AN ABSTRACT OF THE DISSERTATION OF

Marisa Norma Chantal Litz for the degree of Doctor of Philosophy in Fisheries Science presented on December 9, 2016.

Title: Feeding Ecology and Growth of Juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) During Early Marine Residence.

Abstract approved:

_____

Jessica A. Miller

The early marine phase following freshwater emigration has been identified as a critical period in salmonid (*Oncorhynchus* spp.) life history, characterized by high but variable mortality. Consistent with the "growth-mortality" and "bigger-is-better" hypotheses, at least some of the mortality during the critical period appears to be size-dependent – with smaller or slower growing individuals less likely to survive than larger, faster growing conspecifics. Size and growth are flexible morphological traits that vary with prey availability, yet there is incomplete information on the temporal and spatial match/mismatch between juvenile salmonids and their marine prey in the Northern California Current Ecosystem. This work addressed a gap in the understanding of seasonal variability in prey community composition, abundance, and quality during early marine residence. Three studies were conducted using a population of subyearling (age-0) Chinook salmon (*O. tshawytscha*) from the upper

Columbia River in order to evaluate the effects of prey on salmon growth, biochemistry, and performance. The first was a laboratory study that tested for growth rate and swimming speed differences in salmon reared on three treatment diets followed by three fasting treatments to assess the effects of variability in summer diet quality and winter diet quantity. Significant differences in growth were detected among fasting treatments but not diet treatments. Also, larger salmon with more storage lipids swam faster than smaller leaner fish following fasting, indirectly supporting the notion that growth during the critical period provides a carryover benefit important for overwinter survival. Salmon fatty acids and bulk stable isotopes of carbon and nitrogen were measured throughout the experiment to provide estimates of turnover and incorporation rates. The next study was a longitudinal field study that measured variation in salmon size and prey field community throughout the early ocean period (May – September) over two years of high marine survival (2011 and 2012) to better understand the relationship between prey community composition and salmon growth. Maximum growth rates were associated with high biomass of northern anchovy (*Engraulis mordax*) which peaked in abundance at different times in each year. The final bioenergetics modeling study combined data from the laboratory and field studies to evaluate the relative importance of prey availability, prey energy density, and temperature on salmon growth. Variation in feeding rate was related most with growth rate variability and least with prey energy density. Throughout their range, subyearlings can grow at high rates in the ocean (>2% body weight per day) by consuming both invertebrate and marine fish prey. However, when marine fish prey are highly abundant they likely provide an energetic advantage

over invertebrate prey by reducing overall foraging costs. Quantifying the abundance, size, diet, and distribution of juvenile salmonids relative to their prey field throughout early ocean residence will contribute to a better understanding of seasonal differences in trophic interactions that are associated with differences in annual growth and survival rates. Moreover, an integrated approach that combines sampling of prey with measurements of predator growth, diet, fatty acids, and stable isotopes provides a useful framework for assessing trophic dynamics and evaluating the effects of climate variability and change on predator and prey communities.

# Feeding Ecology and Growth of Juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) During Early Marine Residence

by
Marisa Norma Chantal Litz

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented December 9, 2016
Commencement June 2017

Doctor of Philosophy dissertation of Marisa Norma Chantal Litz presented on December 9, 2016

APPROVED:

Major Professor, representing Fisheries Science

Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Marisa Norma Chantal Litz, Author

# ACKNOWLEDGEMENTS

This dissertation is the result of many years of hard work that would not have been possible without the contribution and support of many individuals. I am sincerely indebted to my major advisor, Dr. Jessica A. Miller, who showed a steady and unwavering commitment to my intellectual development. I was fortunate to have her as a mentor and a role model. I am thankful to my committee members – Dr. Louise A. Copeman, Dr. Laurie A. Weitkamp, Dr. Robert M. Suryan, and Dr. Christopher J. Marshall, for accepting nothing less than the best and for their help in honing my critical thinking skills. I am grateful for their insight, patience, and advice, and feel lucky to have benefitted from their wisdom throughout this process. Dr. Thomas P. Hurst and Dr. Kelly J. Benoit-Bird deserve special mention for continually questioning my assumptions and for encouraging me to think more deeply about ocean ecology despite not serving as official committee members. I am a better scientist for our numerous discussions. I appreciate the researchers of the Estuarine and Ocean and Ecology Program at NOAA Fisheries Northwest Fisheries Science Center, especially Kurt L. Fresh, Dr. William T. Peterson, Dr. Richard D. Brodeur, Dr. Kym C. Jacobson, Paul J. Bentley, and Cheryl A. Morgan, for providing me with ship time, office space, and technical support through the completion of my dissertation, and for allowing me to be a contributing member of their group over the years. To the numerous friends, lab-mates, and volunteers who helped out in the field and in the laboratory, your contributions to this work have not gone unnoticed – thank you so much for your time and assistance. Detailed acknowledgements are offered at the end of each chapter. To the Newport surfing community, thank you for your stoke

over the years and for invigorating my research with your commitment to and connection with the coastal ocean. Lastly, thank you to my husband and best friend, Gregory P. Hutchinson, who has been along on this ride with me for over a decade. This work was supported by the Cooperative Institute for Marine Resources Studies', the NOAA Living Marine Resources Cooperative Science Center, and scholarships awarded by the NOAA Educational Partnership Program and Oregon State University.

# CONTRIBUTION OF AUTHORS

Dr. Jessica A. Miller was involved in project overview, experimental design, data analysis, and helped with the writing of Chapters 2 – 4. Dr. Louise A. Copeman helped with the experimental design, laboratory analysis, and writing of Chapters 2 and 3. Dr. Thomas P. Hurst provided technical expertise and helped with the experimental design, data analysis, and writing of Chapter 2. Dr. Laurie A. Weitkamp and Elizabeth A. Daly provided diet data and helped with the data analysis and writing of Chapters 3 and 4. David J. Teel provided genetic analysis of samples and helped with the writing of Chapter 3. Andrew M. Claiborne provided growth data, assisted in field collections, and helped with the writing of Chapter 3. Dr. Richard D. Brodeur and Dr. Adam G. Hansen provided help with the bioenergetics modeling and writing of Chapter 4.

# TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

# LIST OF FIGURES

LIST OF FIGURES (Continued)

# LIST OF TABLES

# LIST OF APPENDICES

# DEDICATION

This dissertation is dedicated to the two people who inspired and supported me the most, Dr. Henry A. R. Litz and Dr. Robert L. Emmett, who both lost their battles with cancer while I was conducting this work.

# CHAPTER 1

## GENERAL INTRODUCTION

Interactions between predators and prey have been a major focus of research in terrestrial and aquatic ecosystems over the last century because they are important for identifying the evolutionary and ecological mechanisms underlying population dynamics (Lotka 1925; Holling 1959; Paine 1969). Predators may reduce prey population sizes directly through consumption or indirectly by impeding their ability to forage and reproduce (Berryman 1992; Lima 1998; Preisser et al. 2005). Likewise, prey populations may impact predator population sizes directly through their abundance or indirectly by influencing the predator's habitat choice, feeding rates, and competitive interactions with other consumers (Charnov 1976; Roughgarden 1983; Cushing 1990). In addition to the overall abundance of prey resources, variability in prey quality may also be an important regulatory mechanism influencing predator population dynamics through time and is often related to environmental variability (Mayntz et al. 2003; Litzow et al. 2006; Österblom et al. 2008). This dissertation explores the interactive effects of prey quantity, prey quality, and the environment on the growth, biochemistry, and aerobic performance of a marine predator.

Pacific salmon (*Oncorhynchus* spp.) and steelhead (*O. mykiss*) populations (salmonids) are culturally and economically important, supporting recreational, tribal, and commercial fisheries along the west coast of North America. Most salmonids adopt an anadromous life history strategy (Rounsefell 1958; Healey 1991; Quinn and Myers 2004) – adults migrate from the ocean into freshwater to spawn, and after a rearing

period, juveniles migrate to the ocean and grow quickly before returning to their natal streams within 1 – 5 years to reproduce. Despite the extended ocean residence period, for many years researchers viewed life in the ocean as a "black box". Research efforts on the ocean ecology of salmonids in recent decades has led to better understanding of the marine processes that drive productivity, and this information is helping fishery managers make informed science-based decisions to help sustain populations.

Work on the ocean ecology of juvenile salmonids over the last 40 years has led to better understanding of processes impacting survival. Arguably one of the most important insights are that the first weeks to months in the ocean through the first ocean winter represent a "critical period" in salmonid life history, when mortality rates are high (>90%) but variable from year to year (Fisher and Pearcy 1988; Pearcy 1992; Pearcy and McKinnell 2007). Mortality during the early marine period is typically attributed to a suite of pressures that include predation, inter- and intra-specific competition, food scarcity, disease, and parasitism (Pearcy 1992; Hutchinson et al. 2002; Sandell et al. 2015).

The importance of survival through the critical period was originally evidenced by strong positive relationships observed between numbers of precocious males, or "jacks" that return to spawn after just a few months in the ocean, relative to the numbers of adults that return in later years (Peterman 1982; Pearcy 1992; Haeseker et al. 2008). However, these associations have become weaker in recent years (Burke et al. 2013). Correlations between ocean conditions (plume volume) in spring and summer, attributes of juveniles (size, condition, diet) in fall, and subsequent adult returns can be high (Miller et al. 2013; Losee et al. 2014; Dale et al. 2017). These relationships suggest that there

may be multiple factors operating throughout early marine life that are regulating survival. Strong relationships between ocean conditions in winter after ocean entry and coho (*O. kisutch*) survival also indicate that physiological condition and energy stores may limit survival during the first ocean winter (Beamish and Mahnken 2001; Logerwell et al. 2003). These observations lend support to the idea that summer mortality can be high but winter mortality may be more directly related to survival to adulthood. Thus, the timing of the critical period, i.e., the point after which mortality is relatively stable and abundance is a good predictor of recruitment, may vary from year to year. Investigations that focus on specific stock groups throughout the early marine period may be more insightful in terms of identifying relevant scales and processes that are regulating survival during early ocean residence.

Marine survival of salmonids is related to oceanographic conditions (Mantua et al. 1997; Logerwell et al. 2003; Stachura et al. 2014). For populations in the Pacific Northwest, ocean conditions are considered more favorable for survival when temperatures are cooler, primary and secondary production are higher, and piscivorous predators less abundant than when ocean conditions are warmer, less productive, and predator abundances higher. The mechanisms underlying this general phenomenon have not entirely been identified, although considerable progress has been made in identifying relevant metrics that are correlated with salmonid survival. Indicators of the ocean environment, which include physical indices at both local (e.g. temperature, upwelling) and ocean basin scales (e.g. Pacific Decadal Oscillation and El Niño), and biological indices of potential prey (e.g. zooplankton and ichthyoplankton) and predators have

proven useful in forecasting salmonid survival when combined in multivariate models (Burke et al. 2013; Peterson et al. 2014).

In a long-term effort to elucidate the mechanisms regulating marine survival of salmonids, ocean surveys have focused on juveniles emigrating from the Columbia River Basin since 1998 (for methods see Brodeur et al. 2005). Complementary studies evaluating community structure in the lower Columbia River estuary (Weitkamp et al. 2012; Teel et al. 2014; Weitkamp et al. 2015), and abundance of zooplankton (Hooff and Peterson 2006), ichthyoplankton (Daly et al. 2013), forage fish (Emmett et al. 2005; Litz et al. 2008; Kaltenberg et al. 2010), and predators (Emmett et al. 2006; Emmett and Krutzikowsky 2008; Evans et al. 2012) in coastal waters have resulted in better understanding of the relationships between juvenile salmonids, the estuarine and pelagic community, and oceanography along the continental shelf.

Most information about juvenile salmonid prey comes from diet studies. Previous work evaluating diet (Daly et al. 2009; Daly and Brodeur 2015; Dale et al. 2017) has identified important prey resources, but information on seasonal and inter-annual variation in the prey field and the relationship between the prey field and the environment remain relatively unknown (but see Schabetsberger et al. 2003; Brodeur and Morgan 2016). This is largely because the prey field has proven difficult to quantitatively sample in the pelagic environment (Brodeur et al. 2011).

Upon ocean entry, juvenile salmonids transition from feeding mostly on invertebrates to mostly on fish (Daly et al. 2009). It has been hypothesized that consuming fish may be more favorable for salmonid growth, although this hypothesis has not been explicitly tested. Size and growth during the early life history phases of many

marine fish species have been shown to correlate with survival (Anderson 1988; Sogard 1997; Houde 2008). Achieving a larger size may reduce the pool of potential predators, and growing quickly enough to pass a size threshold for predation may reduce the amount of time when a fish is vulnerable. Size-selective mortality of smaller salmonids during the first few months in the ocean has been demonstrated in some populations of Pacific salmon (Moss et al. 2005) but other studies have found no evidence that smaller individuals are removed from the population in higher proportions during early ocean entry, especially during years of high survival (Woodson et al. 2013; Claiborne et al. 2014; Gamble 2016). Therefore, if growth has a benefit to survival during early marine residence, it may not be apparent until the first ocean winter.

The primary objective of this work was to examine the intersecting roles of prey quantity, prey quality, and the environment on juvenile Chinook (*O. tshawytscha*) salmon growth and performance during early marine residence. Three studies using subyearlings (juveniles that migrate to sea as age-0 fish) from the same genetic stock of origin in the upper Columbia River Basin (upper Columbia summer-fall Chinook) were designed to address this objective. The investigations included a laboratory rearing experiment (Chapter 2) to test the hypothesis that marine fish prey fatty acids are superior to invertebrate prey fatty acids for salmon growth and performance under both feeding and fasting conditions; a field study (Chapter 3) to quantify seasonal and inter-annual variability in the prey field with respect to coastal oceanography and salmon diet, growth, condition, and biochemistry; and a bioenergetics modeling study (Chapter 4) to better understand the relative contributions of prey quality, prey quantity, and temperature on salmon growth observed in the field. Collectively, this work disentangles elements of

prey and the environment that are driving variation in observed salmon growth rates to provide insight on the energy dynamics underlying predator-prey interactions during early marine residence.

