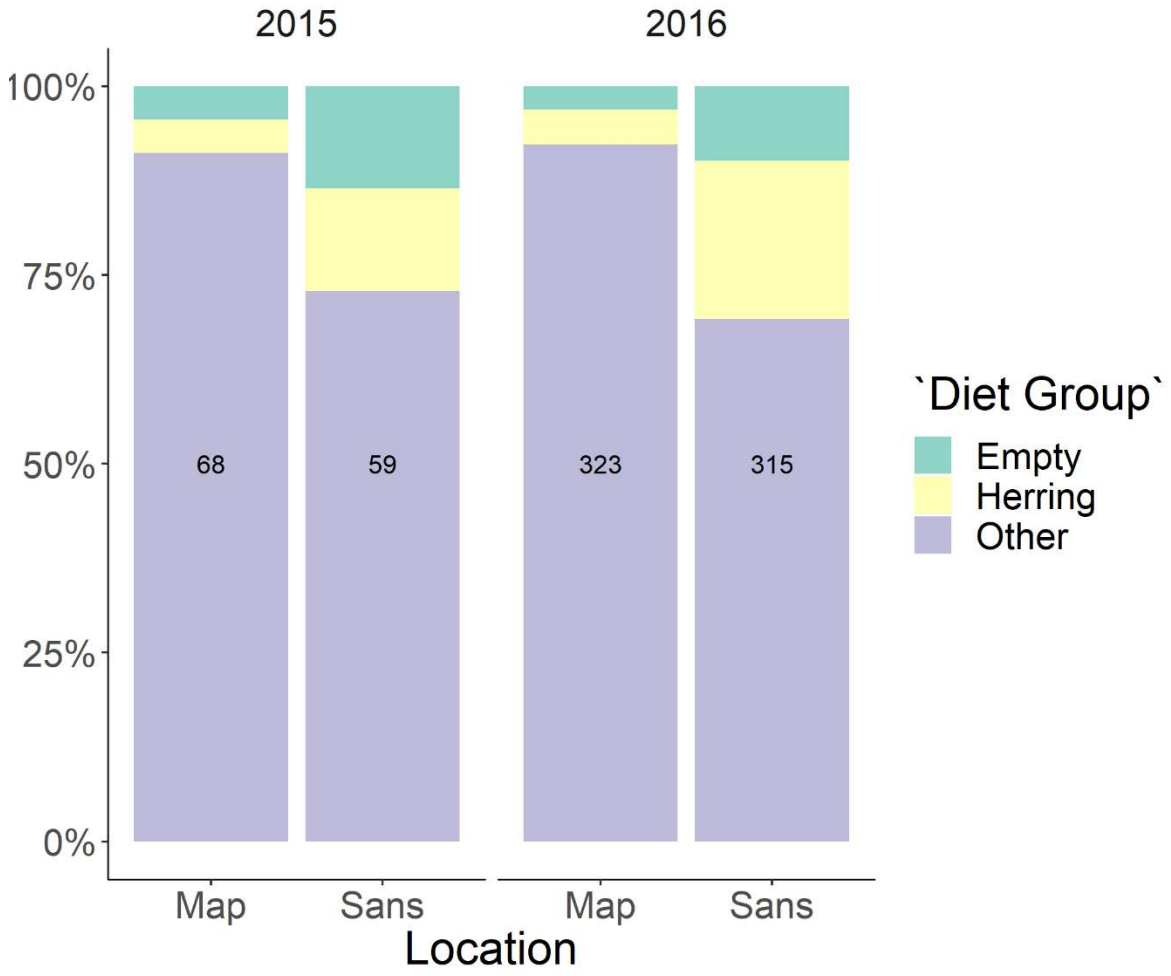


Figure 5.11. Relative proportions of juvenile ocean-type Chinook Salmon sampled at Sansum Narrows (Sans) and Maple Bay (Map) in 2015 and 2016 which had either empty stomachs, contained Pacific Herring, or contained other diet items not including Pacific Herring. Sample sizes for each year and period are overlaid on the bars.

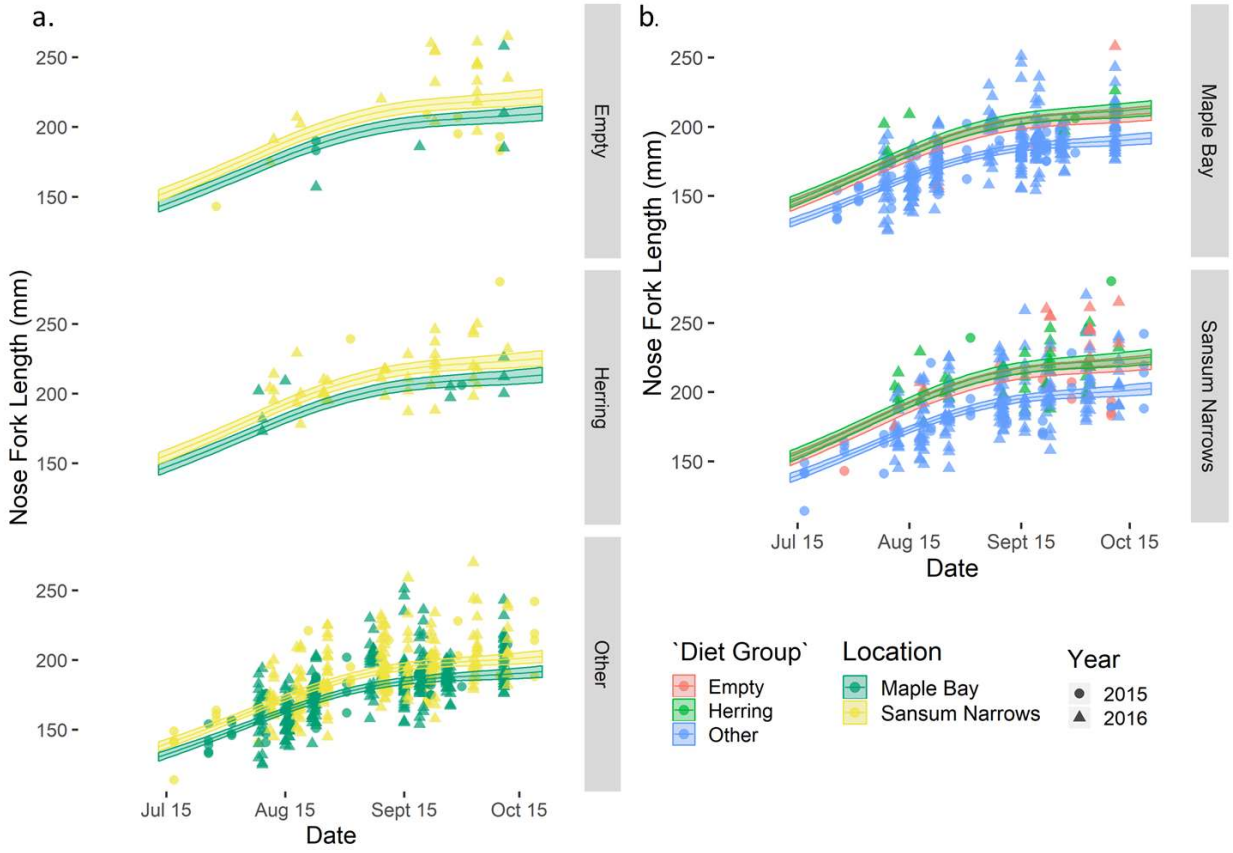


Figure 5.12. Actual (points) and GAM model predictions (lines and ribbons) of juvenile Cowichan River Chinook Salmon FL for three different coarse diet groups (empty stomachs, containing Pacific Herring, and containing other prey) at Sansum Narrows and Maple Bay in 2015 and 2016. Year and origin (hatchery or wild) were non-significant in the model (see text for details); predictions illustrated here are for a wild fish in 2015. Ribbons represent the standard error of model predictions. The left column (a) illustrates differences in predicted FL at different capture sites for each diet group while the right column (b) illustrates differences in predicted FL for different diet groups at each capture site.

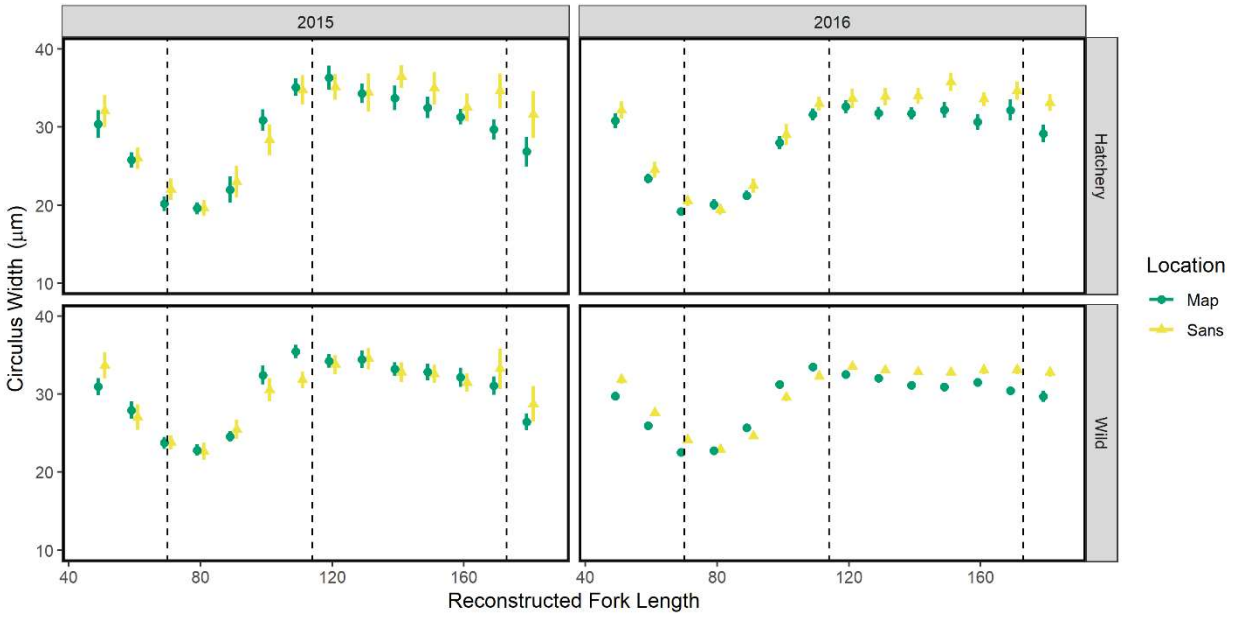


Figure 5.13. Mean (points) and standard error (bars) of circulus width in 10 mm size bins for hatchery- and wild-origin Cowichan River Chinook Salmon captured at Sansum Narrows and Maple Bay in 2015 and 2016. An apparent absence of error bars for some points indicates very small standard errors. Dashed vertical lines indicate the break points of growth regions used for modelling effects of capture site, year and origin on growth rate (Table 5.7).