A hypothesis that served as an overarching framework guiding this work was that marine fish prey are superior to invertebrate prey for salmon growth and survival. The quality of prey, in terms of energy density, may be related to the overall abundance of prey lipids (Iverson et al. 2002), prey lipid classes (Anthony et al. 2000), or prey fatty acids (Litzow et al. 2006). Lipids are rich energy sources that play an important role in energy transfer and growth during the critical period of marine fishes (Houde 2008). The diversity of lipids in marine foodwebs was reviewed in detail by Parrish (2013). In salmonids, lipid classes can be distinguished from one another based on their increasing polarity (Fig 1.1): steryl esters, triacylglycerols, free fatty acids, sterols, and polar lipids. Lipid classes serve different functions – triacylglycerols are important in energy storage whereas sterols and polar lipids are important in maintaining cell structure. The primary constituent of most lipid classes are the fatty acids. The essential fatty acids, which are fatty acids that are obtained from diet and are directly transferred to the consumer with little to no modification, can be used to trace trophic links in marine food webs (Dalsgaard et al. 2003).

In marine fish, the essential fatty acids docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA) are structurally important in maintaining cell membranes and functionally important as precursors for hormones known as eicosanoids (Sargent et al. 1999). Previous research determined that marine fish prey contains more DHA than EPA, yielding DHA:EPA ratios that are >1, whereas invertebrate prey contains more

EPA than DHA; thus invertebrate DHA:EPA ratios are <1 (Daly et al. 2010). Ratios of DHA:EPA that are between 1 and 2 are favorable for larval and juvenile growth and survival in a number of marine fish species (Watanabe 1993; Copeman et al. 2002; Takeuchi 2014), but it is unknown what the effect of dietary DHA:EPA is on juvenile Chinook salmon.

The laboratory rearing experiment (Chapter 2) was conducted in three phases and tested the effects of dietary fatty acids and diet ration on salmon growth, biochemistry, and aerobic performance to better understand the effects of prey quality and quantity on growth during the critical period. In phase one, salmon were reared on treatment diets that included an invertebrate-dominated (krill, *Euphausia pacifica* and *Thysanoessa spinifera*), high EPA diet; a fish-dominated (northern anchovy, *Engraulis mordax*), high DHA diet; and a mixed diet (krill and anchovy, DHA:EPA = 1). The expectation was that salmon reared on the fish-dominated diet would grow faster than salmon reared on the krill-dominated diet.

Diets of consumers can be measured directly through gut contents analysis, but observations are limited to the last meal. Diets can also be measured indirectly through analysis of dietary biomarkers in the tissues of consumers. Dietary biomarkers are chemical compounds characteristic of an organism that can be used to identify trophic links and energy pathways in ecosystems. Two types of chemical biomarkers that have been used in trophic studies are fatty acids and bulk carbon and nitrogen stable isotopes ($\delta^{13}C$ and $\delta^{15}N$). Values of $\delta^{13}C$ can be used to trace carbon sources (e.g. freshwater or marine) at the base of the food web and $\delta^{15}N$ values can be used to infer trophic position, as values increase with each trophic level (Fry 2006). Both fatty acids and stable isotopes

provide information on diet and nutrient sources integrated over weeks to months, and combined are a powerful tool for reconstructing food sources (Dalsgaard et al. 2003; Fry 2006; Vander Zanden et al. 2015).

Salmon fatty acids and stable isotopes were tracked through time during the phase one of the laboratory feeding experiment presented in Chapter 2 to measure lags between consumption and expression in tissues. Growth and lipids were also measured in salmon that were fasted for varying amounts of time, to evaluate the effect of fasting on salmon growth and lipid stores. During the last phase of the experiment, to evaluate whether dietary fatty acids provided a carryover effect in terms of future aerobic performance, critical swimming speeds were measured in fasted salmon. Expectations were that salmon reared on the fish-dominated, high DHA diet would grow larger, have higher triacylglycerol stores, and swim faster than salmon reared on the invertebrate-dominated, high EPA diet.

The field study presented in Chapter 3 was designed to concurrently sample juvenile salmon and their potential prey in coastal waters near the vicinity of the mouth of the Columbia River to evaluate the relative importance of prey quantity versus quality on salmon growth and condition. The seasonal development of the salmon prey field over two years was described in relation to oceanographic conditions using multivariate analysis. Next, changes in salmon size, growth, and stomach contents were measured for comparison with the prey field. Lastly, diet contributions were analyzed using a complementary fatty acid and stable isotope approach to evaluate dietary shifts in relation to an ontogenetic shift in habitat (freshwater to saltwater). This was the first study to

longitudinally sample both salmon and their prey during early marine residence and to utilize dietary biomarkers to make inferences about dietary contributions through time.

Bioenergetics models, based on mass-balance equations, offer a sound theoretical approach for evaluating energy dynamics in individuals and populations (Ney 1993; Chipps and Wahl 2008). Bioenergetics models account for, and allocate, energy consumed by individuals to their respective fates (Winberg 1956):

$$C = M + W + G.$$

In the basic bioenergetics equation, *C* equals energy consumed, *M* represents energy allocated towards metabolism, *W* is waste products, and *G* is growth. The Wisconsin bioenergetics model (Hanson et al. 1997) used in this study accounts for changes in temperature, body size, and food quality through time (on a daily time step) when estimating consumption or growth.

In Chapter 4, results from the laboratory experiment (Chapter 2) and the field study (Chapter 3) were combined in a bioenergetics modeling study to measure the effects of prey quantity, quality, and temperature on salmon growth observed in the field. Salmon reared in the laboratory were used to evaluate performance of a bioenergetics model prior to applying it to field data. The bioenergetics model was then fit to observed growth from June to September during two years to estimate consumption. A sensitivity analysis was conducted to quantify the effects of observed variation in feeding rate (prey quantity), diet energy density (prey quality), and temperature on salmon growth during early marine residence. Results from this study, combined with information from

previous feeding and bioenergetics modeling studies, provide insight on foraging and energy allocation strategies that may be influencing salmonid survival throughout their range.

In the final chapter of this dissertation (Chapter 5) the primary findings of the laboratory experiment (Chapter 2), the field study (Chapter 3), and the bioenergetics modeling study (Chapter 4) were synthesized to highlight the significant contributions of this work and suggest directions for future research. New insight on the critical period is considered with reference to UCSF subyearling Chinook. Lastly, applications and limitations of the techniques employed are discussed in terms of the monitoring and management of Pacific salmon populations, with particular emphasis on the challenges of understanding predator-prey dynamics in a changing climate.

## LITERATURE CITED

Anderson JT (1988) A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J Northw Atl Fish Sci 8, 55–66.

Anthony JA, Roby DD, Turco KR (2000) Lipid content and energy density of forage fishes from the northern Gulf of Alaska. J Exp Mar Biol Ecol 248, 53–78.

Beamish RJ, Mahnken C (2001) A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog Oceanogr 49, 423–437.

Berryman AA (1992) The origins and evolution of predator-prey theory. Ecology 73, 1530–1535.

Brodeur RD, Fisher JP, Emmett RL, Morgan CA, Casillas E (2005) Species composition and community structure of pelagic nekton off Oregon and Washington under variable conditions. Mar Ecol Prog Ser 298, 41–57.

Brodeur RD, Daly EA, Benkwitt CE, Morgan CA, Emmett RL (2011) Catching the prey: sampling juvenile fish and invertebrate prey fields of juvenile coho and Chinook salmon during their early marine residence. Fish Res 108, 65–73.

Brodeur RD, Morgan CA (2016) Influence of a coastal riverine plume on the cross-shelf variability in hydrography, zooplankton, and juvenile salmon diets. Estuar Coasts 39, 1183–1198.

Burke BJ, Peterson WT, Beckman BR, Morgan CA, Daly EA, Litz MNC (2013) Multivariate models of adult Pacific salmon returns. PLoS ONE 8(1), e54134.

Charnov EL (1976) Optimal foraging: The marginal value theorem. Theor Popul Biol 9, 129–136.

Chipps SR, Wahl DH (2008) Bioenergetics modeling in the 21st century: reviewing new insights and revisiting old constraints. Trans Am Fish Soc 137, 298–313.

Claiborne AM, Miller JA, Weitkamp LA, Teel DJ (2014) Evidence for selective mortality in marine environments: the role of fish migration size, timing, and production type. Mar Ecol Prog Ser 515, 187–202.

Copeman LA, Parrish CC, Brown JA, Harel M (2002) Effects of docsahexaenoic, eicosapentaenoic, and arachidonic acids on the early growth, survival, lipid composition and pigmentation of yellowtail flounder (*Limanda ferruginea*): a live food enrichment experiment. Aquaculture 210, 285–304.

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26, 249–293.

Dale KE, Daly EA, Brodeur RD (2017) Interannual variability in the feeding and condition of subyearling Chinook salmon off Oregon and Washington in relation to fluctuating ocean conditions. Fish Oceanogr 26, 1–16.

Dalsgaard J, St. John M, Kattner G, Müeller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46, 224–340.

Daly EA, Brodeur RD, Weitkamp LA (2009) Ontogenetic shifts in diets of juvenile and subadult coho and Chinook salmon in coastal marine waters: Important for marine survival? Trans Am Fish Soc 138, 1420–1438.

Daly EA, Benkwitt CE, Brodeur RD, Litz MNC, Copeman LA (2010) Fatty acid profiles of juvenile salmon indicate prey selection strategies in coastal marine waters. Mar Biol 157, 1975–1987.

Daly EA, Auth TA, Brodeur RD, Peterson WT (2013) Winter ichthyoplankton biomass

as a predictor of early summer prey fields and survival of juvenile salmon in the northern California Current. Mar Ecol Prog Ser 484, 203–217.

Daly EA, Brodeur RD (2015) Warming ocean conditions relate to increased trophic requirements of threatened and endangered salmon. PLoS ONE 10(12), e0144066.

Emmett RL, Brodeur RD, Miller TW, Pool SS, Krutzikowsky GK, Bentley PJ, McCrae J (2005) Pacific sardine (*Sardinops sagax*) abundance, distribution, and ecological relationships in the Pacific Northwest. Calif Coop Ocean Fish Invest Rep 46, 122–143.

Emmett RL, Krutzikowsky GK, Bentley P (2006) Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998–2003: Relationship to oceanographic conditions, forage fishes, and juvenile salmonids. Prog Oceanogr 68, 1–26.

Emmett RL, Krutzikowsky GK (2008) Nocturnal feeding of Pacific hake and jack mackerel off the mouth of the Columbia River, 1998–2004: Implications for juvenile salmon predation. Trans Am Fish Soc 137, 657–676.

Evans AF, Hostetter NJ, Collis K, Lyons DE, Sandford BP, Ledgerwood RD, Sebring S (2012) Systemwide evaluation of avian predation on juvenile salmonids from the Columbia River based on recoveries of passive integrated transponder tags. Trans Am Fish Soc 141, 975–989.

Fisher JP, Pearcy WG (1988) Growth of juvenile coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington, USA, in years of differing coastal upwelling. Can J Fish Aquat Sci 45, 1036–1044.

Fry B (2006) Stable Isotope Ecology. Springer, New York.

Gamble MM (2016) Size-selective mortality and environmental factors affecting early marine growth during marine life stages of sub-yearling Chinook salmon in Puget Sound, Washington. MS Thesis, University of Washington, Seattle.

Haeseker SL, Peterman RM, Su Z, Wood CC (2008) Retrospective evaluation of preseason forecasting models for sockeye and chum salmon. N Am J Fish Manage 28, 12–29.

Hanson PC, Johnson TB, Schindler DE, Kitchell JF (1997) Fish Bioenergetics 3.0 for Windows. Center for Limnology, University of Wisconsin-Madison and the University of Wisconsin Sea Grant Institute. WISCU-T-97–001.

Healey MC (1991) Life history of Chinook salmon (*Oncorhynchus tshawytscha*). In Groot C, Margolis L (eds) Pacific Salmon Life Histories, UBC Press, Vancouver, pp 313–393.

Holling CS (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can Entomol 91, 293–320.

Hooff R, Peterson WT (2006) Copepod biodiversity as an indicator of changes in ocean and climate conditions of the northern California current ecosystem. Limnol Oceanogr 51, 2607–2620.

Houde ED (2008) Emerging from Hjort's shadow. J Northw Atl Fish Sci 41, 53–70.

Hutchinson P, Welch D, Boehlert G, Whelan K (2002) A synthesis of the joint meeting: causes of marine mortality of salmon in the North Pacific and North Atlantic Oceans and in the Baltic Sea. N Pac Anadr Fish Comm Tech Rep 4, 93–96.

Iverson SJ, Frost KJ, Lang SLC (2002) Fat content and fatty acid composition of forage fish and invertebrates in Prince William Sound, Alaska: factors contributing to among and within species variability. Mar Ecol Prog Ser 241, 161–181.

Kaltenberg AM, Emmett RL, Benoit-Bird KJ (2010) Timing of forage fish seasonal appearance in the Columbia River plume and link to ocean conditions. Mar Ecol Prog Ser 419, 171–184.

Lima S (1998) Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv Study Behav 27, 215–290.

Litz MNC, Emmett RL, Heppell SS, Brodeur RD (2008) Ecology and distribution of the northern subpopulation of northern anchovy (*Engraulis mordax*) off the U.S. west coast. Calif Coop Ocean Fish Invest Rep 49, 167–182.

Litzow MA, Bailey KM, Prahl FG, Heinz R (2006) Climate regime shifts and reorganization of fish communities: the essential fatty acid limitation hypothesis. Mar Ecol Prog Ser 315, 1–11.

Logerwell EA, Mantua NJ, Lawson PW, Francis RC, Agostini VN (2003) Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fish Oceanogr 12, 554–568.

Losee J, Miller JA, Peterson WT, Teel DJ, Jacobson KC (2014) Influence of ocean ecosystem variation on trophic interactions and survival of juvenile coho and Chinook Salmon. Can J Fish Aquat Sci 71, 1747–1757.

Lotka AJ (1925) Elements of Physical Biology. Williams and Wilkins, Baltimore.

Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. Bull Am Meteorol Soc 78, 1069–1079.

Maynz D, Toft S, Vollrath F (2003) Effects of prey quality and availability on the life history of a trap-building predator. Oikos 101, 631–638.

Miller JA, Teel DJ, Baptista A, Morgan CA (2013) Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook Salmon (*Oncorhynchus tshawytscha*). Can J Fish Aquat Sci 70, 617–629.

Moss JH, Beauchamp DA, Cross AD, Myers KW, Farley EV Jr, Murphy JM, Helle JH (2005) Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. Trans Am Fish Soc 134, 1313–1322.

Ney JJ (1993) Bioenergetics modeling today – growing pains on the cutting edge. Trans Am Fish Soc 122, 736–748.

Österblom H, Olsson O, Blenckner T, Furness RW (2008) Junk-food in marine ecosystems. Oikos 117, 967–977.

Paine RT (1969) The Pisaster-Tegula interaction: prey patches, predator food preference, and intertidal community structure. Ecology 50, 950–961.

Parrish CC (2013) Lipids in marine ecosystems. ISRN Oceanography 2013 Article ID 604045, 16 pp.

Pearcy WG (1992) Ocean Ecology of North Pacific Salmonids. Washington Sea Grant Program, University of Washington Press, Seattle.

Peterman RM (1982) Model of salmon age structure and its use in preseason forecasting and studies of marine survival. Can J Fish Aquat Sci 39, 1444–1452.

Pearcy WG, McKinnell SM (2007) The ocean ecology of salmon in the northeast Pacific Ocean – an abridged history. In Grimes CB, Brodeur RD, Halderson LJ, McKinnell SM (eds) The Ecology of Juvenile Salmon in the Northeast Pacific Ocean: Regional Comparisons. American Fisheries Society, Bethesda, pp 7–30.

Peterson WT, Fisher JL, Peterson JO, Morgan CA, Burke BJ, Fresh KL (2014) Applied fisheries oceanography: Ecosystem indicators of ocean conditions inform fisheries management in the California Current. Oceanography 27, 80–89.

Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86, 501–509.

Quinn TP, Myers KW (2004) Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited. Rev Fish Biol Fisher 14, 421–442.

Roughgarden J (1983) Competition and theory in community ecology. Am Nat 122, 583–601.

Rounsefell GA (1958) Anadromy in North American Salmonidae. Fish Bull 131, 171–185.

Sandell TA, Teel DJ, Fisher J, Beckman B, Jacobson KC (2015) Infections by *Renibacterium salmoninarum* and *Nanophyetus salmincola* Chapin are associated with reduced growth of juvenile Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Northeast Pacific Ocean. J Fish Dis 38, 365–378.

Sargent J, Bell G, McEvoy L, Tocher D, Estevez A (1999) Recent developments in the essential fatty acid nutrition of fish. Aquaculture 177, 191–199.

Schabetsberger R, Morgan CA, Brodeur RD, Potts CL, Peterson WT, Emmett RL (2003) Prey selectivity and diel feeding chronology of juvenile Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Columbia River plume. Fish Oceanogr 12, 523–540.

Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull Mar Sci 60, 1129–1157.

Stachura MM, Mantua NJ, Scheuerell MD (2014) Oceanographic influences on patterns in North Pacific salmon abundance. Can J Fish Aquat Sci 71, 226–235.

Takeuchi T (2014) Progress on larval and juvenile nutrition to improve the quality and health of seawater fish: a review. Fish Sci 80, 389–403.

Teel DJ, Bottom DL, Hinton SA, Kuligowski DR, McCabe GT, McNatt R, Roegner GC, Stamatiou LA, Simenstad CA (2014) Genetic identification of Chinook salmon in the Columbia River estuary: Stock-specific distributions of juveniles in shallow tidal and freshwater habitats. N Am J Fish Man 34, 621–641.

Vander Zanden MJ, Clayton MK, Moody EK, Solomon CT, Weidel BC (2015) Stable isotope turnover and half-life in animal tissues: a literature synthesis. PLoS ONE 10(1), e0116182.

Watanabe T (1993) Importance of docosahexaenoic acid in marine larval fish. J World Aquacult Soc 24, 152–161.

Weitkamp LA, Bentley PJ, Litz MNC (2012) Seasonal and interannual variation in juvenile salmonids and associated fish assemblage in open waters of the lower Columbia River estuary. Fish Bull 110, 426–450.

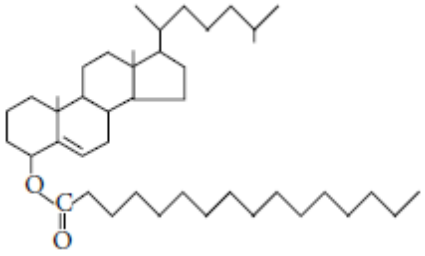
Weitkamp LA, Teel DJ, Liermann M, Hinton SA, Van Doornik DM, Bentley PJ (2015) Stock-specific size and timing at ocean entry of Columbia River juvenile Chinook salmon and steelhead: implications for early ocean growth. Mar Coast Fish 7, 370–392.

Winberg GG (1956) Rate of metabolism and food requirements of fishes. Fish Res Board Can Trans Ser 194.

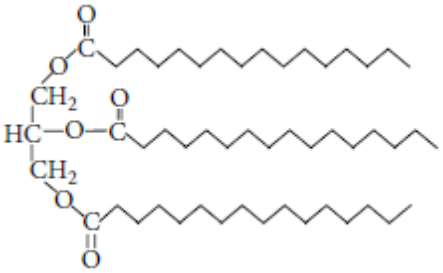
Woodson LE, Wells BK, Weber PK, MacFarlane RB, Whitman GE, Johnson RC (2013) Size, growth, and origin-dependent mortality of juvenile Chinook salmon *Oncorhynchus tshawytscha* during early ocean residence. Mar Ecol Prog Ser 487, 163–175.

**Figure 1.1** Structure of the major lipid classes identified in salmon tissue.

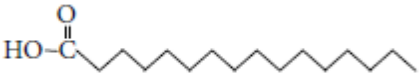
Steryl Ester



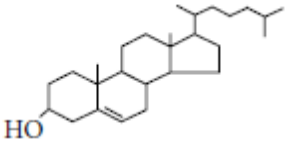
Triacyglererol



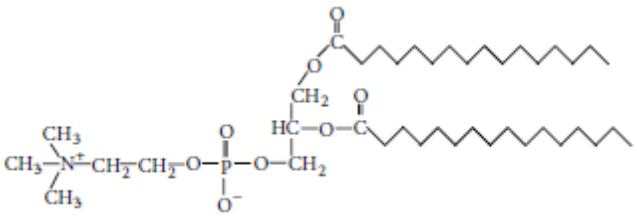
Free Fatty Acid



Sterol



Polar lipid (e.g. phospholipid)



CHAPTER 2

# EFFECTS OF DIETARY FATTY ACIDS ON JUVENILE SALMON GROWTH, BIOCHEMISTRY, AND AEROBIC PERFORMANCE: A LABORATORY REARING EXPERIMENT

Marisa N. C. Litz, Jessica A. Miller, Louise A. Copeman, and Thomas P. Hurst

*Journal of Experimental Marine Biology and Ecology*
Online ISSN: 0022-0981
In review

ABSTRACT

A three-phase experiment measured the effects of prey quality and diet ration on juvenile Chinook salmon (*Oncorhynchus tshawytscha*) performance. The first phase was designed to evaluate the effect of dietary levels of two essential fatty acids (EFAs), docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA) on salmon growth. Salmon were reared for 12 weeks on three diets varying in proportions of krill (*Thysanoessa spinifera* and *Euphausia pacifica*) and northern anchovy (*Engraulis mordax*). Supplements of DHA and EPA were added to the formulated diets to achieve DHA:EPA ratios (0.6, 0.9, and 1.5) representative of naturally occurring prey. Growth rates over 12 weeks were not significantly different among diet treatments, which may be because EFAs were provisioned above required amounts. Salmon maintained DHA at high levels (>20% of total fatty acids) across all treatments and sampling periods, whereas EPA reflected dietary concentrations after 12 weeks. Fatty acids were incorporated into salmon muscle at varying rates but on average reflected diet after 1 to 2 months, similar to bulk stable isotopes of carbon and nitrogen. The second phase of the experiment was designed to evaluate fasting effects on salmon size, growth, and lipid storage over 4 weeks. Salmon were either fed for 4 weeks, fasted for 4 weeks, or fasted for 2 weeks and then fed for 2 weeks. Fed fish were heavier, grew faster, and had significantly more storage lipids than fasted fish. The third phase was designed to evaluate aerobic performance in fasted fish. Critical swim speeds were found to be positively related to salmon body size and storage lipids, but not prior diet quality, evidence that larger salmon with higher energy reserves may be better suited for overwinter survival due to their ability to swim faster than smaller, leaner individuals.

## INTRODUCTION

In addition to the overall quantity of available prey, aspects of prey quality are known to influence the growth, survival, and abundance of marine populations (Alverson 1992; Mazur et al. 2007; Renkawitz et al. 2015). Prey quality can vary in terms of total energy density (e.g. lipids), biochemical composition (e.g. fatty acids), or both. Lipids are naturally occurring organic compounds that are important in energy storage, cell membrane structure, and in the biosynthesis of molecules used to regulate many physiological processes (Sargent et al. 1999; Tocher 2003; Arts et al. 2009). Fatty acids, the primary constituent of some lipid classes, are highly variable across marine prey (Budge et al. 2002; El-Sabaawi et al. 2009; Daly et al. 2010) and may also vary seasonally within a species, as has been noted in different systems (Iverson et al. 2002; Litz et al. 2010).

Fatty acid composition in fishes is highly affected by their diet (Saito et al. 1996; Mjaavatten et al. 1998; Copeman et al. 2013). Essential fatty acids (EFAs), such as docosahexaenoic acid (22:6n-3; DHA), eicosapentaenoic acid (20:5n-3; EPA), arachidonic acid (20:4n-6; ARA), linoleic acid (18:2n-6; LA), and α-linolenic acid (18:3n-3; ALA) must be obtained through diet, and insufficient amounts can lead to a suite of developmental failures and eventual death (Sargent et al. 1995; Izquierdo 1996; Tocher 2010). Requirements for EFAs vary by species and life stage, yet DHA is often cited as the most important EFA during larval and juvenile phases because of its role in neural growth and development which impacts feeding efficiency, vision, behavior, and survival (Watanabe 1993; Bell et al. 1995; Takeuchi 2014). Ratios of DHA to EPA, which reflect relative proportions of these two functionally different EFAs, are

commonly used to evaluate EFA requirements in larval and juvenile marine fish, with dietary ratios of DHA:EPA = 2 generally considered optimal (Sargent et al. 1999; Copeman et al. 2002; Wu et al. 2003), although intermediate levels (DHA:EPA ≈ 1) have been shown to be sufficient in many species (Rodriguez et al. 1997; Copeman and Laurel 2010; Tocher 2015).

Pacific salmon (*Oncorhynchus* spp.) migrate from freshwater to the ocean as juveniles, and transition from feeding on mostly invertebrate prey to mostly marine fish prey (Brodeur 1991; Daly et al. 2009; Dale et al. 2017). Mortality during the first few months following freshwater emigration is high, although the principle drivers (e.g. decreased growth, increased predation) may vary regionally, temporally, and by species (Hartt 1980; Pearcy 1992; Beamish et al. 2004). Several studies have shown that mortality may be size-selective (Moss et al. 2005; Claiborne et al. 2011; Miller et al. 2013), and that early marine growth (Tomaro et al. 2012) and accumulation of storage lipids throughout the first summer (Beamish and Mahnken 2001) are related to survival. Because storage lipids are easily catabolized to provide metabolic energy for growth and swimming (Sheridan 1994), the amount or composition of stored lipids may be important in determining fish survival during periods of restricted ration, such as during their first winter (Schultz and Conover 1999; Tocher 2003; Hurst 2007a). Higher survival of larger juveniles with greater lipid stores in fall is predicted by the "critical size, critical period" hypothesis (Beamish and Mahnken 2001; Beamish et al. 2001; Farley et al. 2007), which posits that smaller salmon with lower energy storage and higher metabolic rates are more likely to deplete their energy reserves and be more vulnerable to starvation or predation than larger salmon during the first ocean winter.

Through time, marine fish prey comprises a larger proportion of juvenile Chinook (*O. tshawytscha*) salmon diet, which may be related to faster growth since larger salmon tend to consume more fish (Brodeur 1991; Schabetsberger et al. 2003; Daly et al. 2009). Invertebrates frequently consumed by juveniles during early marine residence include hyperiid and gammarid amphipods, crab larvae, and krill (*Thysanoessa spinifera* and *Euphausia pacifica*); common fish prey are age-0 northern anchovy (*Engraulis mordax*; hereafter anchovy) and rockfish (*Sebastes* spp.), among others (Brodeur 1991; Daly et al. 2009; Dale et al. 2017). On average, Daly et al. (2010) found that DHA occurs in higher proportions (21% total fatty acids) in marine fish prey than invertebrate prey (14% of total fatty acids), but EPA occurs in higher proportions in invertebrates (29% of total fatty acids) compared to fish (21% of total fatty acids), yielding average DHA:EPA ratios that range from 0.2 – 0.7 for invertebrates and 0.5 – 1.4 for fish. Based on these measurements, it is expected that marine fish prey are nutritionally favorable for juvenile salmon development because they are closer to the DHA:EPA ratios ≥1 that have been identified as superior for juvenile growth and survival in other species (NRC 2011; Takeuchi et al. 2014).