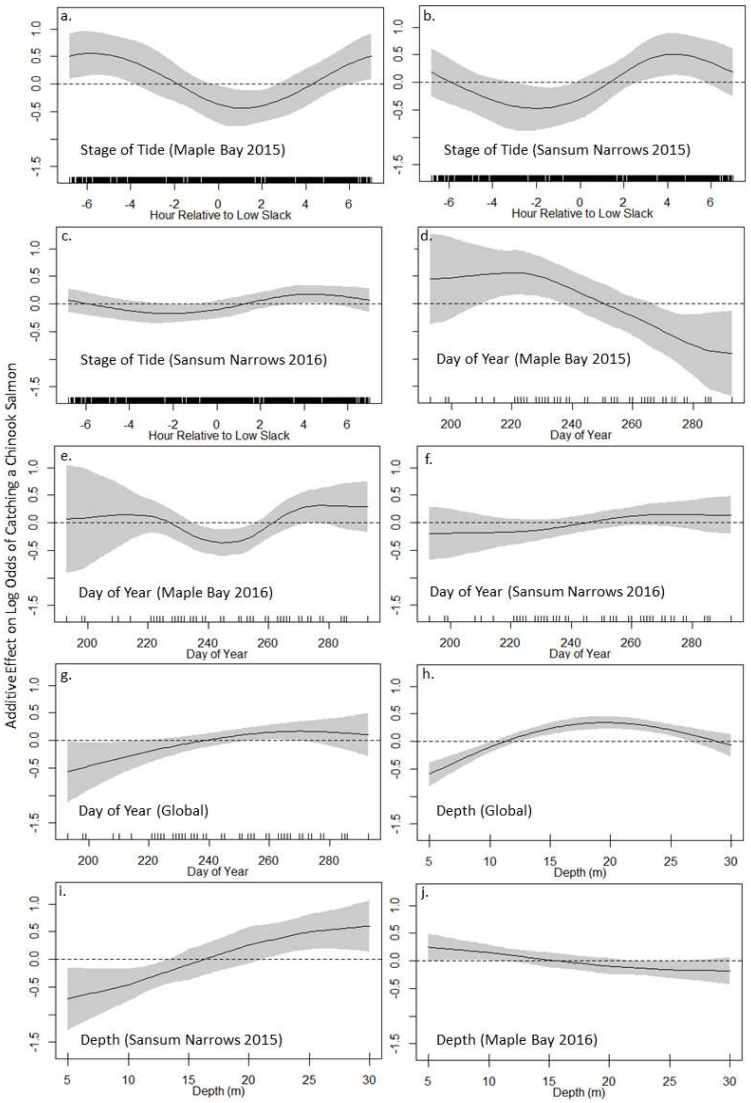


Figure 5.14. Plots for all significant ($p < 0.05$) smooth terms in a generalized additive mixed effects model (GAMM) relating the log-odds of catching a first ocean year Chinook Salmon to site, hour of the day, day of the year, depth, and stage of the tide (see Table 5.8 for all regression statistics). Significant smooth terms were the site and year-specific effects of stage of the tide at a. Maple Bay in 2015, b. Sansum Narrows in 2015, and c, Sansum Narrows in 2016; day of the year at d. Maple Bay in 2015, e. Maple Bay in 2016, and f. Sansum Narrows in 2016; and depth h. globally, i. at Sansum Narrows in 2015 and j. Maple Bay in 2016. The global smooth term for day of the year (g.) was marginally non-significant ($P = 0.077$) but is illustrated here to facilitate interpretation of site-specific smooth terms which are significantly different from this underlying trend (d-f). Site specific smooth terms for depth also reflect differences from the global trend (h). Shaded regions indicate 2 x the standard error of the smooth.

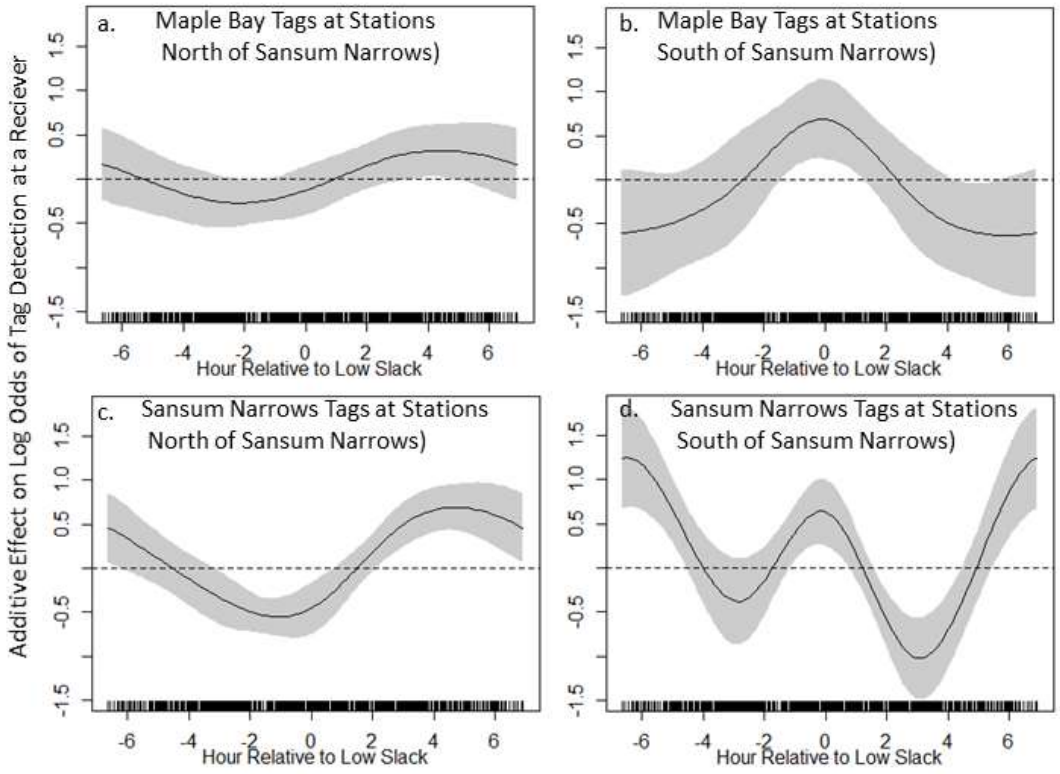
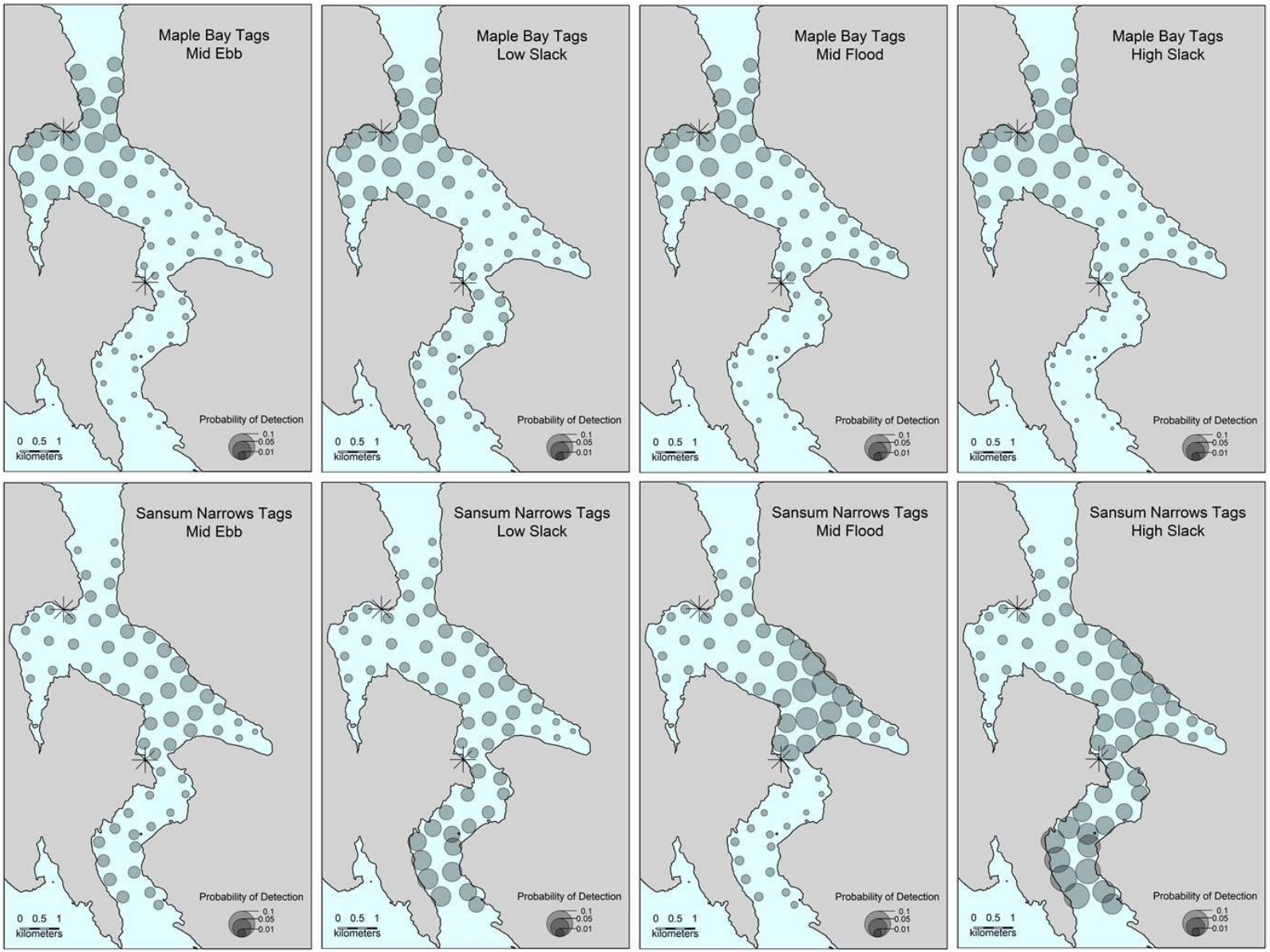


Figure 5.15. Plots for all significant ($p < 0.05$) one dimensional smooth terms in a generalized additive mixed effects model (GAMM) relating the log-odds of detecting acoustic tagged juvenile Chinook Salmon during mobile tracking to tagging site, listening station group, the interaction of tagging site with a two dimensional spatial smooth and the interaction of stage of the tide with listening station group and tagging site (see Table 5.9 for all regression statistics). Significant one dimensional smooth terms were the tagging site and station group specific effects of stage of the tide for a. Maple Bay tags at stations north of Sansum Narrows, b. Maple Bay tags at stations south of Sansum Narrows, c, Sansum Narrows tags at stations north of Sansum Narrows, and d, Sansum Narrows tags at stations South of Sansum Narrows. Shaded regions indicate 2 x the standard error of the smooth.


Maple Bay Tags
Mid Ebb
Maple Bay Tags
Low Slack
Maple Bay Tags
Mid Flood
Maple Bay Tags
High Slack
Sansum Narrows Tags
Mid Ebb
Sansum Narrows Tags
Low Slack
Sansum Narrows Tags
Mid Flood
Sansum Narrows Tags
High Slack
Probability of Detection
0.1
0.05
0.01
0 0.5 1
kilometers

1

Figure 5.16. (previous page) Predicted probability of detecting a juvenile Chinook Salmon tagged at Maple Bay (top row) or Sansum Narrows (bottom row) at each of 60 listening stations across four stages of the tide (columns) during mobile tracking as predicted by a binomial generalized additive mixed model (see text for details). Stars indicate locations of Maple Bay (top) and Sansum Narrows (bottom) tagging sites.

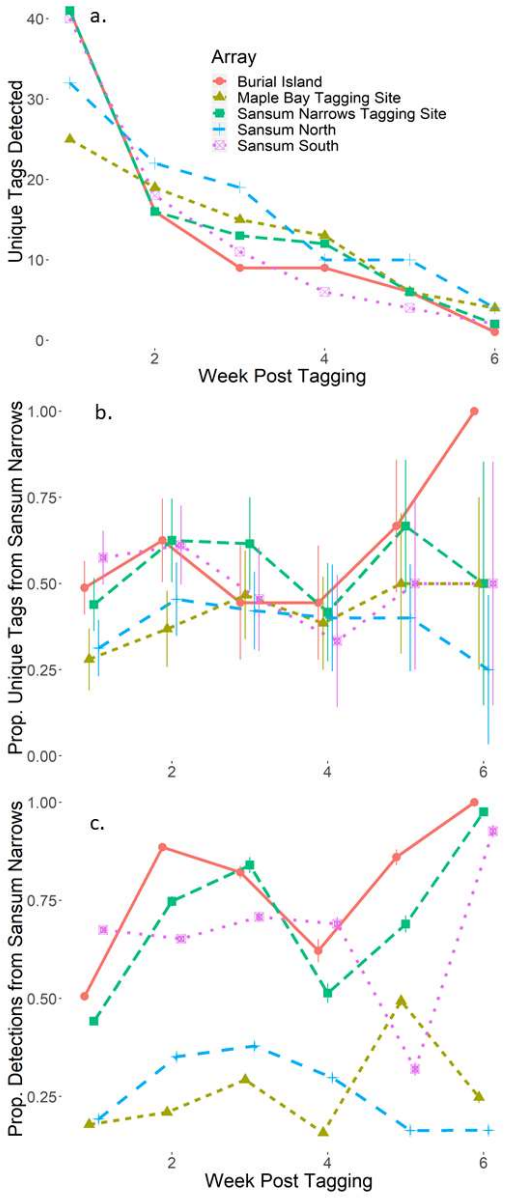


Figure 5.17. Weekly total number of unique tags (a), proportion of unique tags applied at Sansum Narrows (b), and proportion of total detections that were for tags applied at Sansum Narrows (c) for detections at each of five receiver arrays (Figure 5.6) in the vicinity of Maple Bay and Sasnum Narrows. Error bars in b and c are standard error of proportions.