Fatty acids, along with bulk stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), can be used as biomarkers that integrate information about a predator's diet over timescales of weeks to months (Dalsgaard et al. 2003; Fry 2006; Parrish 2013). The fatty acid biomarker approach is based on the observation that fatty acids produced by primary producers (Ackman et al. 1968) or synthesized *de novo* by primary consumers (Lee et al. 1971) are transferred conservatively through pelagic food webs, and can provide insight into trophic interactions in the marine environment. Stable isotopes are useful in that $\delta^{13}C$

varies with sources of carbon and $\delta^{15}N$ varies with nutrient source and trophic position (Fry 2006). Integrating fatty acid and isotope biomarker data can supplement stomach content analysis and strengthen interpretation of diet data in the field, but accurate estimates of time lags between consumption and expression of biomarkers in tissues are limited. Better understanding of biomarker incorporation rates could improve interpretation of field studies of fatty acids and stable isotope ratios, especially in species that undergo ontogenetic shifts in habitat and diet during development.

The primary objective of the current study was to evaluate whether a fish-dominated diet high in DHA would lead to faster growth in juvenile salmon than a krill-dominated diet high in EPA. Our other objectives were to evaluate fasting effects on salmon growth and lipid stores and to determine whether the fish diet provided a carryover benefit to salmon, in critical swimming speeds, relative to the other diets. To address these objectives, we conducted a three-phase laboratory experiment using age-0 Chinook salmon (Fig 2.1). The first phase of the experiment consisted of a controlled feeding study lasting 12 weeks (the feeding study), where fish were reared on diets varying in proportions of krill and anchovy. Throughout the feeding study, fatty acids and bulk stable isotopes were measured to quantify time for a diet shift to be reflected in the relevant salmon tissue biomarkers. The second phase of the experiment was designed to assess size and biochemical changes during periods of food deprivation (the fasting study). In the last phase of the experiment, critical swimming speeds were measured in previously fasted fish to examine whether nutritional history provided a carryover effect in terms of future exercise performance (the swimming study). Collectively, results from

this experiment provide novel insight into the growth, lipid stores, and biochemical signatures of feeding and food-deprived juvenile salmon.

## METHODS

### *Fish rearing*

Juvenile fall Chinook salmon from brood year 2012 (mass ≈ 5 g) were obtained from Priest Rapids Hatchery located along the bank of the Columbia River immediately downstream of Priest Rapids Dam in Washington, USA (46.63° N, 119.86° W). Salmon were transported to the Hatfield Marine Science Center in Newport, Oregon (44.60° N, 124.05° W) and approximately 40 fish were transferred to each of nine 568-L round aquaculture tanks with a constant flow of charcoal-filtered freshwater (mean 14.8 ± 0.5 °C standard error SE). All tanks were equipped with continuous-flow air supply and the lab lighting system was adjusted monthly to approximate a natural light cycle. Fish were fed a low lipid (12.5% lipid by dry weight) commercial hatchery diet (Otohime Fish Diet® extruded pellets) offered once daily at approximately 2% of the total fish weight in each tank based on size measurements made every 4 – 6 weeks. Rations were adjusted weekly between size measurements by assuming an increase of ~1.5% in body weight (BW) per day based on the growth model of Iwama and Tautz (1981).

Salmon were allowed to acclimate to lab conditions for 4 weeks before being gradually introduced to seawater over 1 week. Seawater was pumped from Yaquina Bay, Oregon, sand filtered to 50 µm, and sterilized using ultraviolet light. Once at full strength, seawater temperature averaged (± SE) 11.6 ± 2.2 °C, salinity was 32.1 ± 0.7, and dissolved oxygen was 7.4 ± 0.6 ml $L^{-1}$ over the duration of the experiment. Once all

salmon completed smoltification (n = 377), 10 fish from each tank (n = 90) were randomly selected and injected with a passive integrated transponder (PIT) tag. Tagged fish were measured through time but were not sampled for lipids and stable isotopes. This was done to monitor changes in individual size and growth throughout the experiment for comparison with size and growth measured from tank averages. After tagging, all salmon began feeding on a formulated acclimation diet for 6 weeks so they could adjust to gelatin food prior to the feeding study. Natural mortality rates (fish $wk^{-1}$) did not vary across treatments or phase of the experiment for tagged (untagged) salmon and were 0.7(0.5) for the acclimation period, 3.8(6.7) for the feeding study, 1.3(2.0) for the ration study, and 0(0.3) for the swimming study.

*Feeding study*

During the first phase of the experiment, three tanks of fish were randomly assigned to one of three treatments and fish were reared for 12 weeks on the formulated treatment diets (Table 2.1). Treatment diets contained similar ingredients and differed by the addition of krill (K diet), krill and anchovy (KA diet), or anchovy (A diet). Diets had similar amounts of lipid per wet weight (20.1 – 26.1 mg $g^{-1}$), but their fatty acid composition was further modified by the addition of EPA oil (Epax® 1050 TG) or DHA oil (Epax® 6015 TG) so that DHA:EPA ratios equaled 0.6 for the K diet, 0.9 for the KA diet, and 1.5 for the A diet (Table 2.2). The diets were blended to create a homogenous texture, bound with gelatin, and frozen. Thawed and grated food was offered once daily to fish at approximately 2% of the total fish weight per tank and adjusted weekly based

on an estimated weight gain of 1.5% BW per day (Iwama and Tautz 1981). Fish were observed until all food was consumed, which typically took <2 min.

To evaluate subsequent changes in size, one fish from each tank (n = 9) was weighed (nearest 0.1 g) and measured for fork length (FL, mm) at the start of the study. All fish were measured at weeks 2, 6, and 12. Tank averages from week 2 onward were considered an experimental unit (n = 3 per treatment). Normality and homogeneity of all measurements were checked by Shapiro-Wilk and Bartlett's tests, respectively. Growth rates (mm $d^{-1}$) were determined from FL by regression and compared among treatments by two-way analysis of covariance (ANCOVA) with the main effects of diet treatment, time, and their interaction. Instantaneous specific growth rates (SGR % BW $d^{-1}$) were also measured:

$$SGR = \left(\frac{\left(lnW_f - lnW_i\right)}{t} \times 100\right),$$

where $\ln W_f$ and $\ln W_i$ are the natural logarithm of the final and initial weight and $t$ is the time (days) between observations. Salmon FL, mass, and growth were compared during each sampling date for tagged and untagged fish using t-tests. Because measurements at each sampling period were not considered independent, tank-averaged size and SGR were compared across treatments and sampling dates using two-way repeated measures analysis of variance (ANOVA) and Tukey post-hoc tests with a Bonferroni correction factor. For this analysis, diet treatment and time were the between-subjects factors, and all models included an error term for repeated subjects. The analysis was conducted using

linear mixed-effects models constructed using the "nlme" (Pinheiro et al. 2016) and "multcomp" (Hothorn et al. 2008) packages available for R 3.2.3 (R Core Team 2015).

*Fasting study*

In the second phase of the experiment (weeks 12 – 16), treatment rations were adjusted so that one tank of fish from each diet treatment was fasted for 0, 2, or 4 weeks. The 4-week study included three treatments: 1) fed for 4 weeks, no fasting; 2) fasted for 2 weeks, fed for 2 weeks; and 3) fasted for 4 weeks. Fed fish received their previous diet treatment. This was done to assess how fasting would impact salmon size, growth, and lipid stores. Because we detected no differences in FL, mass, or growth among feeding treatments at the end of the feeding study, differences in tank-averaged size, growth, and lipids at the end of the fasting study were analyzed among ration treatments irrespective diet treatment using one-way ANOVA and Tukey post-hoc tests. Three of the 26 fish evaluated for growth and lipids had values more than 2 SD away from treatment means and were removed prior to analysis.

*Swimming study*

Critical swimming speed ($U_{crit}$ mm $s^{-1}$) is a standard measurement to assess aerobic performance in fish (Plaut 2001). In the third phase of the experiment (the swimming study – weeks 16 to 20), critical swimming speeds were measured in 12 fish after they were fasted for 4 weeks. The 12 fish had received different rations during the fasting study from weeks 12 to 16. The swimming study was conducted to determine if salmon previously reared on the fish-dominated, high DHA diet outperformed fish reared

on the krill-dominated, EPA diet or the intermediate diet. To measure $U_{crit}$, we used a 5,678 L recirculating water bath with three 5-hp, 1,750 rpm pumps that forced water to a 1,000 L header tank (see Hurst 2007b for a complete description). The three swimming chambers, each 15 cm in diameter and 115 cm long, were submerged in the water bath within an acrylic cylinder connected to the header tank. A baffle in front of the header tank prevented any turbulence from entering the swimming chambers. The upstream ends of the swimming chambers were sealed by rigid styrene screen to prevent fish from escaping. The downstream ends were sealed using 8 mm cloth mesh fastened with a hose clamp. Water temperatures averaged 8.8 ± 0.6 SE °C across trials. Flow velocities were monitored with an electromagnetic flowmeter (Marsh-McBirney Flo-Mate model 2000) located 5 cm downstream of the swim chambers.

During swimming trials, a single salmon was transferred into each chamber and acclimated during a 15-min period at an initial flow velocity of 50 mm $s^{-1}$. Flow velocities were increased every 10 min by 50 mm $s^{-1}$ until fish could no longer swim and maintained contact with the downstream mesh for more than 10 s. At that point, velocity and time spent swimming at that velocity were recorded, then the downstream barrier was detached and the fish was removed from the chamber. Salmon were tested twice on successive days and their average $U_{crit}$ calculated. Critical swimming velocities were determined according to the equation:

$$U_{crit} = V + \left(\frac{vT}{t}\right),$$

where $V$ is the highest speed maintained for a full time interval, $v$ is the velocity increment (50 mm $s^{-1}$), $t$ is the time interval (10 min), and $T$ is the amount of time spent at the fatigue velocity (Brett 1964). The $U_{crit}$ velocities were not corrected for blocking effects as recommended by Bell and Terhune (1970) as the cross-sectional area of the fish was <2% of the swimming chamber area. Critical swimming speed was evaluated using regression with previous diet treatment, ration, fish size (FL), and storage lipids included independently as main effects and added one at a time by forward selection. The most parsimonious model was chosen based on lowest Akaike Information Criterion (AIC) value (Burnham and Anderson 2002).

*Lipid and stable isotope analysis*

Baseline characteristics were described from a sample of one fish randomly selected from each tank immediately prior to the start of the feeding study. Salmon were then sampled for lipids and bulk carbon ($^{13}C$) and nitrogen ($^{15}N$) stable isotopes at weeks 2, 4, 6, 8, and 12 (3 fish per tank). Additional samples were collected for lipid analysis after 1 week of the feeding study, at the end of the fasting study (week 16), and at the end of the swimming study (week 20, 2 – 3 fish per tank), resulting in a total of 209 lipid samples at nine sampling periods and 144 stable isotope samples at six sampling periods. Fatty acid composition was measured on all lipid sampling dates; lipid classes were measured at the start, middle, and end of the feeding study (weeks 0, 6, 12), at the end of the fasting study (week 16), and the end of the swimming study (week 20). For lipids, dorsal muscle tissue from the left side was sampled by first removing the skin and then

sampling muscle (0.36 – 1.09 g wet weight) just under the dorsal fin. For isotopes, dorsal muscle was similarly collected from the right side of the fish (0.34 – 1.31 g wet weight).

Samples were analyzed for whole lipids, lipid classes, and fatty acid composition at the Hatfield Marine Science Center in Newport, Oregon. Tissue samples were stored in chloroform under nitrogen at –80 °C for less than 6 months prior to extraction using a modified Folch procedure (Folch et al. 1957; Parrish 1999; Copeman et al. 2016). Lipid classes: steryl esters (SE), triacylglycerols (TAG), free fatty acids (FFA), sterols (ST), and polar lipids (PL) were determined using thin layer chromatography and flame ionization detection (TLC/FID) with a MARK V Iatroscan (Iatron Laboratories, Tokyo, Japan) as described by Lu et al. (2008). Lipid extracts (5-10 µl) were spotted on duplicate silica gel covered Chromarods and developed using three solvent stages to separate lipid classes. Following the last development stage, rods were scanned and the output was analyzed using Peak Simple software (ver. 3.67, SRI Inc.). Data were compared to lipid standards (Sigma-Aldrich, St. Louis, MO, USA), including a TAG standard developed from walleye pollock liver using the methods of Miller et al. (1998) with the addition of a final elution of 15 ml of hexane:diethyl ether:formic acid solution (80:20:0.1). Lipid classes were expressed in absolute (mg $g^{-1}$ wet weight) and relative amounts (% of total lipids).

Fatty acid methyl esters (FAME) were prepared by transesterification using sulfuric acid according to Budge et al. (2006) and analyzed on an HP 7890 GC FID equipped with an autosampler and a DB wax+ GC column (Agilent Technologies, Inc., U.S.A.) according to Copeman et al. (2016). The column temperature began at 65 °C for 0.5 min and was increased to 195 °C (40 °C $min^{-1}$), held for 15 min then increased again

(2 °C $min^{-1}$) to a final temperature of 220 °C. Final temperature was held for 1 min. The carrier gas was hydrogen, flowing at a rate of 2 ml $min^{-1}$. Injector temperature was set at 250 °C and the detector temperature was constant at 250 °C. Peaks were identified using retention times based upon Supelco standards (37 Component FAME, BAME, PUFA 1, PUFA 3). Nu-Check Prep GLC 487 quantitative fatty acid mixed standard was used to develop correction factors for individual fatty acids. Chromatograms were integrated using Chem Station (version A.01.02, Agilent).

Samples for stable isotope analysis were processed at the Oregon State University Stable Isotope Laboratory. Samples were rinsed with deionized water, placed in a pre-weighed aluminum boat and dried at 60 °C for 48 h. After drying, the aluminum weigh boats were reweighed and the final dry weight of each sample determined by difference. Dried muscle tissue was ground into a fine powder and 1.0 ± 0.1 g was packed into a pre-weighed tin capsule. Prepared samples were loaded into a Costech Zero Blank Autosampler along with the isotopic lab standards that were calibrated against international standards (USGS40, ANU Sucrose, and IAEA-N2). Samples were then flashed combusted at >1000 °C using a Carlo Erba NA1500 elemental analyzer and the resulting $CO_2$ and $N_2$ analyzed by continuous-flow mass spectrometry using a DeltaPlus isotope ratio mass spectrometer. Stable isotope values were expressed as:

$$\delta^{13}C \text{ or } \delta^{15}N = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000,$$

where *R* is $^{13}C$:$^{12}C$ or $^{15}N$:$^{14}N$.