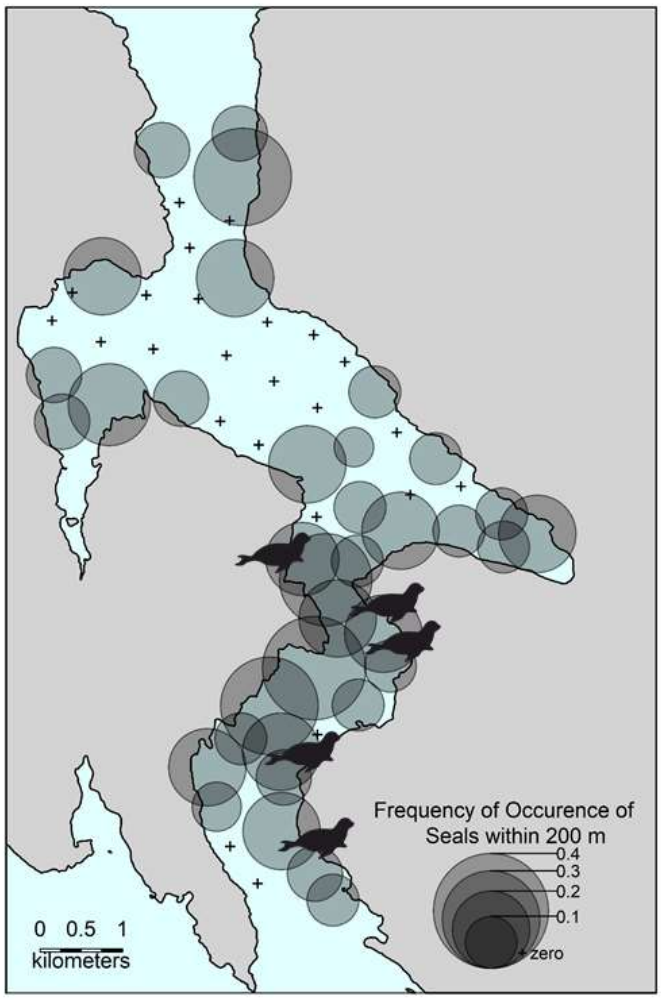


Figure 5.18. Frequency of observations of seals within 200 m of the vessel at the end of each mobile tracking stop across 10 days of monitoring between 16 Sept and 27 Sept 2017. Seal silhouettes indicate locations where seals were observed hauled out on the shoreline.

Chapter 6 – Conclusions and Future Directions

6.1 Democratizing Pacific Salmon marine ecology research

Scientific disciplines differ vastly in the cost and complexity of equipment and approaches required for their pursuit. Foundational work in community ecology that required no more equipment than gumboots, a crowbar, and a piece of string (Paine 1966) is not disparaged for its simplicity. Fisheries oceanography, including research on the marine ecology of Pacific Salmon, is neither simple nor cheap. In freshwater and estuarine systems, where research using small vessels and human-powered fishing gears are practical, non-governmental organizations (NGOs; e.g. Chalifour et al. 2019) and First Nations (e.g. Atlas et al. 2017) have been successful in leading research initiatives into factors influencing Pacific Salmon productivity. Once Pacific Salmon move out of littoral habitats, logistical challenges have meant that research on their ecology has largely been the province of state agencies (but see Carr-Harris et al. 2015 and James et al. 2020 for examples of marine sampling programs by non-state organizations).

The work presented in this dissertation, particularly the microtrolling approach described in Chapter 2, demonstrates that at least in some settings, meaningful research on the ecology of juvenile Pacific Salmon at sea can be conducted economically by stakeholders with more limited resources. The largest vessel used as part of this research program (with the exception of the vessel used to deploy acoustic tag receivers) was 6.7 m in length. Oceanographic gear was deployed by hand or using an inexpensive recreational trap puller and microtrolling gear was deployed using downriggers costing approximately $500. Obviously, some ecological questions, for example those pertaining to winter ecology on the high seas (Harris 2020), will always require the resources available only to larger (federal or state) agencies. However, I hope that more First Nations and NGOs will apply microtrolling and small vessel oceanography to investigate the ecology of juvenile Pacific Salmon in coastal waters.

In addition to its accessibility to stakeholders with limited resources, microtrolling can be useful to larger agencies where moderate numbers of samples are required, non-lethal sampling (or sampling fish immediately upon death) is necessary, or spatial and temporal flexibility are critical. One such application of microtrolling is the acoustic tagging of multiple species of

Pacific Salmon off the Washington Coast as part of the Salmon Ocean Behaviour and Distribution Program (SOBAD) of the National Marine Fisheries Service since summer of 2019 (Joseph Smith pers. comm.). Microtrolling has also been used by the Molecular Genetic Laboratory at the DFO Pacific Biological Station to obtain winter samples of juvenile Pacific Salmon from Quatsino Sound and Clayquot Sound for genomics-based assessment of physiological status and pathogen loads (Andrew Bateman, pers. comm.). A two-year project by the US Geological Survey recently (2018-2019) employed microtrolling to investigate trophic relationships of Chinook and Coho Salmon in Puget Sound (Beauchamp et al. 2020). The Pacific Salmon Foundation, BC Conservation Foundation, Fisheries and Oceans Canada, and the University of Victoria have also just begun using microtrolling to apply PIT tags as part of a three-year investigation of potential survival bottlenecks for juvenile Chinook and Coho Salmon originating from rivers in the Salish Sea.

Expanded application of hook and line sampling of juvenile Pacific Salmon at sea requires continued evaluation of the assumptions of this approach. Vulnerability of fish to hook and line gear is regulated by both internal and external factors, meaning that a random sample of the population is generally not obtained (Lennox et al. 2017). The results reported in Chapter 2 suggest that microtrolling may be biased against smaller fish. Comparison of nose to fork lengths of juvenile Chinook Salmon captured by microtrolling and purse seining during a two day period in September 2016 appear to support this conclusion, with the size distribution of microtroll-captured fish exhibiting a positive skew not present for purse seine-captured fish (K. Pellett and W. Duguid, unpublished data). The significant differences in size of juvenile Chinook Salmon captured on identical sized but different coloured lures (Chapter 4) reinforces the potential for hook and line sampling to introduce bias. Where biases introduced by hook and line sampling could compromise study conclusions, comparative sampling by microtrolling and a less selective method such as trawling may be warranted to assess potential biases.

6.2 Continued challenges for assessing recent growth of salmon in the field

Relating recent growth of juvenile Pacific Salmon sampled in the field to spatiotemporal variability in environmental conditions requires methods to index recent growth of individual fish (Ferriss et al. 2014, Journey et al. 2016, 2020, Davis et al. 2020). Unfortunately, all currently

available growth indices have some drawbacks, particularly where non-lethal sampling is required. The results reported in Chapter 3 confirm that insulin like growth factor-1 (IGF1) is superior to RNA to DNA ratio (RD) and scale circulus spacing as an index of recent growth. However, non-lethally drawing an adequate sample of blood from small fish (< 120 mm) is generally not possible (Ferriss et al. 2014), and drawing blood from larger juvenile salmon may have unknown impacts on post-release survival.

While RD did a reasonable job of indexing recent growth in juvenile Chinook Salmon in the laboratory experiment reported in Chapter 3, it performed poorly in the field. During the field sampling in 2015 (Chapter 4) RD was sampled from Chinook Salmon using the methods described in Chapter 3, but due to technical issues, results were not analyzed or reported. Biopsy of fish in the field using a very small (1.5 mm) diameter biopsy punch proved challenging, and the biopsies obtained often appeared heterogenous and smaller than the diameter of the punch. Of 358 samples, 89 (24.9%) were rejected due to CVs of duplicate RNA or DNA measurements exceeding 15% or due to RNA concentrations that were too low to measure (cases where the fluorescence attributed to RNA was lower than the intercept of the standard curve, resulting in illogical negative values for RD). By comparison, only 25 of 263 (9.5%) samples analyzed in Chapter 3 were rejected based on the same criteria. Twelve of 273 remaining samples (4.4%) had RD values lower than 1.0, while the lowest value reported for Chinook Salmon in Chapter 3 was 1.4. Due to concern regarding the validity of results, RD values were not used in subsequent analyses. The possibility that the use of a very small biopsy punch may result in non-representative sampling of white muscle tissue is discussed in Chapter 3. This problem could have been more pronounced with the larger fish sampled in the field where a thicker layer of subcutaneous lipid and wider myomeres and associated bands of connective tissue would be present. It is also possible that UV exposure and the inability to maintain an RNAse-free environment in field conditions resulted in RNA degradation. Due to these uncertainties, it is not recommended that RD of non-lethally sampled muscle tissue be used as a growth index for small fish sampled in the field.

Spacing of the outer scale circuli (second outermost in Chapter 3 and mean of second and third outermost in Chapter 4) proved to be a useful index of recent growth. However, this index

is somewhat limited by the need to account for the dependence of circulus spacing on fish size that was identified in Chapter 3. This limitation also applies to IGF1, for while no relationship between IGF1 and initial size was detected in Chapter 3, such a relationship has been reported in previous work (Shimizu et al. 2009). Including fish size as a covariate in models explaining variation in these growth indices (or otherwise accounting for this relationship) may obscure significant patterns if larger fish are also growing faster (Ferriss et al. 2014). Given the strong links between size and piscivory reported in this dissertation (Chapters 4 and 5) and between piscivory and growth reported in the literature (Litz et al. 2017, Davis et al. 2020), a positive relationship between size and growth rate of juvenile Chinook Salmon may be common. The possibility that circulus spacing is dependent on size only for small Chinook Salmon close to smoltification is discussed in Chapter 3. Given the logistical advantages of circulus spacing as a growth index, further work is warranted to investigate whether the relationship between circulus spacing and growth rate becomes independent of fish size after some threshold.

The approach applied in Chapter 5 to index growth rate over defined size intervals using circulus spacing circumvents the dependence of circulus spacing on fish size. However, this method cannot be used to index recent growth at the time of capture. Also, given the dependence of circulus deposition rate on growth rate reported in Chapter 3, and in the literature for other salmonids (Bilton and Robins 1971, Fisher and Pearcy 1990, Beakes et al. 2014, Haraldstad et al. 2016), extreme care should be exercised in using circulus counts as a proxy for days prior to capture (e.g. Gamble et al. 2018, Davis et al. 2020).

Assessing the recent growth of juvenile Pacific Salmon captured in the ocean is likely to remain a challenge. More experimental work should be conducted on fish at the same size and season, and growing at comparable rates, as those that will be sampled in the field. Such work will be challenging to achieve and may require the application of mesocosm approaches.