Instrument error was ± 0.1‰ for C and ± 0.2‰ for N. Samples with atomic C:N ratios > 3.5 (n = 9) were lipid corrected using the following equation by Post et al. (2007) for aquatic organisms:

$$\delta^{13}C_{normalized} = \delta^{13}C - 3.32 + 0.99 \times C{:}N.$$

This was done to account for the lipid depletion effect in which high levels of lipids can cause significant depletion in $^{13}C$ irrespective of the source $\delta^{13}C$ (McConnaughey and McRoy 1979).

*Changes in salmon biochemistry*

We evaluated changes in salmon biochemistry throughout the experiment. Lipid classes and total lipids per wet weight were compared among treatments at the middle and end of the feeding study (weeks 6 and 12) using multivariate analysis of variance (MANOVA) and Tukey post-hoc tests. To evaluate whether percentages of EPA, DHA, and DHA:EPA in salmon tissue varied among treatments through the feeding study (weeks 1, 2, 4, 6, 8, and 12), values were compared by repeated measures ANOVA and Tukey post-hoc tests with a Bonferroni correction using linear mixed effects models. Salmon stable isotope measurements ($\delta^{13}C$ and $\delta^{15}N$) were compared throughout the feeding study at weeks 2, 4, 6, 8, and 12 using the same method.

To evaluate whether salmon muscle reflected dietary fatty acids and stable isotopes at the end of the feeding study, Pearson correlation analysis was used to examine

the relationship between dietary and salmon EPA, DHA, DHA:EPA, $\delta^{13}C$, and $\delta^{15}N$ at the end of week 12. To estimate turnover and incorporation rates, fatty acids and isotopes were plotted through time and fit to a nonlinear exponential rise to maximum model (Cober et al. 2006; Copeman et al. 2013; Mohan et al. 2016):

$$Y_t = Y_0 + a(1 - e^{-bt}),$$

where $Y_t$ equals percent fatty acid or isotope ratio ($\delta^{13}C$ and $\delta^{15}N$) at time *t*, $Y_0$ is the value at time 0, *a* is the total change in value after the diet is switched, and *b* refers to the initial slope of the curve (% or ‰ $d^{-1}$). We used the parameter *b* to calculate turnover time (ln2/*b*, half-life in days), which is commonly presented in the stable isotope literature (Vander Zanden et al. 2015) and total time to reach equilibrium (1/*b*, in days), which is more commonly presented in the fatty acid literature (Copeman et al. 2013; Mohan et al. 2016).

Experimentally-derived isotopic discrimination factors (i.e. differences in the isotopic ratio between the consumer and diet) were calculated by subtracting mean diet $\delta^{13}C$ or $\delta^{15}N$ from model estimates at saturation ($Y_0 + a$). Finally, to test whether fasting had an effect on EPA, DHA, and DHA:EPA values, tank averages were compared at the beginning and end of the swimming study (weeks 16 and 20) using one-way ANOVA.

## RESULTS

### *Feeding study*

Tagging did not appear to affect the growth rates of juvenile salmon during the feeding study (weeks 0 to 12): we found there were no significant (t-tests, all $p < 0.40$) differences in FL, mass, or growth between tagged and untagged fish at any sampling period. Therefore, results are represented using tank average values based on measurements of all tagged and untagged fish combined. Chinook salmon increased in size from an average of 108 mm and 13.9 g at the start of the feeding study to 135 mm and 33.1 g by the end of week 12 (Fig 2.2). There were no significant differences among treatments in FL (repeated measures ANOVA, $F = 0.02$, $p = 0.98$), mass ($F = 0.50$, $p = 0.63$), or SGR ($F = 3.20$, $p = 0.11$). However, across treatments salmon significantly increased in FL (repeated measures ANOVA, $F = 601.01$, $p < 0.01$), mass ($F = 303.74$, $p < 0.01$), and SGR ($F = 32.66$, $p < 0.01$) from weeks 2 to 12. Specific growth rates increased from an average of 0.84% BW $d^{-1}$ from weeks 2 to 6 to 1.28% BW $d^{-1}$ from weeks 6 to 12. This pattern in growth rate occurred despite the fish receiving equivalent weight-specific rations (2% $d^{-1}$) throughout. For length-based growth, there was a significant (ANCOVA, $F = 3.81$, $p = 0.04$) interaction effect of treatment and time. Salmon feeding on the krill-dominated, high EPA (K) diet and the fish-dominated, high DHA (A) diet grew slightly faster (K = 0.38 mm $d^{-1}$ and A = 0.37 mm $d^{-1}$) than salmon feeding on the intermediate (KA) diet (0.29 mm $d^{-1}$), even though FL differences by the end of the feeding study were not significant.

*The fasting study*

At the end of second phase of the experiment, the fasting study (weeks 12 to 16), there were significant differences among fish that were fasted for 0 out of 4 weeks total,

fasted for 2 weeks and then fed for 2 weeks, or fasted continuously for 4 weeks in mass (ANOVA $F = 12.10$, $p = 0.01$), length-based growth ($F = 6.39$, $p = 0.03$), SGR ($F = 20.12$, $p < 0.01$), and storage lipids (% TAG; $F = 6.61$, $p = 0.03$), but not FL ($F = 4.21$, $p = 0.07$) or total lipids per wet weight ($F = 0.76$, $p = 0.84$). Tukey post-hoc tests revealed that fish fasted for 0 out of 4 weeks had significantly greater mass ($p = 0.01$), growth (length-based $p = 0.03$; SGR $p < 0.01$), and storage lipids ($p = 0.03$) compared to fish that were fasted for 4 weeks (Fig 2.3). There were no significant (Tukey $p > 0.05$) differences in size, growth, or lipids between fish that were fasted for 0 or 2 out of 4 weeks. Interestingly, FL and length-based growth rates increased in fish that were fasted for 4 weeks, whereas mass and SGR decreased.

*The swimming study*

Maximum swimming speed ($U_{crit}$) of juvenile salmon in our study averaged 631 mm $s^{-1}$ (± 44 mm $s^{-1}$ SD), corresponding to 4.3 body lengths $s^{-1}$ (± 0.5 body lengths $s^{-1}$ SD), and was best explained by the amount of TAG with FL included as a covariate ($R^2 = 0.88$, $F = 11.1$, $p = 0.04$, $AIC = 51.32$). Fastest swimming speeds were obtained by larger fish with greater fat stores (Fig 2.4). Although salmon reared on the fish-dominated (A) diet tended to be larger and have higher levels of TAG than fish from other treatments (both associated with higher swim speeds), previous diet treatment or ration (as categorical main effects) did not have a significant effect on swim speed.

*Changes in salmon biochemistry*

Lipid classes and total lipids per wet weight were not significantly different among treatments in the middle (6 weeks) (MANOVA, Pillai = 1.66, $p = 0.34$) or at the end (12 weeks) of the feeding study (MANOVA, Pillai = 1.47, $p = 0.60$; Fig 2.5). Polar lipids and TAG contributed most to the salmon lipid pool, ranging from 19.2 to 54.0% of total lipids across all samples. Across treatments, total muscle lipids decreased by an average of 18% from week 0 to week 6 and increased by 27% from week 6 to week 12, suggesting that salmon changed their energy allocation strategy.

Percentages of EPA significantly (repeated measures ANOVA, $F = 9.4$, $p < 0.01$) increased with the interaction of time and diet during the feeding study. The largest overall change in salmon fatty acid composition was the increase in EPA from 6.5% of total fatty acids at the start of the feeding study to 17.6% at the end of the study in fish feeding on the krill-dominated (K) diet (Fig 2.6a). Based on multiple comparisons (Tukey post-hoc tests with Bonferroni correction), EPA values were significantly ($p < 0.01$) greater in the high EPA (K) and intermediate (KA) treatment salmon than in the high DHA (A) treatment salmon by week 8, and all treatments had EPA values that were significantly different from one another by week 12 (all $p < 0.01$; Fig 2.6). By the end of the feeding study, salmon and dietary EPA values were significantly and positively correlated (EPA $r = 0.99$, $p < 0.01$), indicating that salmon maintained EPA in amounts proportional to diet percentages, even though amounts of EPA in the diet were greater (18.6 – 38.0% of total fatty acids) than amounts found in fish (7.7 – 18.3%).

In contrast to EPA, amounts of salmon DHA did not significantly (repeated measures ANOVA, $F = 3.5$, $p = 0.10$) vary across treatments and were consistently as high or higher (>25% of fatty acids) than dietary amounts of DHA (21.4 to 27.0% of total

fatty acids) throughout the feeding study. Evidence that fish were not taking up DHA relative to dietary proportions was the poor relationship ($r = 0.28$, $p = 0.47$) between dietary and salmon DHA values at the end of the feeding study. However, because EPA varied across treatments, DHA:EPA ratios varied significantly (repeated measures ANOVA, $F = 3.0$, $p = 0.01$) by the interaction of treatment and time. Salmon feeding on the krill-dominated (K) diet had an average DHA:EPA ratio of 1.5 by the end of the feeding study, which was significantly (Tukey, $p < 0.01$) lower than salmon feeding on the intermediate (KA) and fish-dominated (A) diets (DHA:EPA = 2.8 and 3.6, respectively). Fasting did not appear to have an effect on EPA, DHA, or DHA:EPA values, as there were no significant (ANOVA, all $F < 0.90$, $p > 0.36$) differences in those fatty acid amounts or ratios across tanks from the start to the end of the swimming study (weeks 16 to 20).

By the end of the feeding study (week 12), correlations between salmon and dietary $\delta^{13}C$ ($r = 0.67$) and $\delta^{15}N$ ($r = 0.87$) were both positive and significant ($p < 0.05$), indicating that salmon tissue reflected the differing carbon sources and trophic levels occupied by marine invertebrate prey and marine fish prey in the treatment diets. For $\delta^{15}N$, there was a significant (repeated measures ANOVA, $F = 8.26$, $p < 0.01$) interaction between time and diet. Salmon feeding on the fish-dominated (A) diet had significantly (Tukey $p < 0.01$) higher average $\delta^{15}N$ values in weeks 8 (12.2‰) and 12 (12.4‰) than salmon feeding on the krill-dominated (K) diet (11.8‰ in week 8 and 11.7‰ in week 12), but there were no significant (Tukey, $p > 0.05$) differences in $\delta^{15}N$ between fish (A) and intermediate (KA) treatments through time. Values of $\delta^{13}C$ varied significantly with time (repeated measures ANOVA, $F = 181.6$, $p < 0.01$), but did not vary with diet ($F =$

1.9, $p = 0.23$). Average $\delta^{13}C$ values were significantly (Tukey, $p = 0.04$) less negative in salmon feeding on the fish-dominated (A) diet (-18.2‰) than salmon feeding on the krill-dominated (K) diet (-18.4‰) by the end of the feeding study (Fig 2.7).

**Turnover and discrimination values**

We fit nonlinear regression models to salmon EPA, DHA, and DHA:EPA through 12 weeks of the feeding study to estimate the number of days it took muscle fatty acids to reach equilibrium with dietary fatty acids (Fig 2.8 and Table 2.3). All models were significant ($R^2 = 0.31$ to 0.89, $p < 0.05$), with the exception of DHA in the krill-dominated (K) treatment and DHA:EPA in the fish-dominated (A) treatment, whose average values did not change through time. Turnover (half-life) estimates varied by treatment and fatty acid, and averaged 46 days across all treatments and fatty acids (range = 7 to 151 days). Average time to equilibrium was 67 days (range = 10 to 218 days).

We also fit nonlinear regression models to bulk stable isotope signatures through time (Fig 2.9 and Table 2.4). Models were significant ($R^2 = 0.31$ to 0.91, $p < 0.05$) for all stable isotope models except for $\delta^{15}N$ in the fish-dominated (A) treatment, whose average values did not change through time. Turnover (half-life) estimates varied less by treatment than fatty acids, averaging 42 days across $\delta^{13}C$ and $\delta^{15}N$ in all treatments (range = 8 to 66 days). Average time to equilibrium was 61 days (range = 12 to 95 days). Average turnover time and time to equilibrium estimates were similar for fatty acids and bulk stable isotopes, indicating that they integrated diet information in salmon muscle tissue over approximately the same amount of time.

Isotopic discrimination values were calculated at the end of the feeding experiment (week 12) as the difference between diet and consumer $\delta^{13}C$ and $\delta^{15}N$ values at equilibrium (average value through time for $\delta^{15}N$ in the A treatment). Carbon isotope discrimination values (‰) were 0.37, 0.59, and 0.76 for the krill-dominated (K), intermediate (KA), and fish-dominated (A) treatment diets, and nitrogen isotope discrimination values were 4.21, 4.49, and 4.07. For $\delta^{15}N$, discrimination values were higher than the 3.4‰ discrimination value typically associated with aquatic organisms (Post 2002).

## DISCUSSION

Juvenile Chinook salmon grow rapidly in the ocean following freshwater emigration as they transition from feeding mostly on invertebrates to mostly age-0 marine fishes. Invertebrates contain more EPA while marine fishes have more DHA. This study was conducted to evaluate the effects of dietary fatty acids and feeding ration on salmon growth, lipids, and swim speed to determine if prey quality has direct or indirect (i.e. carryover) effect on salmon performance during the juvenile phase. Across diet treatments, EPA contributed 19 – 38% and DHA contributed 21 – 27% of total dietary fatty acids, yielding DHA:EPA ratios that ranged from 0.6 to 1.5. At these levels, there was no detectable effect of diet on salmon growth, suggesting that EPA and DHA were provisioned at sufficient levels across treatments. Consequently, we conclude that other factors such as prey quantity, prey availability, and prey digestibility may be equally or more important than prey quality in determining juvenile Chinook salmon growth during early marine residence.