6.3 The importance of Pacific Herring

An important result of this dissertation was evidence for complex relationships between age-0 Pacific Herring and juvenile Chinook Salmon. I found that Pacific Herring were the most important prey of juvenile Chinook Salmon by mass (Chapter 4) but that only large juvenile

Chinook Salmon were preying upon Pacific Herring, possibly due to gape limitation (Chapters 4 and 5). Juvenile Chinook Salmon which had consumed Pacific Herring were faster growing and had fuller stomachs than those which had consumed other prey (Chapter 4). The detailed case study of Sansum Narrows and Maple Bay (Chapter 5) also suggested that larger juvenile Chinook Salmon may be co-locating with age-0 Pacific Herring schools at fine spatial and temporal scales. Such co-location could have the potential to expose juvenile salmon to greater risk from predators also targeting juvenile Pacific Herring.

The Salish Sea Marine Survival Project sought to uncover factors that could explain perceived synchronous declines of marine survival of Chinook and Coho Salmon and Steelhead in the Salish Sea that differed from patterns in adjacent coastal regions (Pacific Salmon Foundation 2015). For Chinook Salmon, subsequent analysis of survival time series has suggested that trends were in fact not synchronous (Ruff et al. 2017) although survival had in most cases declined in recent years. Nevertheless, in looking for potential mechanisms that could be important to salmon survival at the scale of the Salish Sea, Pacific Herring are a likely suspect. The Strait of Georgia is the site of the largest spawning aggregation of Pacific Herring in Canada (DFO 2018), and age-0 fish are believed to rear within the Salish Sea for at least their first year (Boldt et al. 2018). Pacific Herring are dominant forage fish in the surface waters of both the Strait of Georgia (Beamish et al. 2012) and Puget Sound (Greene et al. 2015). The results presented in Chapters 4 and 5 are consistent with a growing body of evidence for the importance of piscivory to the growth potential of juvenile Chinook Salmon (Litz et al. 2017, Davis et al. 2020). Further, they are consistent with the results of Chamberlin et al. (2017), which suggested that growth advantages of piscivory on Pacific Herring may be available only to larger juvenile Chinook Salmon. In Chapter 4 I discuss some of the factors which could have led to shifts in the predator to prey size ratios of Chinook Salmon and Pacific Herring over time, including loss of diversity of spawning populations, warming temperatures, and density dependent growth effects. Investigating not only mechanisms controlling local abundance of age-0 Pacific Herring, but also their size relative to co-occurring Chinook and Coho Salmon is an important area for future research in the Salish Sea.

Age-0 Pacific Herring are widely distributed in the Salish Sea in summer but tend to be nearshore and close to bottom during the day, leading surveys of abundance to be conducted at night (Boldt et al. 2018). While habitat preferences of Pacific Herring have been studied in Prince William Sound (Lewandoski and Bishop 2017), I am not aware of any similar work in the Salish Sea, although Shaffer et al. (2020) found that both juvenile Pacific Salmon and juvenile Pacific Herring were more abundant within kelp forests than in adjacent kelp free habitat in the Strait of Juan de Fuca. More research is needed both to assess the generality of the association between juvenile Chinook Salmon and age-0 Pacific Herring inferred from the case study presented in this dissertation (Chapter 5) and to better understand the fine-scale distribution of age-0 Pacific Herring in the Salish Sea.

The relationships between age-0 Pacific Herring and juvenile Chinook Salmon described in this dissertation raise the possibility of feedback loops that could impact survival of juvenile Chinook Salmon. Where age-0 Pacific Herring abundance is locally (or regionally) low, reduced density dependence could lead to larger individual herring (Reum et al. 2013). These large herring would then be accessible only to the largest juvenile Chinook Salmon which might also require greater search and handling times. Low abundances of Pacific Herring, a primary prey of harbour seals (Thomas et al. 2017), could also increase predation pressure on juvenile Chinook Salmon in general, and on large individuals with higher subsequent survival potential (Beamish and Mahnkin 2001) in particular due to their co-location with scarce harbour seal prey. If low age-0 Pacific Herring density was a consequence of mechanisms which had also impacted abundance or growth of juvenile Chinook Salmon (Beamish et al. 2012), these feedback loops could be superimposed on already poor recruitment prospects. Pacific Herring have the potential to modulate and integrate top-down and bottom-up effects on juvenile Pacific Salmon survival, and these hypothetical relationships warrant further investigation.

6.4 Interacting factors regulate marine growth potential of Pacific Salmon at multiple scales

Growth and size of juvenile Pacific Salmon varies at basin (Ferriss et al. 2014, Journey et al. 2016), sub-basin (Davis et al. 2020, Journey et al. 2020), and interannual (Duffy and Beauchamp 2011, Tomaro et al. 2012, Graham et al. 2019) scales. In this dissertation I focused

on variation in distribution, size, diet and growth of juvenile ocean-type Chinook Salmon within a single sub-basin of the Salish Sea (the Southern Gulf Islands) at a scale of kilometers to tens of kilometers through the late summer and fall of the first year at sea. In Chapter 4 I report that size, diet and growth rate of ocean-type Chinook Salmon all differed among five sites in the Southern Gulf Islands. While I found no support for the hypothesis that fish selected or grew faster in locally more stratified regions, sites where Pacific Herring were more important in the diet had larger, faster growing fish. A high-resolution focus on two of these sites (approximately 4 km apart) in Chapter 5 confirmed this pattern, and further suggested that larger, faster growing, more piscivorous juvenile Chinook salmon from within a single stock (Cowichan River) may be spatiotemporally co-locating with schools of age-0 Pacific Herring. While I did not detect significant spatial patterns in observations of surfaced seals in Chapter 5, co-location of large juvenile salmon with age-0 Pacific Herring has potential to influence predation exposure (see previous section). Reconstruction of prior growth rates from scale circuli of juvenile Cowichan River Chinook Salmon suggested that fish which were larger and faster growing in late summer had also been larger and faster growing earlier in life, likely including prior to migrating to the ocean. While further work is required, circulus spacing patterns were also consistent with these larger fish having entered the ocean later. Taken together these results suggest that the growth rate of juvenile Chinook Salmon is regulated by multiple external and internal factors and their interactions (Figure 6.1).

A key limitation of this dissertation was its restricted spatial scope and lack of replication. Nevertheless, this work suggests testable hypotheses going forward. One of these is that juvenile Chinook Salmon captured in association with aggregations of age-0 Pacific Herring should in general be larger and faster growing than those from the same stock captured at the same time and location but not associated with age-0 Pacific Herring. This could be tested with a spatially stratified microtrolling program that either targeted microtrolling on Pacific Herring aggregations identified visually or by sonar or that sampled with replication inside and outside of age-0 Pacific Herring habitat hotspots. Analyzing stock- or life-history-specific size of juvenile Chinook Salmon from Strait of Georgia Trawl surveys (Beamish 2000) or age-0 Pacific Herring surveys (Boldt et al 2018) with tow-level CPUE of Pacific Herring as a covariate could also test this hypothesis. As alluded to in 6.3 (above) classification of what constitutes good age-0 Pacific

Herring habitat within the Salish Sea remains a challenge. In Chapters 4 and 5 I discussed reasons why the tidal jet at Sansum Narrows might concentrate forage fish. The results presented in Chapter 5 suggest that the mechanism was not upwelling of zooplankton from depth as suggested by Zamon (2002, 2003) for San Juan Passage. Areas where tidal currents interact with topography, including tidal narrows, may also facilitate efficient foraging for planktivores due to a flux of plankton past areas providing shelter from the current (feed rest hypothesis, Genin 2004). Consistent presence of age-0 Pacific Herring at sites where tidal currents interact with topography is 'common knowledge' among recreational fishers in the Salish Sea, and given the results of Zamon (2002, 2003) and this dissertation, it is a phenomenon that warrants further study.

6.5 Unusual Conditions in 2015 and 2016

The North Pacific experienced an unprecedented heat wave from the winter of 2013-14 until the winter of 2015-16 (Di Lorenzo et al. 2016). Sea surface temperature in coastal British Columbia in 2015 and 2016 were the highest of any years between 1935 and 2018 based on timeseries collected at coastal lighthouses (Chandler 2019). Juvenile Chinook Salmon (Neville 2017) and age-0 Pacific Herring (Boldt et al. 2018) were also larger than average in fall surveys conducted by DFO in the Strait of Georgia. Warm ocean conditions in the year of outmigration have been associated with poor smolt to adult survival of Pacific Salmon (Beamish et al. 2009, Sharma et al. 2013). However, escapements of adult Chinook Salmon to the Cowichan River from 2017 to 2019 (the primary return years for fish sampled in 2015 and 2016) were in the top five returns from 1988 to 2019 (Kevin Pellett, DFO, unpublished data). These exceptional conditions raise questions about the generality of the results reported in this dissertation. At the scale of the Salish Sea, climate impacts stratification through effects on freshwater inputs, surface warming and wind mixing. The open water of the Strait of Georgia, which can be strongly stratified in summer (Journey et al. 2020), is an important rearing area for juvenile Pacific Salmon (Beamish et al. 2000, Beamish et al. 2011). Our study area in the Southern Gulf Islands was sheltered from strong wind-driven mixing, and local variation in water column properties was primarily influenced by tidal mixing that would be consistent across interannual variation in ocean temperature. The lack of a clear relationship between water column

stratification and size, diet or growth of juvenile Chinook Salmon reported in Chapter 4 should not be interpreted as evidence that stratification, including climate driven variation in stratification, is not important at other spatial scales (Burke et al. 2013, Journey et al. 2016, Journey et al. 2020). While age-0 Pacific Herring were larger than average in 2015 and 2016, 4 years since 1992 had greater mean lengths than reported in 2015 (1998, 2005, 2007, and 2010; Boldt et al. 2018). Our key result of apparent size-dependence of predation by juvenile Chinook Salmon on age-0 Pacific Herring is therefore likely applicable beyond our study years. Indeed, Chamberlin et al. (2017) hypothesized a link between size mediated foraging on Pacific Herring and growth advantages to large juvenile Chinook Salmon based on sampling conducted in Puget Sound in 2011. The results presented in this dissertation are one step in a process of understanding juvenile Pacific Salmon marine ecology that will require the integration of multiple spatial and temporal scales, including interannual variation.

6.6 References

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6.7 Figures

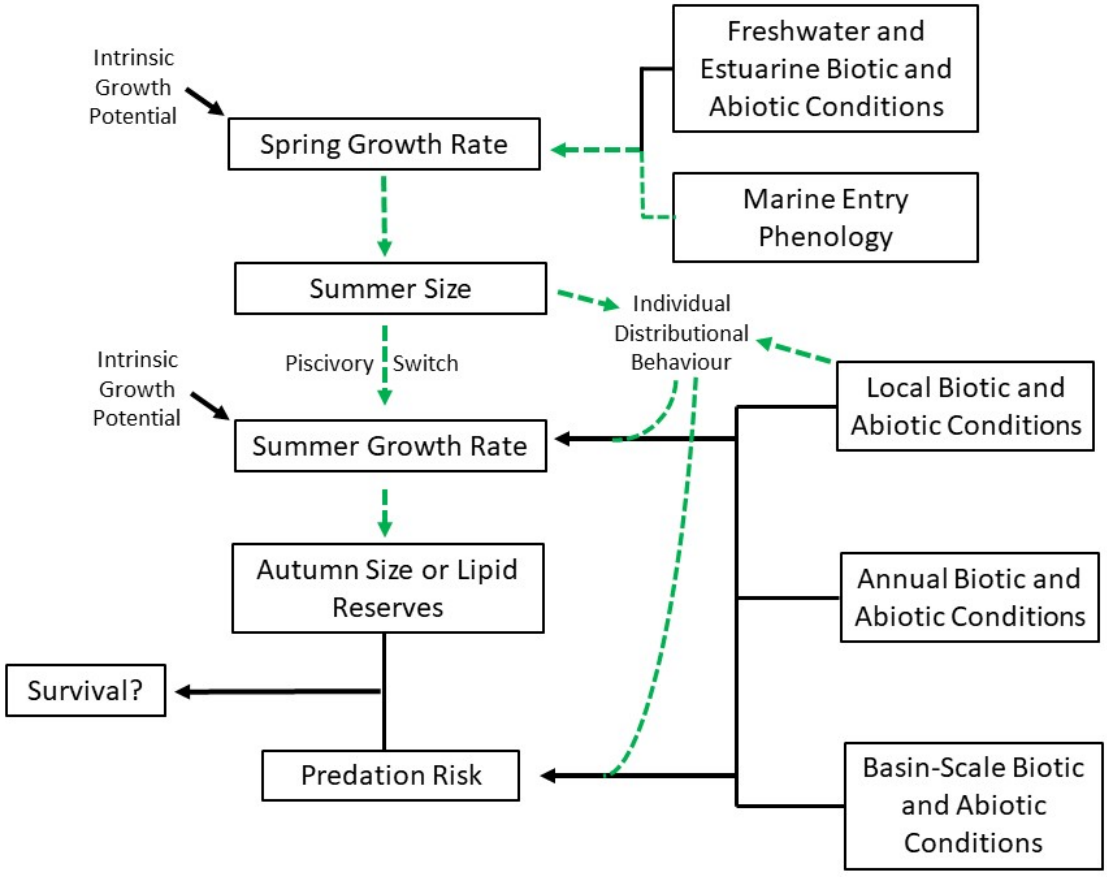

Figure 6.1. Schematic representation of factors influencing summer growth rate, and in turn survival, of juvenile Chinook Salmon in the Salish Sea. Green dashed lines indicate relationships which are at least partially supported by results of this dissertation. A key result of this dissertation is that individual distributional behaviour with respect to local scale habitat features may be related to individual size and diet and may influence growth and predation exposure.

Appendices

7.1 Appendix 1 - Supplementary Material for Chapter 4

Table 7.1. Pacific Biological Station molecular genetics laboratory Chinook Salmon stock codes and region and/or life history type groupings reported in the present study. The number of individuals assigned to each stock is indicated (N). An additional twelve fish originally identified as Chinook Salmon were determined by genetics to be Chinook-Coho Salmon hybrids (Araujo et al. in prep), one was a Coho Salmon mis-identified as a Chinook Salmon, and two samples failed to amplify.

DFO Stock Codes	Stock Grouping	N
Cowichan	Cowichan River	209
Clearwater	Fraser/Thompson Stream Type	3
Elkin_R	Fraser/Thompson Stream Type	3
Louis	Fraser/Thompson Stream Type	1
McGregor	Fraser/Thompson Stream Type	8
Nazko	Fraser/Thompson Stream Type	1
Raft_R	Fraser/Thompson Stream Type	2
Tete_Jaune	Fraser/Thompson Stream Type	2
U_Coldwat_SP	Fraser/Thompson Stream Type	1
Chilliwack_F	Lower Fraser Ocean Type	30
Harrison	Lower Fraser Ocean Type	25
Chemainus	Other East Coast VI	2
Nanaimo_F	Other East Coast VI	1
Nanaimo_SU	Other East Coast VI	2
Puntledge_F	Other East Coast VI	20
Green@Kendal_F	Puget Sound	1
Nooksack_SP@Ke	Puget Sound	4
Snohomish_R	Puget Sound	18
Soos_Cr_H	Puget Sound	15
L_Shuswap	South Thompson Ocean Type	6
Nitinat	West Coast VI	6
Totals		360

Table 7.2. Mean and standard deviation (SD) of an index of biomass concentration (units ~ g/m^3) for potential zooplankton prey of juvenile Chinook Salmon sampled with vertical 30 m tows with a 0.5 m diameter 350 µm ring net between 9 July and 23 October 2015 at five sites in the Southern Gulf Islands of the Salish Sea (Table 4.1). Only taxa occurring in more than 10 tows are included. Sample size (N) indicates the number of tows per site and month, two tows were conducted each day.

Month	Taxonomic Group	Cowichan Bay			Maple Bay			Saanich Inlet			Sansum Narrows			Satellite Channel		
July		N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
	Copepod	6	0.00167	0.00077	4	0.00032	0.00026	4	0.01290	0.02161	6	0.00246	0.00197	6	0.00551	0.00582
	Decapod Megalopa	6	0.00652	0.00317	4	0.00217	0.00096	4	0.00523	0.00290	6	0.00085	0.00070	6	0.00258	0.00226
	Decapod Zoea	6	0.04206	0.02011	4	0.01366	0.00773	4	0.01453	0.00722	6	0.00508	0.00294	6	0.01130	0.00714
	Euphausiid	6	0.00005	0.00006	4	0.00001	0.00001	4	0.00006	0.00010	6	0.00005	0.00009	6	0.00020	0.00024
	Gammarid	6	0.00000	0.00000	4	0.00641	0.00250	4	0.00015	0.00031	6	0.00617	0.00747	6	0.00020	0.00045
	Hyperoche sp.	6	0.00098	0.00079	4	0.00073	0.00086	4	0.00078	0.00075	6	0.00023	0.00033	6	0.00046	0.00033
	Larval Fish	6	0.00016	0.00038	4	0.00003	0.00003	4	0.00008	0.00009	6	0.00001	0.00001	6	0.00002	0.00003
	Polychaete	6	0.00061	0.00053	4	0.00005	0.00006	4	0.00004	0.00005	6	0.00003	0.00003	6	0.00003	0.00005
	Themisto pacifica	6	0.00011	0.00013	4	0.00014	0.00017	4	0.00040	0.00012	6	0.00081	0.00108	6	0.00068	0.00063
August																
	Copepod	8	0.00446	0.00836	8	0.00055	0.00054	8	0.02505	0.04076	4	0.00047	0.00024	10	0.00934	0.01019
	Decapod Megalopa	8	0.00532	0.00691	8	0.00231	0.00108	8	0.00191	0.00122	4	0.00167	0.00142	10	0.00134	0.00093
	Decapod Zoea	8	0.02763	0.01081	8	0.02050	0.00990	8	0.01284	0.01102	4	0.00854	0.00660	10	0.01253	0.00660
	Euphausiid	8	0.00003	0.00004	8	0.00006	0.00009	8	0.00017	0.00019	4	0.00005	0.00004	10	0.00024	0.00024
	Gammarid	8	0.00043	0.00122	8	0.00580	0.00529	8	0.00101	0.00236	4	0.00547	0.00635	10	0.00015	0.00036
	Hyperoche sp.	8	0.00198	0.00191	8	0.00083	0.00049	8	0.00104	0.00088	4	0.00063	0.00014	10	0.00053	0.00045
	Larval Fish	8	0.00000	0.00000	8	0.00015	0.00026	8	0.00003	0.00004	4	0.00015	0.00027	10	0.00001	0.00003
	Polychaete	8	0.00123	0.00054	8	0.00009	0.00008	8	0.00006	0.00007	4	0.00008	0.00006	10	0.00006	0.00006
	Themisto pacifica	8	0.00035	0.00031	8	0.00041	0.00042	8	0.00021	0.00016	4	0.00035	0.00021	10	0.00103	0.00069
September																
	Copepod	6	0.00096	0.00095	8	0.00144	0.00147	6	0.00229	0.00220	8	0.00052	0.00033	6	0.00216	0.00158
	Decapod Megalopa	6	0.00141	0.00138	8	0.00036	0.00027	6	0.00084	0.00111	8	0.00047	0.00033	6	0.00183	0.00179
	Decapod Zoea	6	0.00716	0.00297	8	0.00485	0.00251	6	0.00796	0.00557	8	0.00222	0.00175	6	0.01011	0.00943
	Euphausiid	6	0.00005	0.00008	8	0.00036	0.00075	6	0.00022	0.00027	8	0.00009	0.00010	6	0.00019	0.00019
	Gammarid	6	0.00000	0.00000	8	0.00237	0.00442	6	0.00000	0.00000	8	0.00112	0.00142	6	0.00000	0.00000
	Hyperoche sp.	6	0.00276	0.00263	8	0.00097	0.00066	6	0.00166	0.00165	8	0.00103	0.00083	6	0.00055	0.00045
	Larval Fish	6	0.00005	0.00012	8	0.00005	0.00014	6	0.00000	0.00000	8	0.00000	0.00001	6	0.00012	0.00019
	Polychaete	6	0.00079	0.00096	8	0.00008	0.00016	6	0.00018	0.00021	8	0.00008	0.00009	6	0.00007	0.00008
	Themisto pacifica	6	0.00032	0.00042	8	0.00022	0.00015	6	0.00045	0.00036	8	0.00029	0.00041	6	0.00082	0.00049
October																
	Copepod	4	0.00011	0.00009	4	0.00039	0.00017	4	0.00040	0.00017	4	0.00042	0.00043	2	0.00175	0.00059
	Decapod Megalopa	4	0.00064	0.00082	4	0.00050	0.00060	4	0.00088	0.00097	4	0.00006	0.00011	2	0.00000	0.00000
	Decapod Zoea	4	0.00201	0.00060	4	0.00267	0.00230	4	0.00291	0.00249	4	0.00059	0.00048	2	0.00123	0.00046
	Euphausiid	4	0.00006	0.00006	4	0.00015	0.00010	4	0.00016	0.00004	4	0.00013	0.00013	2	0.00015	0.00006
	Gammarid	4	0.00000	0.00000	4	0.00128	0.00093	4	0.00077	0.00102	4	0.00226	0.00320	2	0.00000	0.00000
	Hyperoche sp.	4	0.00076	0.00029	4	0.00018	0.00030	4	0.00060	0.00050	4	0.00017	0.00012	2	0.00037	0.00053
	Larval Fish	4	<0.00001	<0.00001	4	0.00000	0.00000	4	0.00000	0.00000	4	0.00000	0.00000	2	0.00000	0.00000
	Polychaete	4	0.00017	0.00017	4	0.00015	0.00009	4	0.00002	0.00004	4	0.00000	0.00000	2	0.00000	0.00000
	Themisto pacifica	4	0.00010	0.00009	4	0.00003	0.00005	4	0.00077	0.00018	4	0.00035	0.00040	2	0.00033	0.00007

Table 7.3. Mean and standard deviation (SD) of partial fullness indices for prey categories of juvenile ocean-type, Strait of Georgia origin Chinook Salmon sampled between 9 July and 23 October 2015 at five sites in the Southern Gulf Islands of the Salish Sea (Table 4.1). Only taxa belonging to analysis categories (Table 4.3) occurring in more than 10% of stomachs were included. Sample size (N) indicates the number of non-empty juvenile Chinook Salmon stomachs sampled per site and period.