Minimum dietary requirements for essential fatty acids (EFAs) vary between marine and freshwater fishes and are currently unknown for juvenile Chinook salmon (Tocher 2010). Nutritional guidelines state that polyunsaturated fatty acids (EPA, DHA, but also LA and ALA) should be provisioned in total at 1 – 2% of Pacific salmon diet by weight (NRC 2011; Tocher 2015). Dietary EFAs were provided above this level across all treatments, which may be why we did not detect any differences in growth. There is some evidence from rainbow trout (*O. mykiss*) that ALA may be the only essential fatty acid required, as anadromous species may have evolved the ability to biosynthesize EPA and DHA from ALA (Tocher 2010). Additional information on the minimum and optimum dietary EFA requirements for growth and health in juvenile Chinook salmon will be needed to understand the consequences of prey fatty acids on salmon growth in both field and aquaculture settings.

Our findings indicate that Chinook salmon may synthesize DHA from other fatty acids such as LA and ALA. We found that ALA proportions decreased through time across all treatments. We also found that salmon had proportionally more DHA than was found in diets, regardless of dietary DHA amounts, implying that either DHA was being selectively retained or synthesized. Evidence that DHA was probably not being retained was found during the swimming study, when DHA concentrations did not significantly change during fasting. If DHA was being retained during fasting, concentrations would be expected to increase due to decreased storage lipids, and saturated and monounsaturated fatty acids would be expected to decrease as they were mobilized for energy (Pierce and McWilliams 2014), but DHA amounts did not decrease. Rearing salmon on diets that contain variable amounts of AL and ALA, but not EPA or DHA,

may help determine if Chinook salmon utilize these fatty acids to biosynthesize EPA and DHA during development, and could be useful in differentiating biochemical pathways between similar anadromous species.

Requirements for DHA by marine fishes, including salmon during the marine phase, may be a reflection of the phytoplankton community and primary production within the ecosystems where they evolved. Japanese amberjack (*Seriola quinqueradiata*) has among the highest DHA requirement of any fish, whereas Pacific cod (*Gadus macrocephalus*) has among the lowest (Takeuchi 2014). Japanese amberjack are found in oligotrophic waters of the Northwestern Pacific, from Japan to Hawaii, where productivity is low and dominated by heterotrophic dinoflagellates, which are rich in DHA, whereas Pacific cod and Pacific salmon are more frequently associated with highly productive coastal systems dominated by diatoms, which are rich in EPA (Parrish 2013). The finding that Pacific cod require less DHA than a similar species, Atlantic cod (*Gadus morhua*) (Copeman and Laurel 2010), further suggests that there may be a habitat component to EFA dietary requirements.

Although salmon growth did not vary with dietary fatty acids in this study, fasting had a significant effect on fish size, growth, and lipid storage. We also found that larger fish with more storage lipids outperformed smaller fish in critical swimming trials following 4 weeks of fasting, indirectly relating potential survival to nutritional status. Mechanistically, faster swimming fish may have an advantage over slower swimming fish during periods of restricted ration because they may be better at evading pursuing predators, capturing elusive prey, and moving more quickly towards areas of increased productivity while relying on increased lipid stores. The result that larger fish with more

energy stores outperformed smaller fish provides support for the "critical size, critical period" hypothesis (Beamish and Mahnken 2001; Beamish et al. 2001; Farley et al. 2007) – the idea that salmon year-class strength may be determined after the first ocean summer when individuals that fail to grow large enough to meet metabolic demands do not survive. To further test this hypothesis, a cohort could be repeatedly sampled through the overwintering period and attributes from survivors compared with attributes of fish in the fall (using otoliths or other metrics). If larger fish with more energy stores survive at a higher rate, they would be expected to be over-represented in the surviving population.

The onset of piscivory is often accompanied by an increase in growth rate that typically translates into larger size and greater survival throughout life for piscivorous fishes (Juanes 1994; Mittelbach and Persson 1998). While it may be intuitive to conclude that growth rate increases may be due to increased quality of prey consumed by piscivores, our results suggest that this may not be the case. Juvenile salmon feeding on marine fish prey may grow faster than salmon feeding on invertebrates because of the energetic advantages of feeding on fish. Krill contain less lipid overall by wet weight ($6.28 \pm 1.02$ SE mg $g^{-1}$) than anchovy ($10.75 \pm 0.93$ SE mg $g^{-1}$; Litz, unpublished data), and because of differences in mean size, salmon must find and capture several krill to equal the mass of a single anchovy. In the field, differences between searching for, pursuing, capturing, handling, and digesting multiple invertebrates compared to a single anchovy may explain why salmon may grow faster when feeding on fish. This study compared growth performance on a fish-dominated to krill-dominated diet while controlling for differences in lipid content, ration, and digestibility. Under these controlled conditions, there were no growth differences among treatments. Higher growth

rates in salmon feeding on marine fish prey relative to invertebrates observed in the field may reflect differences in salmon activity and consumption as opposed to differences in prey quality.

This study improves our understanding of the biochemical changes that occur in juvenile Chinook salmon during a diet shift. An integrated approach that uses fatty acids and stable isotopes in addition to stomach content analysis to re-create dietary history is becoming more widely used in trophic studies (Budge et al. 2008; El-Sabaawi et al. 2009; Copeman et al. 2016). Despite this, quantitative estimates of how fatty acids and stable isotopes differ in their incorporation times are lacking. Uncertainty about the temporal period over which fatty acids and stable isotopes integrate information about diet can confound interpretation of data on migration, food webs, and trophic position (Vander Zanden et al. 2015; Hertz et al. 2016). This study found that isotopic turnover in muscle tissue averaged 42 days, which was similar (39 days) to another study examining anadromous rainbow trout (Heady and Moore 2013). The average turnover estimate from this study of 42 days was close to the modeled estimate of 47 days based on mean fish mass (13.9 g) at diet switch: ln [half-life] = ln[body mass, g] + 3.28 from Vander Zanden et al. (2015). Strong coherence between our laboratory-derived turnover estimates and the modeled value suggests that turnover may be approximated for juvenile salmon from mass at the diet switch.

We expected that salmon fatty acids would be at equilibrium with their diet by the end of the 12-week feeding study based on biochemical data collected during feeding studies on other juvenile species (Budge et al. 2011; Copeman et al. 2013; Mohan et al. 2016). We found that different dietary fatty acids reached equilibrium in muscle tissue at

different times depending on the overall change in fatty acid concentration and the rate of initial change (*b* parameter) captured by our nonlinear models. Across treatments, the rate of EPA uptake ranged from 0.5 to 5.0% $d^{-1}$, yielding equilibrium estimates that ranged from 20 to 218 days (average = 95 days). For DHA, the rates were faster at 9.4 and 10.3% $d^{-1}$ (equilibrium times of 10 and 11 days). Uptake rate of LA in muscle tissue of two gadid speces, Pacific cod and walleye Pollock (*Theragra chalcogramma*), was found to be 2.0% $d^{-1}$ in the laboratory (Copeman et al. 2013), and in Atlantic croaker (*Micropogonias undulates*), uptake of LA was between 1.0 and 2.0% $d^{-1}$ (Mohan et al. 2016). In those other studies, time to equilibrium ranged from 44 to 81 days. These results suggest that there may not be a universal uptake rate across fatty acids, species, and tissue types, but that the rate and time to equilibrium likely depends upon dietary fatty acid concentration and the consumer's initial fatty acid composition and ability to biosynthesize or selectively retain fatty acids.

Accurate estimates of trophic position are required to re-create food webs used in ecosystem models, which are becoming increasing used in fisheries management (Collie et al. 2016). Estimates of trophic position in aquatic ecosystems are usually calculated by examining $\delta^{15}N$ and assuming a discrimination value of 3.4‰ between trophic levels (Post 2002). Recent studies (Hussey et al. 2014; Hertz et al. 2014) have cautioned against this assumption and have shown that there is a significant negative association between dietary $\delta^{15}N$ and a consumer's discrimination value. In our feeding study, discrimination values ranged from 4.1 to 4.5‰ and were probably >3.4‰ because of the relatively low $\delta^{15}N$ values of the treatment diets (7.0 – 8.2‰) with respect to naturally occurring prey, that typically have $\delta^{15}N$ values greater than 9.0‰ (Miller et al. 2010). Further laboratory

studies could establish trophic discrimination values across a range of prey types varying in trophic position to confirm this observation and these values could prove useful in the development of stable isotope mixing models to estimate salmon diets in the field.

Changes in juvenile Chinook salmon lipids were evaluated under both feeding and fasting conditions. Salmon lipids decreased during the first half of the feeding study as salmon added length, increased in the second half of the feeding study as salmon added weight, and then decreased proportionately with ration through the fasting and swimming studies as energy stores were mobilized to meet energetic demands. Juvenile Chinook salmon are known to shift energy allocation from somatic growth to energy storage during the first ocean summer (MacFarlane and Norton 2002; MacFarlane 2010), which may be an adaptive response to balance growth and metabolic demands (Allen et al. 2016). There is a need to better understand the trade-offs between growth and energy storage in juvenile salmon, and the environmental cues that regulate them, in order to identify thresholds in size, growth, or body condition that may determine whether or not salmon survive through the critical first year at sea.

*Conclusions*

In this three-phase experiment, we evaluated the effects of dietary fatty acids and fasting on juvenile Chinook salmon growth, lipids, and aerobic performance. During the 12-week feeding study there were no significant differences in size or growth among juveniles reared on formulated diets with ratios of DHA:EPA that were high (1.5, A diet), intermediate (0.9, KA diet), or low (0.6, K diet), indicating that EFAs provisioned at >50% of total dietary fatty acids has no significant effect on Chinook salmon growth.

During the 4-week fasting study, fed salmon were heavier, grew faster, and had significantly more storage lipids than fasted fish. Results of the swimming study found a significant positive association between swimming speed, TAG and fish FL, implying that lipid stores may have a carryover effect in future performance following periods of food deprivation. In winter months when food resources may be scarce, larger, fatter salmon are expected to survive better than smaller, leaner fish (Beamish and Mahnken 2001; Farley et al. 2007; Hurst 2007a).

This study also quantified temporal changes in the fatty acid and stable isotope profiles of juvenile Chinook salmon reared on different diets. We found that uptake of dietary fatty acids varied depending on fatty acid and dietary concentration, but that on average fatty acids and bulk stable isotopes reflected diet within 1 to 2 months following a diet shift. This work marks an important step in refining understanding about how juvenile Chinook salmon integrate diet into size, growth, energetic storage, and aerobic performance during early marine residence, a critical period in salmon life history. Knowledge about the temporal lags between diet and biochemistry could lead to more accurate predictions and assessment of the consequences of prey on juvenile Chinook salmon growth, condition, and possibly survival.

## ACKNOWLEDGEMENTS

The Chinook salmon used in this study were reared at Priest Rapids Hatchery, operated by the Washington Department of Fish and Wildlife with funds from Grant County Public Utility District and the U.S. Army Corps of Engineers. Authorization for use of the salmon came from M. Kimbel, J. Easterbrooks, M. Lewis, and G. Pearson. We would

like to thank M. Arkoosh, J. Dietrich, G. Hutchinson, J. Porquez, A. Barry, L. Tomaro, T. Murphy, and E. Fedewa for their assistance with fish transport and animal husbandry. Thanks also to S. Haines, P. Iseri, E. Hanneman, M. Ottmar, A.J. Phillips, and A. Phillips for their assistance in formulating diets and with the critical swimming speed experiment. Samples were processed with the technical assistance of J. Porquez, A. Sremba, K. Klink, and J. McKay. Statistical advice was provided by B. Brinz, N. Sard, and D. M. Hawkyard. This work was supported by a NOAA Living Marine Resources Cooperative Science Center Technical Advisory Board grant (13-07) awarded to J. Miller, R. Emmett, L. Copeman, A. Place, and M. Litz, and by the Bill Wick Marine Fisheries Award presented by the Hatfield Marine Science Center. This study was conducted with approval from Oregon State University's Institutional Animal Care and Use Committee under Animal Care and Use Protocol 4430.

## LITERATURE CITED

Ackman RG, Tocher CS, McLachlan J (1968) Marine phytoplankter fatty acids. J Fish Res Board Can 25, 1603–1620.

Allen D, Rosenfeld J, Richards J (2016) Physiological basis of metabolic trade-offs between growth and performance among different strains of rainbow trout. Can J Fish Aquat Sci 73, 1493–1506.

Alverson DL (1992) A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): The conflict arena. Rev Aquat Sci 6, 203–256.

Arts MT, Brett MT, Kainz MJ (2009) Lipids in Aquatic Ecosystems. Springer, New York.

Beamish RJ, Mahnken C (2001) A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog Oceanogr 49, 423–437.

Beamish RJ, Poier KL, Mahnken C (2001) Evidence of the validity of the critical size and critical period hypothesis. N Pac Anadr Fish Comm 564, 1–16.

Beamish RJ, Mahnken C, Neville CM (2004) Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. Trans Am Fish Soc 133, 26–33.

Bell WH, Terhune DB (1970) Water tunnel design for fisheries research. Fish Res Bd Can Tech Rep 195. Fisheries Research Board of Canada, Nanaimo.

Bell MV, Batty RS, Dick JR, Fretwell K, Navarro JC, Sargent JR (1995) Dietary deficiency of docosahexaenoic acid impairs vision at low light intensities in juvenile herring (*Clupea harengus* L.). Lipids 30, 443–449.

Brett JR (1964) The respiratory metabolism and swimming performance of young sockeye salmon. J Fish Res Bd Can 21, 1183–1226.

Brodeur RD (1991) Ontogenetic variation in the type and size of prey consumed by juvenile coho, *Oncorhynchus kisutch*, and Chinook, *O. tshawytscha*, salmon. Environ Biol Fish 30, 303–315.

Budge SM, Iverson SJ, Bowen WD, Ackman RG (2002) Among and within species variability in fatty acid signatures of marine fish and invertebrates on the Scotian Shelf, Georges Bank and southern Gulf of St. Lawrence. Can J Fish Aquat Sci 59, 886–898.