Period	Category	Cowichan Bay			Maple Bay			Saanich Inlet			Sansum Narrows			Satellite Channel		
July - August		N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
	Cephalopod	42	0.00187	0.00903	42	0.00445	0.02037	22	0.00087	0.00301	19	0.01290	0.03923	28	0.00036	0.00188
	Copepod	42	0.00011	0.00030	42	0.00043	0.00074	22	0.00014	0.00031	19	0.00066	0.00216	28	0.00016	0.00035
	Decapod Megalopa	42	0.04136	0.05536	42	0.03579	0.04265	22	0.03538	0.03697	19	0.00596	0.01301	28	0.02749	0.04612
	Decapod Zoea	42	0.00817	0.01359	42	0.00953	0.01134	22	0.00763	0.01870	19	0.00132	0.00290	28	0.00856	0.02532
	Euphausiid	42	0.00012	0.00075	42	0.00062	0.00270	22	0.00126	0.00307	19	0.00175	0.00525	28	0.00077	0.00298
	Fish	42	0.00991	0.02173	42	0.00364	0.00830	22	0.00058	0.00196	19	0.00198	0.00389	28	0.04918	0.16155
	Gammarid	42	0.00018	0.00089	42	0.00027	0.00090	22	0.00115	0.00483	19	0.00529	0.02214	28	0.00067	0.00165
	Herring	42	0.00523	0.03138	42	0.00539	0.02741	22	0.00454	0.02128	19	0.02168	0.09449	28	0.00699	0.03599
	Hyperia medusarum	42	0.00323	0.00497	42	0.00745	0.01395	22	0.00227	0.00510	19	0.00254	0.00334	28	0.00319	0.00582
	Hyperoche sp.	42	0.00642	0.01071	42	0.00780	0.00868	22	0.00320	0.00516	19	0.00462	0.01185	28	0.00373	0.00893
	Themisto pacifica	42	0.00660	0.02278	42	0.00015	0.00034	22	0.00002	0.00010	19	0.00020	0.00074	28	0.00029	0.00056
	Unid. or Oth. Amphipod	42	0.00023	0.00087	42	0.00030	0.00089	22	0.00083	0.00225	19	0.00010	0.00033	28	0.00066	0.00191
September - October																
	Cephalopod	11	0.00706	0.01699	23	0.00473	0.01528	29	0.00330	0.01731	31	0.01789	0.07208	13	0.00756	0.01973
	Copepod	11	0.00000	0.00000	23	0.00135	0.00284	29	0.00004	0.00010	31	0.00005	0.00014	13	0.00003	0.00007
	Decapod Megalopa	11	0.00153	0.00472	23	0.02887	0.05517	29	0.00454	0.00797	31	0.00365	0.00764	13	0.00783	0.01505
	Decapod Zoea	11	0.00064	0.00210	23	0.00714	0.01057	29	0.00070	0.00157	31	0.00083	0.00173	13	0.00018	0.00024
	Euphausiid	11	0.00000	0.00000	23	0.00000	0.00002	29	0.00174	0.00614	31	0.00827	0.02462	13	0.00059	0.00148
	Fish	11	0.02304	0.04157	23	0.00172	0.00341	29	0.00196	0.00585	31	0.01046	0.03163	13	0.00242	0.00576
	Gammarid	11	0.00000	0.00000	23	0.00019	0.00091	29	0.00139	0.00283	31	0.00057	0.00249	13	0.00054	0.00120
	Herring	11	0.00213	0.00705	23	0.00387	0.01856	29	0.02052	0.08551	31	0.02194	0.09635	13	0.01853	0.06680
	Hyperia medusarum	11	0.00000	0.00000	23	0.00056	0.00111	29	0.00181	0.00235	31	0.00022	0.00058	13	0.00150	0.00246
	Hyperoche sp.	11	0.00029	0.00065	23	0.00959	0.01206	29	0.00434	0.00813	31	0.00176	0.00288	13	0.00884	0.02463
	Themisto pacifica	11	0.00000	0.00000	23	0.00090	0.00236	29	0.00016	0.00045	31	0.00023	0.00087	13	0.00058	0.00074
	Unid. or Oth. Amphipod	11	0.00003	0.00007	23	0.00217	0.00456	29	0.00212	0.00271	31	0.00036	0.00080	13	0.00097	0.00166

Table 7.4. Taxonomically nested, hierarchical summary of gravimetric composition and frequency of occurrence of prey identified in all 322 Chinook Salmon with non-empty stomachs sampled between 9 July and 23 October 2015 at five sites in the Southern Gulf Islands of the Salish Sea (Table 4.1).

Phylum	Class/Subphylum	Order/Subclass	Infraorder	Stage	Family	Species	Mass (g)	Mass %	Occurrence
Arthropoda							50.892	35.94%	279
	Arachnida						0.005	0.00%	1
	Crustacea						49.980	35.30%	278
		Amphipoda					14.571	10.29%	248
					Caprellidae		0.002	0.00%	1
					Gammaridae		1.167	0.82%	43
						Cyphocaris challengeri	0.105	0.07%	2
					Hyperiidae		12.038	8.50%	241
						Hyperia medusarum	3.479	2.46%	128
						Hyperoche medusarum	7.247	5.12%	215
						Themisto pacifica	1.309	0.92%	78
		Copepoda					0.348	0.25%	92
		Cumacea					0.000	0.00%	1
		Decapoda					31.726	22.41%	243
			Anomura				2.791	1.97%	125
				Zoeae	Paguridae		0.000	0.00%	1
				Zoeae	Porcellanidae		2.062	1.46%	79
				Megalopae	Paguridae		0.020	0.01%	14
				Megalopae	Porcellanidae		0.709	0.50%	80
			Brachyura				28.733	20.29%	235
				Zoeae			4.155	2.93%	159
				Megalopae			24.257	17.13%	229
				Megalopae	Cancridae		16.258	11.48%	203
				Megalopae	Grapsidae		0.332	0.23%	87
				Megalopae	Majidae		0.116	0.08%	48
				Megalopae	Pinnotheridae		0.289	0.20%	95
				Megalopae	Xanthidae	*Lophopanopeus bellus*	5.375	3.80%	147
				Post-larval	Pinnotheridae		0.308	0.22%	12
			Caridea				0.101	0.07%	31
				Zoeae			0.020	0.01%	16
				Post-larval			0.082	0.06%	15
		Euphausiacea					2.895	2.04%	46
				Furcilia	Euphausiidae		0.000	0.00%	2
				Zoeae	Euphausiidae		0.000	0.00%	1
				Post-larval	Euphausiidae		2.895	2.04%	44
		Isopoda					0.001	0.00%	1
		Mysida			Mysidae		0.110	0.08%	3
		Thecostraca3					0.327	0.23%	19
	Insecta						0.906	0.64%	17
					Diptera		0.003	0.00%	1
					Hymenoptera		0.207	0.15%	4
	Pycnogonida	Pantopoda					0.001	0.00%	1
Chordata	Osteichthyes						74.314	52.48%	162
		Clupeiformes					55.836	39.43%	41
					Clupeidae	*Clupea pallasi*	54.580	38.54%	38
					Engraulidae	*Engraulis mordax*	1.257	0.89%	3
		Myctophiformes			Myctophidae		2.954	2.09%	2
		Perciformes			Embiotocidae		4.353	3.07%	2
		Pleuronectiformes			Pleuronectidae		0.309	0.22%	10
		Scorpaeniformes			Sebastidae		0.015	0.01%	1
		Sygnathiformes			Sygnathidae	*Syngnathus leptorhynchus*	0.798	0.56%	21
Cnidaria							NA	NA	4
	Hydrozoa	Siphonopora					NA	NA	3
Ctenophora	Tentaculata	Cydippida			Pleurobrachidae	*Pleurobrachia sp.*	NA	NA	1
Mollusca							14.929	10.54%	54
	Bivalvia						0.003	0.00%	2
	Cephalopoda						14.870	10.50%	36
		Octopoda					6.445	4.55%	22
		Teuthida					7.357	5.20%	11
	Gastropoda						0.056	0.04%	18
		Pteropoda (informal)					0.052	0.04%	14
Polychaeta							0.271	0.19%	23
Unidentifiable or Non-Animal							0.882	0.62%	68
Totals							141.600	100.00%	322

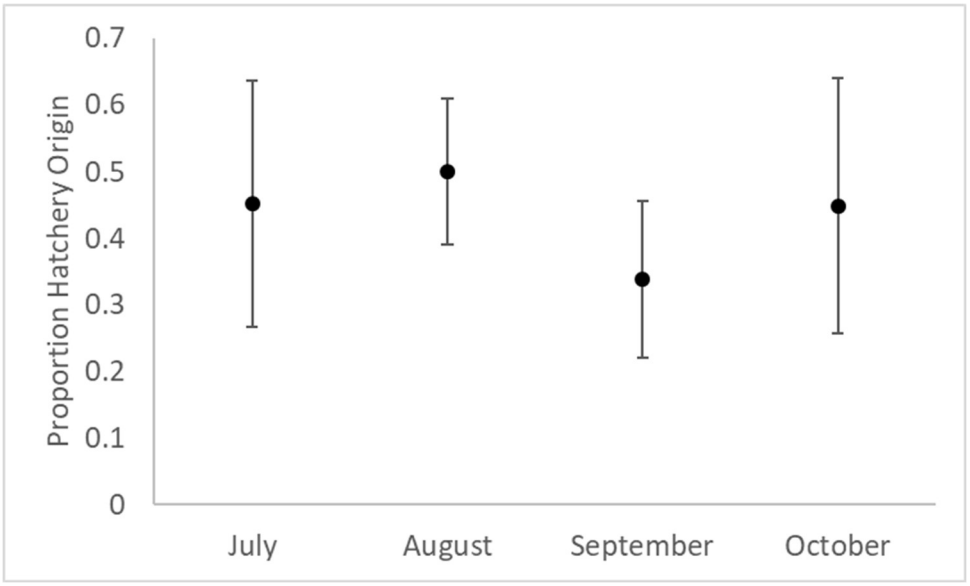

Figure 7.1. Monthly proportion of juvenile Cowichan River origin Chinook Salmon which were of hatchery origin (as indicated by an adipose clip, coded wire tag, or both). Fish were captured between 9 July and 23 October 2015 at five sites in the Southern Gulf Islands of the Salish Sea.

7.2 Appendix 2 – Supplementary Material for Chapter 5

Table 7.5. Details of acoustic zooplankton fish profiler transects, see Figure 5.2 for transect locations.

Date	Start Time	End Time	Site	Letter	Length (m)	Speed (m/s)	Retained for Analysis
2017-08-30	8:56:21	9:03:17	Maple Bay	R	771	1.85	No
2017-08-30	10:47:34	10:54:00	Maple Bay	B	708	1.84	Yes
2017-08-30	10:54:00	10:58:56	Maple Bay	C	423	1.43	Yes
2017-08-30	10:58:56	11:09:00	Maple Bay	D	1269	2.10	Yes
2017-08-30	11:09:00	11:16:20	Maple Bay	R	808	1.84	Yes
2017-08-30	11:57:50	12:06:30	Maple Bay	B	736	1.41	No
2017-08-30	12:06:30	12:10:30	Maple Bay	C	455	1.90	No
2017-08-30	12:10:30	12:21:06	Maple Bay	D	1274	2.00	Yes
2017-08-30	12:21:06	12:28:25	Maple Bay	R	789	1.80	No
2017-08-30	13:18:20	13:25:30	Maple Bay	B	691	1.61	No
2017-08-30	13:25:30	13:29:30	Maple Bay	C	407	1.70	No
2017-08-30	13:29:30	13:40:16	Maple Bay	D	1245	1.93	Yes
2017-08-30	13:40:16	13:46:36	Maple Bay	G	718	1.89	Yes
2017-08-30	13:46:36	13:49:00	Maple Bay	F	258	1.79	No
2017-08-30	14:21:44	14:28:56	Maple Bay	B	693	1.60	Yes
2017-08-30	14:28:56	14:32:51	Maple Bay	C	399	1.70	Yes
2017-08-30	14:32:51	14:42:56	Maple Bay	D	1226	2.03	Yes
2017-08-30	14:42:56	14:49:50	Maple Bay	G	737	1.78	Yes
2017-08-30	14:49:50	14:52:06	Maple Bay	F	258	1.90	Yes
2017-08-30	15:22:30	15:29:20	Maple Bay	B	716	1.75	Yes
2017-08-30	15:29:20	15:33:00	Maple Bay	C	414	1.88	Yes
2017-08-30	15:33:00	15:38:00	Maple Bay	O	621	2.07	Yes
2017-08-30	15:38:00	15:44:00	Maple Bay	N	734	2.04	Yes
2017-08-30	15:44:00	15:50:46	Maple Bay	G	717	1.77	Yes
2017-08-30	15:50:46	15:53:46	Maple Bay	F	234	1.30	Yes
2017-08-30	16:37:50	16:44:41	Maple Bay	B	720	1.75	Yes
2017-08-30	16:44:41	16:48:26	Maple Bay	C	427	1.90	Yes
2017-08-30	16:48:26	16:58:50	Maple Bay	D	1257	2.01	Yes
2017-08-30	16:58:50	17:05:00	Maple Bay	G	719	1.94	Yes
2017-08-30	17:05:00	17:07:42	Maple Bay	F	273	1.69	Yes
2017-08-31	9:20:30	9:29:25	Sansum Narrows	I	1093	2.04	Yes
2017-08-31	9:46:20	10:00:30	Sansum Narrows	E	1720	2.02	Yes
2017-08-31	10:00:30	10:03:50	Sansum Narrows	A	356	1.78	No
2017-08-31	10:54:25	11:03:13	Sansum Narrows	I	1121	2.12	Yes
2017-08-31	11:03:13	11:08:17	Sansum Narrows	K	635	2.09	Yes
2017-08-31	11:26:19	11:30:20	Sansum Narrows	A	378	1.57	No
2017-08-31	12:02:00	12:07:21	Sansum Narrows	H	670	2.09	Yes
2017-08-31	12:07:21	12:15:10	Sansum Narrows	J	881	1.88	Yes
2017-08-31	12:15:10	12:21:18	Sansum Narrows	L	767	2.09	Yes
2017-08-31	12:21:18	12:35:11	Sansum Narrows	E	1754	2.11	Yes
2017-08-31	12:35:11	12:38:51	Sansum Narrows	A	376	1.71	Yes
2017-08-31	13:17:05	13:27:36	Sansum Narrows	I	1122	1.78	Yes
2017-08-31	13:27:36	13:32:30	Sansum Narrows	K	614	2.09	Yes
2017-08-31	13:32:30	13:39:11	Sansum Narrows	L	770	1.92	Yes
2017-08-31	13:39:11	13:48:35	Sansum Narrows	M	1204	2.14	Yes
2017-08-31	13:48:35	13:52:43	Sansum Narrows	A	377	1.52	Yes
2017-08-31	14:24:10	14:29:58	Sansum Narrows	H	684	1.97	Yes
2017-08-31	14:29:58	14:38:49	Sansum Narrows	J	907	1.71	Yes
2017-08-31	14:38:49	14:46:33	Sansum Narrows	L	764	1.65	Yes
2017-08-31	14:46:33	15:01:22	Sansum Narrows	E	1749	1.97	No
2017-08-31	15:01:22	15:04:50	Sansum Narrows	A	363	1.74	Yes
2017-08-31	15:35:40	15:45:00	Sansum Narrows	I	1099	1.96	Yes
2017-08-31	15:45:00	15:50:25	Sansum Narrows	K	641	1.97	Yes
2017-08-31	15:50:25	15:56:40	Sansum Narrows	L	774	2.06	Yes
2017-08-31	15:56:40	16:05:40	Sansum Narrows	M	1205	2.23	Yes
2017-08-31	16:05:40	16:10:00	Sansum Narrows	A	379	1.46	No
2017-08-31	16:42:40	16:48:35	Sansum Narrows	H	682	1.92	Yes
2017-08-31	16:48:35	16:56:30	Sansum Narrows	J	901	1.90	Yes
2017-08-31	16:56:30	17:03:00	Sansum Narrows	L	756	1.94	Yes
2017-08-31	17:03:00	17:16:45	Sansum Narrows	E	1745	2.12	Yes
2017-08-31	17:16:45	17:21:00	Sansum Narrows	A	364	1.43	Yes
2017-09-04	9:01:40	9:07:54	Maple Bay	B	735	1.97	Yes
2017-09-04	9:07:54	9:11:23	Maple Bay	C	449	2.15	Yes
2017-09-04	9:11:23	9:21:22	Maple Bay	D	1227	2.05	No
2017-09-04	9:21:22	9:27:35	Maple Bay	G	759	2.03	Yes
2017-09-04	9:27:35	9:30:03	Maple Bay	F	285	1.92	Yes
2017-09-04	10:24:25	10:27:08	Maple Bay	P	347	2.13	Yes
2017-09-04	10:27:08	10:30:37	Maple Bay	Q	446	2.13	Yes
2017-09-04	10:30:37	10:36:08	Maple Bay	O	658	1.99	No
2017-09-04	10:36:08	10:42:17	Maple Bay	N	765	2.07	Yes
2017-09-04	10:42:17	10:48:41	Maple Bay	R	789	2.05	Yes
2017-09-04	11:18:19	11:24:33	Maple Bay	B	728	1.95	Yes
2017-09-04	11:24:33	11:28:13	Maple Bay	C	445	2.02	Yes
2017-09-04	11:28:13	11:38:53	Maple Bay	D	1224	1.91	No

Date	Start Time	End Time	Site	Letter	Length (m)	Speed (m/s)	Retained for Analysis
2017-09-04	11:38:53	11:45:30	Maple Bay	G	752	1.89	Yes
2017-09-04	11:45:30	11:48:00	Maple Bay	F	272	1.81	Yes
2017-09-04	12:23:47	12:26:54	Maple Bay	P	372	1.99	Yes
2017-09-04	12:26:54	12:30:20	Maple Bay	Q	447	2.17	No
2017-09-04	12:30:20	12:36:00	Maple Bay	O	646	1.90	No
2017-09-04	12:36:00	12:42:40	Maple Bay	N	782	1.96	Yes
2017-09-04	12:42:40	12:49:33	Maple Bay	R	795	1.93	Yes
2017-09-04	13:18:30	13:24:45	Maple Bay	B	728	1.94	Yes
2017-09-04	13:24:45	13:28:03	Maple Bay	C	447	2.26	Yes
2017-09-04	13:28:03	13:38:48	Maple Bay	D	1225	1.90	Yes
2017-09-04	13:38:48	13:45:54	Maple Bay	G	734	1.72	Yes
2017-09-04	13:45:54	13:48:31	Maple Bay	F	277	1.76	Yes
2017-09-04	14:23:45	14:26:35	Maple Bay	P	363	2.13	Yes
2017-09-04	14:26:35	14:30:05	Maple Bay	Q	450	2.14	Yes
2017-09-04	14:30:05	14:35:45	Maple Bay	O	652	1.92	Yes
2017-09-04	14:35:45	14:42:33	Maple Bay	N	751	1.84	Yes
2017-09-04	14:42:33	14:48:31	Maple Bay	R	762	2.13	Yes
2017-09-04	15:34:00	15:40:10	Maple Bay	B	721	1.95	Yes
2017-09-04	15:40:10	15:43:50	Maple Bay	C	442	2.01	No
2017-09-04	15:43:50	15:54:25	Maple Bay	D	1219	1.92	Yes
2017-09-04	15:54:25	16:00:00	Maple Bay	G	748	2.23	Yes
2017-09-04	16:00:00	16:02:30	Maple Bay	F	286	1.91	Yes
2017-09-04	16:51:00	16:54:00	Maple Bay	P	366	2.03	Yes
2017-09-04	16:54:00	16:57:40	Maple Bay	Q	462	2.10	Yes
2017-09-04	16:57:40	17:02:40	Maple Bay	O	653	2.18	Yes
2017-09-04	17:02:40	17:08:30	Maple Bay	N	764	2.18	Yes
2017-09-04	17:08:30	17:16:05	Maple Bay	R	816	1.79	Yes
2017-09-04	17:57:15	18:02:45	Maple Bay	B	710	2.15	Yes
2017-09-04	18:02:45	18:05:20	Maple Bay	C	418	2.70	Yes
2017-09-04	18:05:20	18:14:15	Maple Bay	D	1233	2.30	Yes
2017-09-04	18:14:15	18:19:45	Maple Bay	G	739	2.24	Yes
2017-09-04	18:19:45	18:21:50	Maple Bay	F	265	2.12	Yes
2017-09-05	9:58:11	10:03:25	Sansum Narrows	H	668	2.13	Yes
2017-09-05	10:03:25	10:10:10	Sansum Narrows	J	907	2.24	No
2017-09-05	10:10:10	10:16:41	Sansum Narrows	L	747	1.91	Yes
2017-09-05	10:16:41	10:29:22	Sansum Narrows	E	1722	2.26	Yes
2017-09-05	10:29:22	10:32:41	Sansum Narrows	A	363	1.82	Yes
2017-09-05	10:59:32	11:08:33	Sansum Narrows	I	1091	2.02	Yes
2017-09-05	11:08:33	11:13:05	Sansum Narrows	K	642	2.36	Yes
2017-09-05	11:13:05	11:18:37	Sansum Narrows	L	785	2.37	Yes
2017-09-05	11:18:37	11:27:58	Sansum Narrows	M	1198	2.14	Yes
2017-09-05	11:27:58	11:31:08	Sansum Narrows	A	376	1.98	Yes
2017-09-05	11:59:45	12:05:10	Sansum Narrows	H	661	2.04	Yes
2017-09-05	12:05:10	12:12:40	Sansum Narrows	J	907	2.02	Yes
2017-09-05	12:12:40	12:19:45	Sansum Narrows	L	768	1.81	Yes
2017-09-05	12:19:45	12:34:47	Sansum Narrows	E	1739	1.93	Yes
2017-09-05	12:34:47	12:38:24	Sansum Narrows	A	377	1.74	Yes
2017-09-05	13:06:37	13:15:06	Sansum Narrows	I	1100	2.16	Yes
2017-09-05	13:15:06	13:19:58	Sansum Narrows	K	622	2.13	Yes
2017-09-05	13:19:58	13:25:30	Sansum Narrows	L	781	2.35	Yes
2017-09-05	13:25:30	13:36:03	Sansum Narrows	M	1191	1.88	No
2017-09-05	13:36:03	13:39:56	Sansum Narrows	A	379	1.63	Yes
2017-09-05	14:07:50	14:13:40	Sansum Narrows	H	668	1.91	Yes
2017-09-05	14:13:40	14:22:10	Sansum Narrows	J	907	1.78	Yes
2017-09-05	14:22:10	14:28:10	Sansum Narrows	L	777	2.16	Yes
2017-09-05	14:28:10	14:41:10	Sansum Narrows	E	1759	2.25	Yes
2017-09-05	14:41:10	14:45:20	Sansum Narrows	A	394	1.58	Yes
2017-09-05	15:07:49	15:15:50	Sansum Narrows	I	1064	2.21	Yes
2017-09-05	15:15:50	15:21:50	Sansum Narrows	K	637	1.77	Yes
2017-09-05	15:21:50	15:27:50	Sansum Narrows	L	776	2.15	Yes
2017-09-05	15:27:50	15:36:09	Sansum Narrows	M	1209	2.42	Yes
2017-09-05	15:36:09	15:39:14	Sansum Narrows	A	385	2.08	Yes
2017-09-05	16:07:40	16:13:45	Sansum Narrows	H	685	1.88	Yes
2017-09-05	16:13:45	16:21:30	Sansum Narrows	J	928	2.00	Yes
2017-09-05	16:21:30	16:28:02	Sansum Narrows	L	774	1.97	Yes
2017-09-05	16:28:02	16:40:29	Sansum Narrows	E	1758	2.35	Yes
2017-09-05	16:40:29	16:44:22	Sansum Narrows	A	381	1.63	Yes
2017-09-05	17:08:52	17:17:57	Sansum Narrows	I	1074	1.97	Yes
2017-09-05	17:17:57	17:22:15	Sansum Narrows	K	584	2.26	Yes
2017-09-05	17:22:15	17:27:11	Sansum Narrows	L	777	2.63	Yes
2017-09-05	17:27:11	17:35:10	Sansum Narrows	M	1213	2.53	Yes
2017-09-05	17:35:10	17:38:37	Sansum Narrows	A	387	1.87	Yes
2017-09-05	17:59:13	18:04:20	Sansum Narrows	H	675	2.20	Yes
2017-09-05	18:04:20	18:11:27	Sansum Narrows	J	917	2.15	Yes
2017-09-05	18:11:27	18:18:30	Sansum Narrows	L	777	1.84	Yes
2017-09-05	18:18:30	18:30:55	Sansum Narrows	E	1762	2.36	No
2017-09-05	18:30:55	18:34:20	Sansum Narrows	A	393	1.92	Yes
2017-09-06	8:30:41	8:36:50	Maple Bay	B	703	1.91	Yes
2017-09-06	8:36:50	8:40:21	Maple Bay	C	441	2.09	Yes
2017-09-06	8:40:21	8:50:07	Maple Bay	D	1225	2.09	Yes
2017-09-06	8:50:07	8:56:15	Maple Bay	G	736	2.00	Yes