Budge SM, Iverson SJ, Koopman HN (2006) Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. Mar Mam Sci 22, 759–801.

Budge SM, Wooller MJ, Springer AM, Iverson SJ, McRoy CP, Divorky J (2008) Tracing carbon flow in an Arctic marine food web using fatty acid-stable isotope analysis. Oecologia 157, 117–129.

Budge SM, Penney SN, Lall SP (2011) Response of tissue lipids to diet variation in Atlantic salmon (*Salmo salar*): Implications for estimating diets with fatty acid analysis. J Exp Mar Bio Ecol 409, 267–274.

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.

Claiborne AM, Fisher JP, Hayes SA, Emmett RL (2011) Size at release, size-selective mortality, and age of maturity of Willamette River hatchery yearling Chinook salmon. Trans Am Fish Soc 140, 1135−1144.

Cober ER, Fregeau-Reid JA, Butler G, Voldeng HD (2006) Genotype-environment analysis of parameters describing water uptake in Natto Soybean. Crop Sci 46, 2415–2419.

Collie JS, Botsford LW, Hastings A, Kaplan IC, Largier JL, Livingston PA, Plagányi É, Rose KA, Wells BK, Werner FE (2016) Ecosystem models for fisheries management: finding the sweet spot. Fish Fish 17, 101–125.

Copeman LA, Parrish CC, Brown JA, Harel M (2002) Effects of docsahexaenoic, eicosapentaenoic, and arachidonic acids on the early growth, survival, lipid composition and pigmentation of yellowtail flounder (*Limanda ferruginea*): a live food enrichment experiment. Aquaculture 210, 285–304.

Copeman LA, Laurel BJ (2010) Experimental evidence of fatty acid limited growth and survival in Pacific cod larvae. Mar Ecol Prog Ser 412, 259–272.

Copeman LA, Laurel BJ, Parrish CC (2013) Effect of temperature and tissue type on fatty acid signatures of two species of North Pacific juvenile gadids: A laboratory feeding study. J Exp Mar Biol Ecol 448, 188–196.

Copeman LA, Laurel BJ, Boswell KM, Sremba AL, Klinck K, Heintz RA, Vollenweider JJ, Helser TE, Spencer ML (2016) Ontogenetic and spatial variability in trophic biomarkers of juvenile saffron cod (*Eleginus gracilis*) from the Beaufort, Chukchi, and Bering Seas. Polar Biol 39, 1109–1126.

Dale KE, Daly EA, Brodeur RD (2017) Interannual variability in the feeding and condition of subyearling Chinook salmon off Oregon and Washington in relation to fluctuating ocean conditions. Fish Oceanogr 26, 1–16.

Dalsgaard J, St. John M, Kattner G, Müeller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46, 224–340.

Daly EA, Brodeur RD, Weitkamp LA (2009) Ontogenetic shifts in diets of juvenile and subadult coho and Chinook salmon in coastal marine waters: Important for marine survival? Trans Am Fish Soc 138, 1420–1438.

Daly EA, Benkwitt CE, Brodeur RD, Litz MNC, Copeman LA (2010) Fatty acid profiles of juvenile salmon indicate prey selection strategies in coastal marine waters. Mar Biol 157, 1975–1987.

El-Sabaawi R, Dower JF, Kainz M, Mazumder A (2009) Characterizing dietary variability and trophic positions of coastal calanoid copepods: insight from stable isotopes and fatty acids. Mar Biol 156, 225–237.

Farley EV Jr, Moss JH, Beamish RJ (2007) A review of the critical size, critical period hypothesis for juvenile Pacific salmon. N Pac Anadr Fish Comm Bull 4, 311–317.

Folch J, Lees M, Sloane SG (1957) A simple method for the isolation and purification of total lipids from animal tissues. J Biochem 22, 497–509.

Fry B (2006) Stable Isotope Ecology. Springer, New York.

Hartt AC (1980) Juvenile salmonids in the oceanic ecosystem: the critical first summer. In McNeil WJ, Himsworth DC (eds) Salmonid Ecosystems of the North Pacific. Oregon State University Press, Corvallis, pp 25–57.

Heady WN, Moore JW (2013) Tissue turnover and stable isotope clocks to quantify resource shifts in anadromous rainbow trout. Oecologia 172, 21–34.

Hertz E, Robinson JPW, Trudel M, Mazumder A, Baum JK (2014) Estimation of predator-prey mass ratios using stable isotopes: sources of errors. Mar Ecol Prog Ser 516, 1–6.

Hertz E, Trudel M, El-Sabaawi R, Tucker S, Dower JF, Beacham T, Edwards AM, Mazumder A (2016) Hitting the moving target: modelling ontogenetic shifts with stable isotopes reveals the importance of isotopic turnover. J Anim Ecol 85, 681–691.

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50, 346–363.

Hurst TP (2007a) Causes and consequences of winter mortality in fishes. J Fish Biol 71, 315–345.

Hurst TP (2007b) Thermal effects on behavior of juvenile walleye Pollock (*Theragra chalcogramma*): implications for energetics and food web models. Can J Fish Aquat Sci 64, 449–457.

Hussey NE, MacNeil MA, McMeans BC, Olin JA, Dudley SFJ, Cliff G, Wintner SP, Fennessy ST, Fisk AT (2014) Rescaling the trophic structure of marine food webs. Ecol Lett 17, 239−250.

Iwama GK, Tautz AF (1981) A simple growth model for salmonids in hatcheries. Can J Fish Aquat Sci 38, 649–656.

Iverson SJ, Frost KJ, Lang SLC (2002) Fat content and fatty acid composition of forage fish and invertebrates in Prince William Sound, Alaska: factors contributing to among and within species variability. Mar Ecol Prog Ser 241, 161–181.

Izquierdo MS (1996) Essential fatty acid requirements of cultured marine fish larvae. Aquacult Nutr 2, 183–191.

Lee RF, Nevenzel JC, Paffenhöffer G-A (1971) Importance of wax esters and other lipids in the marine food chain: phytoplankton and copepods. Mar Biol 9, 99–108.

Litz MNC, Brodeur RD, Emmett RL, Heppell SS, Rasmussen RS, O'Higgins L, Morris MS (2010) Effects of variable oceanographic conditions on forage fish lipid content and fatty acid composition in the northern California Current. Mar Ecol Prog Ser 405, 71–85.

Lu Y, Ludsin SA, Fanslow DL, Pothoven SA (2008) Comparison of three microquantity techniques for measuring total lipids in fish. Can J Fish Aquat Sci 65, 2233–2241.

MacFarlane RB, Norton EC (2002) Physiological ecology of juvenile chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California. Fish Bull 100, 244–257.

MacFarlane RB (2010) Energy dynamics and growth of Chinook salmon (*Oncorhynchus tshawytscha*) from the Central Valley of California during the estuarine phase and first ocean year. Can J Fish Aquat Sci 67, 1549–1565.

Mazur MM, Wilson MT, Dougherty AB, Buchheister A, Beauchamp DA (2007) Temperature and prey quality effects on growth of juvenile walleye Pollock *Theragra chalcogramma* (Pallas): a spatially explicit bioenergetics approach. J Fish Biol 70, 816–836.

McConnaughey T, McRoy CP (1979) $^{13}C$ label identifies eelgrass (*Zostera marina*) carbon in an Alaskan estuarine food web. Mar Biol 53, 263–269.

Miller CB, Morgan CA, Prahl FG, Sparrow MA (1998) Storage lipids of the copepod *Calanus finmarchicus* from Georges Bank and the Gulf of Maine. Limnol Oceanogr 43, 488–497.

Miller TW, Brodeur RD, Rau G, Omori K (2010) Prey dominance shapes trophic structure of the northern California Current pelagic food web: evidence from stable isotopes and diet analysis. Mar Ecol Prog Ser 420, 15–26.

Miller JA, Teel DJ, Baptista A, Morgan CA (2013) Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook Salmon (*Oncorhynchus tshawytscha*). Can J Fish Aquat Sci 70, 617–629.

Mjaavatten O, Levings CD, Poon P (1998) Variation in the fatty acid composition of juvenile Chinook and coho salmon from Fraser River estuary determined by multivariate analysis; role of environment and genetic origin. Comp Biochem Physiol B 120, 291–309.

Mohan SD, Mohan JA, Connelly TL, Walther BD, McClelland JW (2016) Fatty acid biomarkers and tissue-specific turnover: validation from a controlled feeding study in juvenile Atlantic croaker *Micropogonias undulatus* J Fish Biol 89, 2004–2023.

Moss JH, Beauchamp DA, Cross AD, Myers KW, Farley EV Jr, Murphy JM, Helle JH (2005) Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. Trans Am Fish Soc 134, 1313–1322.

National Research Council (NRC) (2011) Nutrient Requirements of Fish and Shrimp. The National Academies Press, Washington DC.

Parrish CC (1999) Determination of total lipids, lipid classes and fatty acids in aquatic samples. In Arts MT, Wainmann BC (eds) Lipids in Freshwater Ecosystems. Springer, New York, pp 4–19.

Pearcy WG (1992) Ocean Ecology of North Pacific Salmonids. Washington Sea Grant Program, University of Washington Press, Seattle.

Pierce BJ, McWilliams SR (2014) The fat of the matter: How dietary fatty acids can affect exercise performance. Int Comp Biol 54, 903–912.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2016) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-128. http://CRAN.R-project.org/package=nlme.

Plaut I (2001) Critical swimming speed: its ecological relevance. Comp Biochem Phys A 131, 41–50.

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703–718.

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods, and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152, 179–189.

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Renkawitz MD, Sheehan TF, Dixon HJ, Nygaard R (2015) Changing trophic structure and energy dynamics in the Northwest Atlantic: implications for Atlantic salmon feeding at West Greenland. Mar Ecol Prog Ser 538, 197–211.

Rodrìguez C, Pèrez JA, Dìaz M, Izquierdo MS, Fernandez-Palacios H, Lorenzo A (1997) Influence of the EPA/DHA ratio in rotifers on gilthead seabream (*Sparus aurata*) larval development. Aquaculture 150, 77–89.

Saito H, Ishihara K, Murase T (1996) Effect of prey fish lipids on the docosahexaenoic acid content of total fatty acids in the lipid of *Thunnus albacares* yellowfin tuna. Biosci Biotech Bioch 60, 962–965.

Sargent JR, Bell JG, Bell MV, Henderson RJ, Tocher DR (1995) Requirement criteria for essential fatty acids. J Applied Ich 11, 183–198.

Sargent J, Bell G, McEvoy L, Tocher D, Estevez A (1999) Recent developments in the essential fatty acid nutrition of fish. Aquaculture 177, 191–199.

Schabetsberger R, Morgan CA, Brodeur RD, Potts CL, Peterson WT, Emmett RL (2003) Prey selectivity and diel feeding chronology of juvenile Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Columbia River plume. Fish. Oceanogr. 12, 523–540.

Schultz ET, Conover DO (1999) The allometry of energy reserve depletion: test of a mechanism for size-dependent winter mortality. Oecologia 119, 474–483.

Sheridan MA (1994) Regulation of lipid metabolism in poikilothermic vertebrates. Comp Biochem Physiol B 107, 495–508.

Takeuchi T (2014) Progress on larval and juvenile nutrition to improve the quality and health of seawater fish: a review. Fish Sci 80, 389–403.

Tocher DR (2003) Metabolism and functions of lipids and fatty acids in teleost fish. Rev Fish Sci 11, 107–184.

Tocher DR (2010) Fatty acid requirements in ontogeny of marine and freshwater fish. Aquacult Res 41, 717–732.

Tocher DR (2015) Omega-3 long-chain polyunsaturated fatty acids and aquaculture in perspective. Aquaculture 449, 94–107.

Tomaro LM, Teel DJ, Peterson WT, Miller JA (2012) When is bigger better? Early marine residence of middle and upper Columbia River spring Chinook salmon. Mar Ecol Prog Ser 452, 237−252.

Vander Zanden MJ, Clayton MK, Moody EK, Solomon CT, Weidel BC (2015) Stable isotope turnover and half-life in animal tissues: a literature synthesis. PLoS ONE 10(1), e0116182.

Watanabe T (1993) Importance of docosahexaenoic acid in marine larval fish. J World Aquacult Soc 24, 152–161.

Wu FC, Ting YY, Chen HY (2003) Dietary docosahexaenoic acid is more optimal than eicosapentaenoic acid affecting the level of cellular defense responses of the juvenile grouper *Epinephelus malabaricus*. Fish Shellfish Immunol 14, 223–238.

**Figure 2.1** Schematic overview of the 20-week experiment consisting of three phases following a 6-week acclimation period, when all fish were fed an acclimation diet (AD): (1) the feeding study, when salmon were fed either krill (K), krill and anchovy (KA), or anchovy (A) enriched diets for 12 weeks; (2) the fasting study, when fish were either fed continuously for 4 weeks, starved for 2 weeks and then fed for 2 weeks, or starved for 4 weeks; and (3) the swimming study, when fish were fasted for 4 weeks and then had their critical swimming speeds ($U_{crit}$, mm $s^{-1}$) measured.