Date	Start Time	End Time	Site	Letter	Length (m)	Speed (m/s)	Retained for Analysis
2017-09-06	8:56:15	8:58:45	Maple Bay	F	275	1.83	Yes
2017-09-06	9:24:25	9:27:52	Maple Bay	P	362	1.75	Yes
2017-09-06	9:27:52	9:31:50	Maple Bay	Q	452	1.90	Yes
2017-09-06	9:31:50	9:36:42	Maple Bay	O	646	2.21	Yes
2017-09-06	9:36:42	9:43:10	Maple Bay	N	783	2.02	Yes
2017-09-06	9:43:10	9:49:50	Maple Bay	R	790	1.97	Yes
2017-09-06	10:25:05	10:31:55	Maple Bay	B	727	1.77	Yes
2017-09-06	10:31:55	10:35:51	Maple Bay	C	454	1.92	Yes
2017-09-06	10:35:51	10:47:50	Maple Bay	D	1231	1.71	Yes
2017-09-06	10:47:50	10:54:20	Maple Bay	G	752	1.93	Yes
2017-09-06	10:54:20	10:57:07	Maple Bay	F	272	1.63	Yes
2017-09-06	12:15:00	12:18:03	Maple Bay	P	374	2.05	Yes
2017-09-06	12:18:03	12:21:56	Maple Bay	Q	443	1.90	Yes
2017-09-06	12:21:56	12:27:52	Maple Bay	O	652	1.83	Yes
2017-09-06	12:27:52	12:33:47	Maple Bay	N	770	2.17	Yes
2017-09-06	12:33:47	12:48:30	Maple Bay	R	792	0.90	Yes
2017-09-06	13:03:34	13:09:22	Maple Bay	B	733	2.11	Yes
2017-09-06	13:09:22	13:13:40	Maple Bay	C	455	1.76	Yes
2017-09-06	13:13:40	13:23:50	Maple Bay	D	1225	2.01	Yes
2017-09-06	13:23:50	13:30:20	Maple Bay	G	758	1.94	Yes
2017-09-06	13:30:20	13:33:00	Maple Bay	F	281	1.75	Yes
2017-09-06	14:25:11	14:28:14	Maple Bay	P	373	2.04	Yes
2017-09-06	14:28:14	14:31:38	Maple Bay	Q	448	2.20	Yes
2017-09-06	14:31:38	14:36:38	Maple Bay	O	672	2.24	Yes
2017-09-06	14:36:38	14:41:55	Maple Bay	N	754	2.38	Yes
2017-09-06	14:41:55	14:49:00	Maple Bay	R	805	1.89	Yes
2017-09-06	15:22:29	15:28:20	Maple Bay	B	727	2.07	Yes
2017-09-06	15:28:20	15:32:15	Maple Bay	C	448	1.91	Yes
2017-09-06	15:32:15	15:42:40	Maple Bay	D	1235	1.98	Yes
2017-09-06	15:42:40	15:48:58	Maple Bay	G	760	2.01	Yes
2017-09-06	15:48:58	15:51:20	Maple Bay	F	273	1.92	Yes
2017-09-06	17:20:35	17:23:48	Maple Bay	P	366	1.89	Yes
2017-09-06	17:23:48	17:27:43	Maple Bay	Q	446	1.90	Yes
2017-09-06	17:27:43	17:33:40	Maple Bay	O	667	1.87	Yes
2017-09-06	17:33:40	17:39:50	Maple Bay	N	764	2.06	Yes
2017-09-06	17:39:50	17:46:23	Maple Bay	R	793	2.02	Yes
2017-09-07	8:21:45	8:26:53	Sansum Narrows	H	674	2.19	Yes
2017-09-07	8:26:53	8:34:04	Sansum Narrows	J	915	2.12	Yes
2017-09-07	8:34:04	8:41:00	Sansum Narrows	L	755	1.81	Yes
2017-09-07	8:41:00	8:52:24	Sansum Narrows	E	1735	2.54	Yes
2017-09-07	8:52:24	8:56:30	Sansum Narrows	A	377	1.53	Yes
2017-09-07	9:34:07	9:44:20	Sansum Narrows	I	1098	1.79	Yes
2017-09-07	9:44:20	9:49:40	Sansum Narrows	K	635	1.98	Yes
2017-09-07	9:49:40	9:55:20	Sansum Narrows	L	759	2.23	Yes
2017-09-07	9:55:20	10:04:00	Sansum Narrows	M	1232	2.37	Yes
2017-09-07	10:04:00	10:07:55	Sansum Narrows	A	402	1.71	Yes
2017-09-07	10:48:29	10:54:25	Sansum Narrows	H	658	1.85	Yes
2017-09-07	10:54:25	11:02:20	Sansum Narrows	J	910	1.92	Yes
2017-09-07	11:02:20	11:08:45	Sansum Narrows	L	743	1.93	Yes
2017-09-07	11:08:45	11:22:35	Sansum Narrows	E	1736	2.09	Yes
2017-09-07	11:22:35	11:26:05	Sansum Narrows	A	404	1.93	Yes
2017-09-07	12:02:45	12:11:35	Sansum Narrows	I	1084	2.05	Yes
2017-09-07	12:11:35	12:16:30	Sansum Narrows	K	633	2.15	Yes
2017-09-07	12:16:30	12:22:43	Sansum Narrows	L	765	2.05	Yes
2017-09-07	12:22:43	12:32:38	Sansum Narrows	M	1211	2.03	Yes
2017-09-07	12:32:38	12:35:45	Sansum Narrows	A	391	2.09	Yes
2017-09-07	13:03:28	13:08:40	Sansum Narrows	H	663	2.13	Yes
2017-09-07	13:08:40	13:16:01	Sansum Narrows	J	907	2.06	Yes
2017-09-07	13:16:01	13:22:10	Sansum Narrows	L	731	1.98	Yes
2017-09-07	13:22:10	13:37:22	Sansum Narrows	E	1715	1.88	Yes
2017-09-07	13:37:22	13:40:39	Sansum Narrows	A	393	1.99	No
2017-09-07	14:17:35	14:25:35	Sansum Narrows	I	1065	2.22	Yes
2017-09-07	14:25:35	14:30:37	Sansum Narrows	K	647	2.14	Yes
2017-09-07	14:30:37	14:36:04	Sansum Narrows	L	762	2.33	Yes
2017-09-07	14:36:04	14:45:06	Sansum Narrows	M	1208	2.23	Yes
2017-09-07	14:45:06	14:49:50	Sansum Narrows	A	408	1.44	Yes
2017-09-07	15:23:34	15:29:16	Sansum Narrows	H	669	1.96	Yes
2017-09-07	15:29:16	15:37:15	Sansum Narrows	J	922	1.92	Yes
2017-09-07	15:37:15	15:44:40	Sansum Narrows	L	752	1.69	Yes
2017-09-07	15:44:40	15:57:40	Sansum Narrows	E	1698	2.18	Yes
2017-09-07	15:57:40	16:01:50	Sansum Narrows	A	370	1.48	Yes
2017-09-07	16:59:56	17:08:33	Sansum Narrows	I	1067	2.06	Yes
2017-09-07	17:08:33	17:13:30	Sansum Narrows	K	628	2.12	Yes
2017-09-07	17:13:30	17:19:11	Sansum Narrows	L	759	2.23	Yes
2017-09-07	17:19:11	17:27:45	Sansum Narrows	M	1221	2.38	Yes
2017-09-07	17:27:45	17:31:30	Sansum Narrows	A	404	1.80	Yes

7.3 Appendix 3 - Comparison of Field and Lab Assessment of Juvenile Salmon Diet Composition

7.3.1 *Background*

We sampled diets of juvenile Chinook Salmon non-lethally by gastric lavage in the Southern Gulf Islands of the Salish Sea in 2015 (see Chapter 4) and 2016 (see Chapter 5). In 2015 diets were sampled for 324 Chinook Salmon (results for 262 of these fish are reported in detail in Chapter 4) while in 2016 we sampled diets for 731 juvenile Chinook Salmon. In both years, the products of gastric lavage were examined in the field with the naked eye and the presence or absence of broad taxonomic categories of potential prey was assessed. The taxonomic categories assessed varied slightly between years with the coarsest level of identification across years being cephalopods, copepods, hyperiid amphipods, decapods, gammarid amphipods, fish, polychaetes, euphausiids, insects, and pteropods. Stomach contents of juvenile salmon sampled in 2015 were also subjected to a detailed quantitative analysis in the lab, with stomach contents counted, separated into taxonomic groups, and weighed (see Chapter 4). To validate the use of field presence and absence observations as a metric of diet composition in 2016 we compared laboratory and field assessment of diets for the juvenile Chinook Salmon sampled in 2015. Diets of one Coho Salmon and twelve Chinook/Coho Salmon hybrids sampled in 2015 were also included in this analysis for a total sample size of 337.

7.3.2 *Methods*

For each juvenile salmon diet sample examined in the lab in 2015 we summed the mass of stomach contents in each category assessed for presence or absence in the field. We then calculated the gravimetric proportion of the diet of each fish that was not accounted for by prey categories scored as “present” in the field. We calculated the mean proportion of individual diets that were missed by presence and absence sampling and the aggregate proportion of the diet that was missed by presence and absence sampling. We also assessed how often a prey category was scored as present in the field and subsequently not identified in the lab and how often a prey category was scored as absent in the field but subsequently was detected in the lab. The “other” category was not included in these analyses.

7.3.3 *Results and Conclusion*

Assignment of prey group presence in the field was relatively accurate, ranging from no false positive assignments for fish and decapods to 22% false positive assignments for polychaetes (Table A1). Failure to detect presence in the field was more common, ranging from 5% of occurrences of hyperiid amphipods to 71% of occurrences of polychaete worms. Despite some relatively high false negative rates for assessment of prey group presence in the field, only a small gravimetric proportion of the diet was missed during field assessments. An average of 7.0% of the stomach contents of individual fish was constituted by prey categories not scored as present in the field. For individual prey taxa, the proportion of the overall contribution to diets that was missed during field assessments was below 12% for all groups except polychaetes and pteropods (which together represented less than 0.25% of diets). When all prey was aggregated by mass, a total of 1.9% of the aggregate mass was missed during assessment for presence in the field. The "other" category, which was not included in the comparison between field assessment and lab assessment of diets, constituted 1.9% of the overall mass of stomach contents analyzed in the lab.

While prey category presence was frequently missed in the field, a high gravimetric proportion of the diet was covered by field assessment (mean 93% of individual diets and 98.1% of aggregate diets).

7.3.4 *Tables*

Table 7.6 Comparison of lab and field identification of 10 different prey categories in 337 juvenile salmon for which products of gastric lavage were examined both in the field and in the lab in 2015.

	Cephalopod	Copepod	Hyperiid	Decapod	Gammarid	Fish	Polychaete	Euphausiid	Insect	Pteropod
Count of Presence In Field	36	59	244	237	31	118	9	39	17	8
Field Presence Not Confirmed in Lab	2	1	4	1	1	0	2	5	2	1
Proportion False Field Presence	6%	2%	2%	0%	3%	0%	22%	13%	12%	13%
Count of Presence in Lab	36	94	252	253	44	165	24	47	19	15
Lab Presence Missed in Field	2	36	12	17	14	47	17	13	4	8
Proportion Missed in Field	6%	38%	5%	7%	32%	28%	71%	28%	21%	53%
Proportion of Mass Missed in Field	0.2%	6.0%	0.9%	0.3%	11.6%	2.6%	34.7%	4.3%	1.6%	49.1%
Proportion of Overall Diet*	10.03%	0.25%	8.93%	23.75%	0.80%	53.39%	0.18%	1.96%	0.67%	0.04%