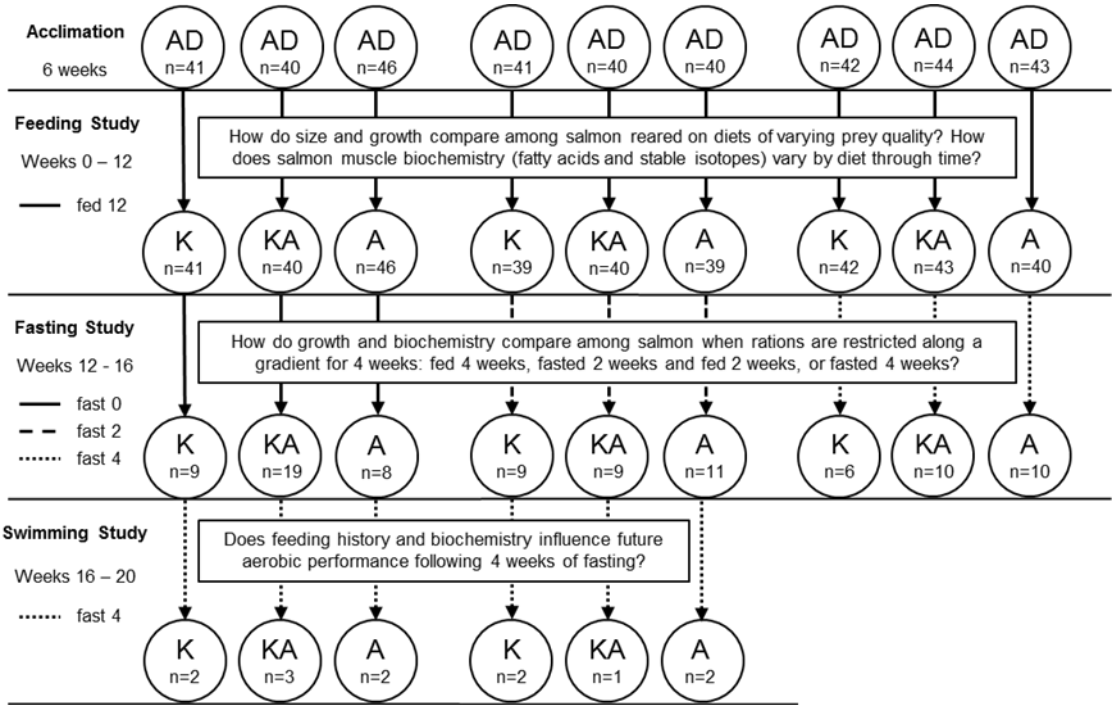


**Figure 2.2** Observed and average a) fork length and b) mass of fish at weeks 0, 2, 6, and 12 through the feeding study. Treatments are means ± standard error calculated from tanks feeding on krill (K), krill and anchovy (KA), or anchovy (A) diets.

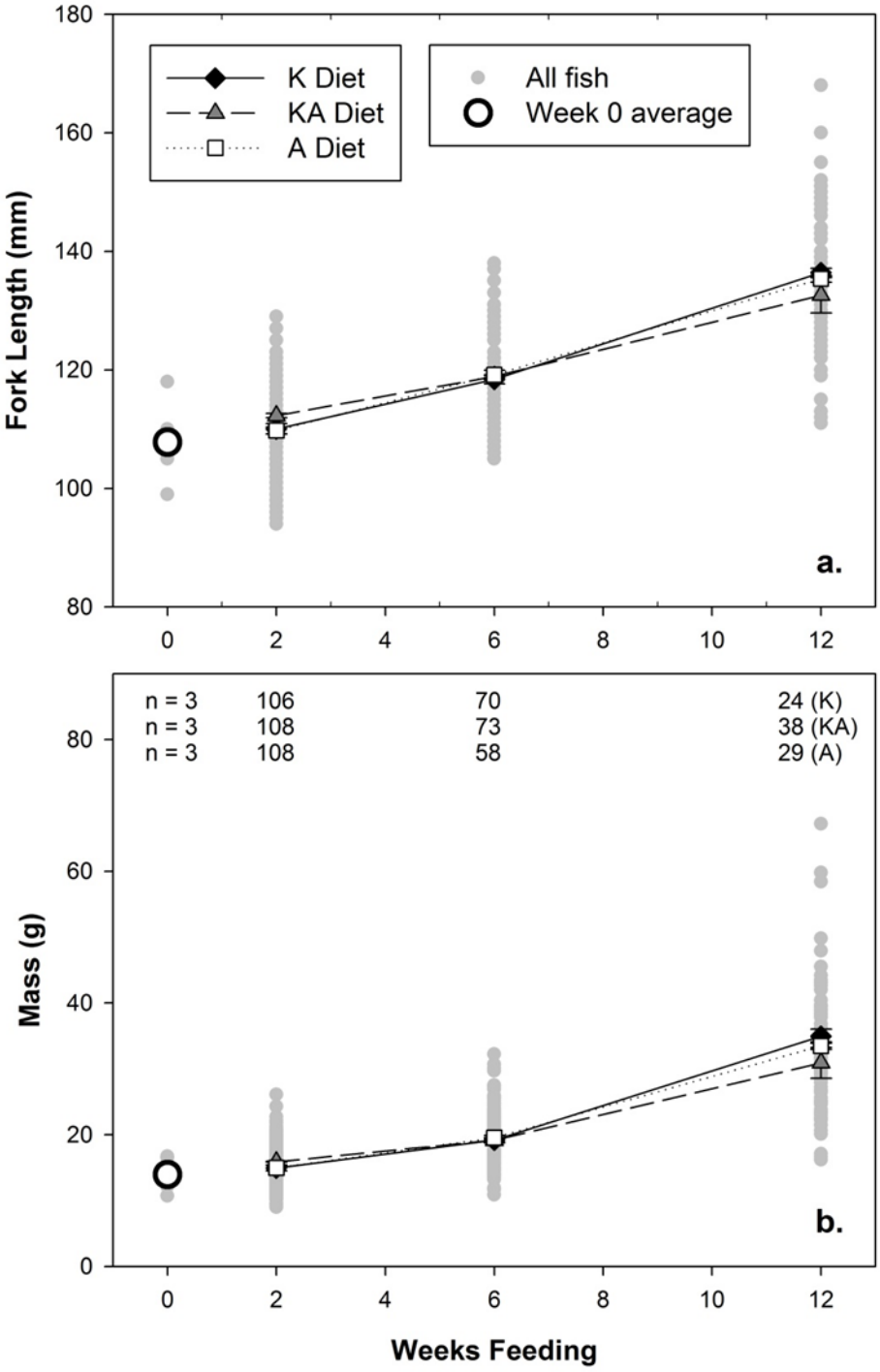


**Figure 2.3** Box plots showing treatment (n = 3 tanks per treatment) range, median (straight line), and mean (dashed line) a) fork length, b) mass, c) growth rate, d) specific growth rate (SGR), e) triacylglycerols (% TAG), and f) total lipids (mg $g^{-1}$) following ration treatments. Different letters above boxes indicate statistical significance (one-way ANOVA and Tukey post-hoc tests $p < 0.05$).

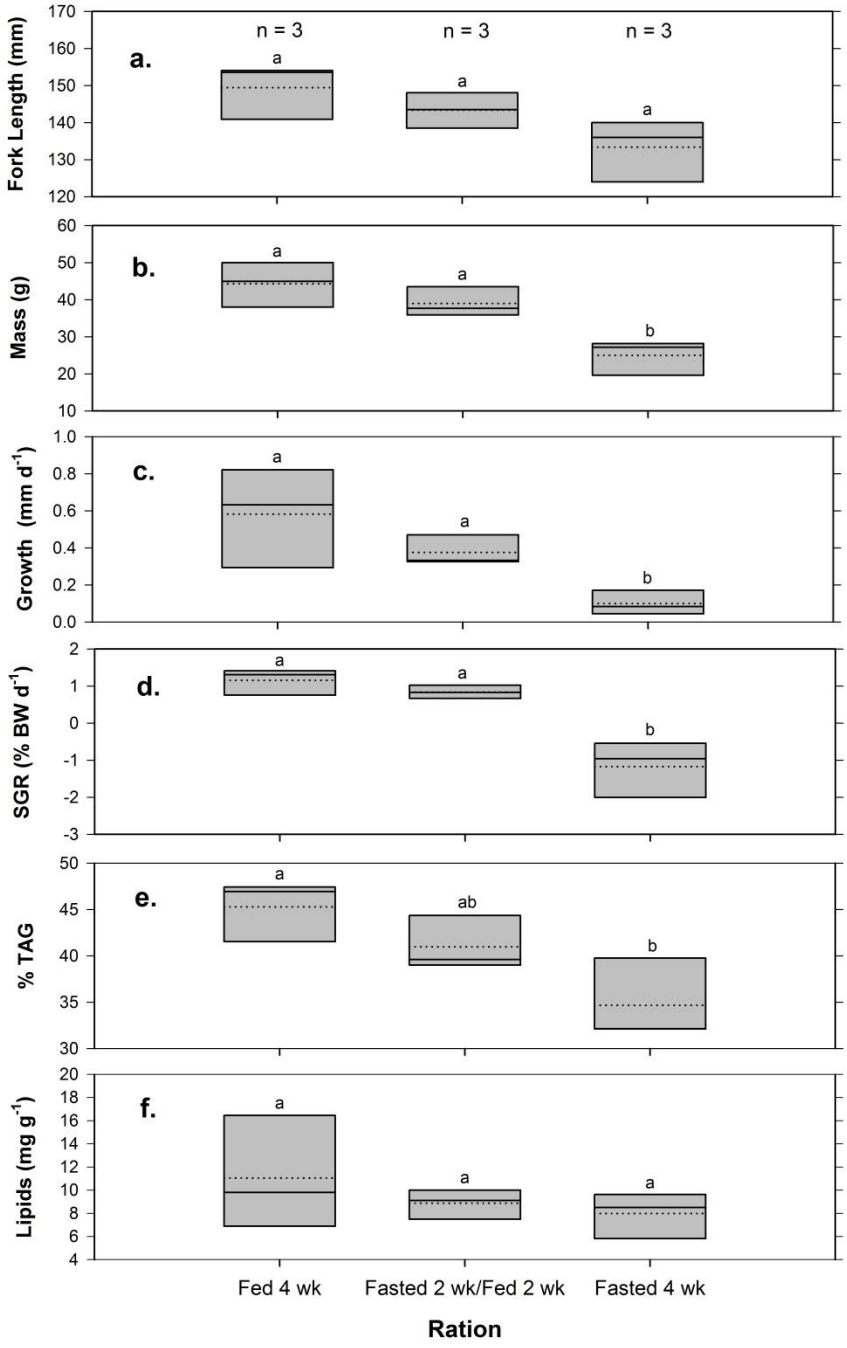


**Figure 2.4** Scatterplot of treatment (n = 2 tanks per treatment) means with bidirectional error bars for a) triacylglycerols (% TAG) or b) fork length and critical swimming speeds ($U_{crit}$ mm $s^{-1}$) of Chinook salmon after feeding on krill (K), krill and anchovy (KA), or anchovy (A) enriched diets for 16 weeks followed by 4 weeks of fasting.

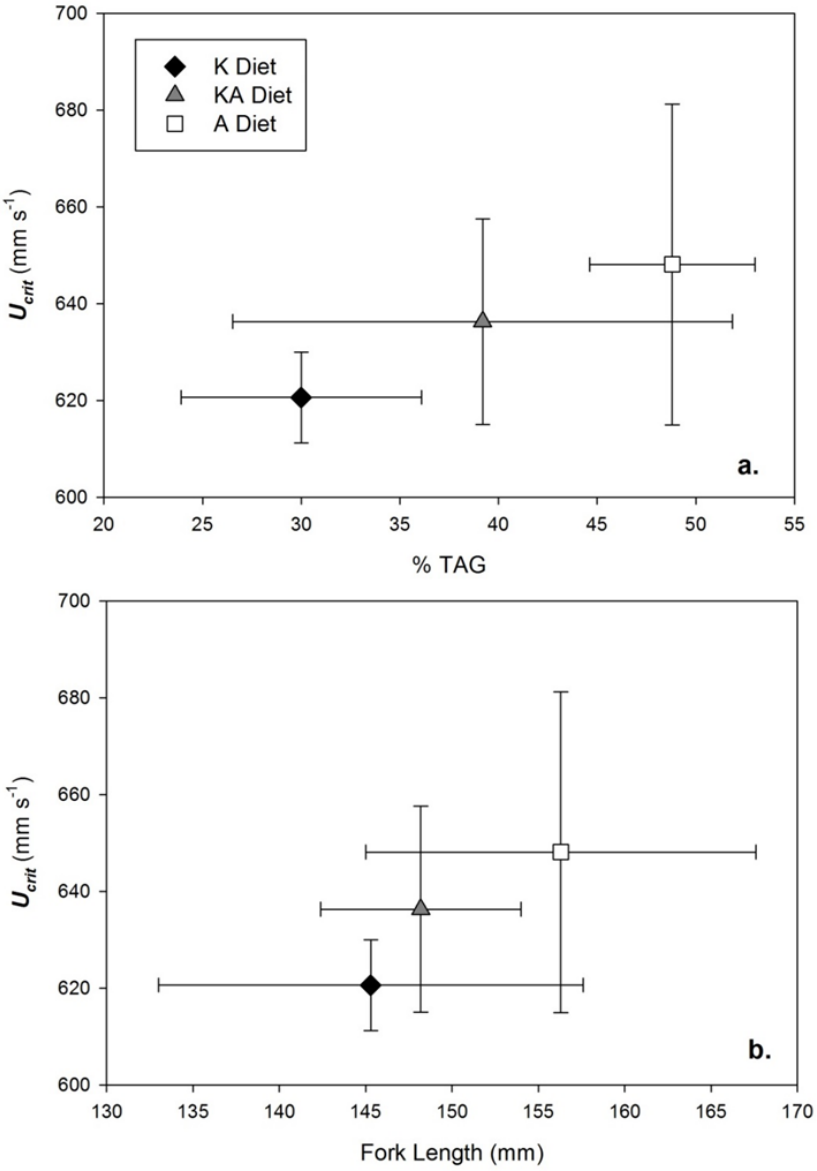


**Figure 2.5** Lipid classes per wet weight (mg $g^{-1}$) in muscle tissue of salmon feeding on krill (K), krill and anchovy (KA), or anchovy (A) enriched diets at weeks 0, 6, and 12. Lipid classes are steryl esters (SE), triacylglycerols (TAG), free fatty acids (FFA), sterols (ST), and polar lipids (PL). Week 0 baseline values are an average ± standard error SE of all tanks (n = 9) and weeks 6 and 12 represent treatment means ± SE (n = 3 tanks per treatment).

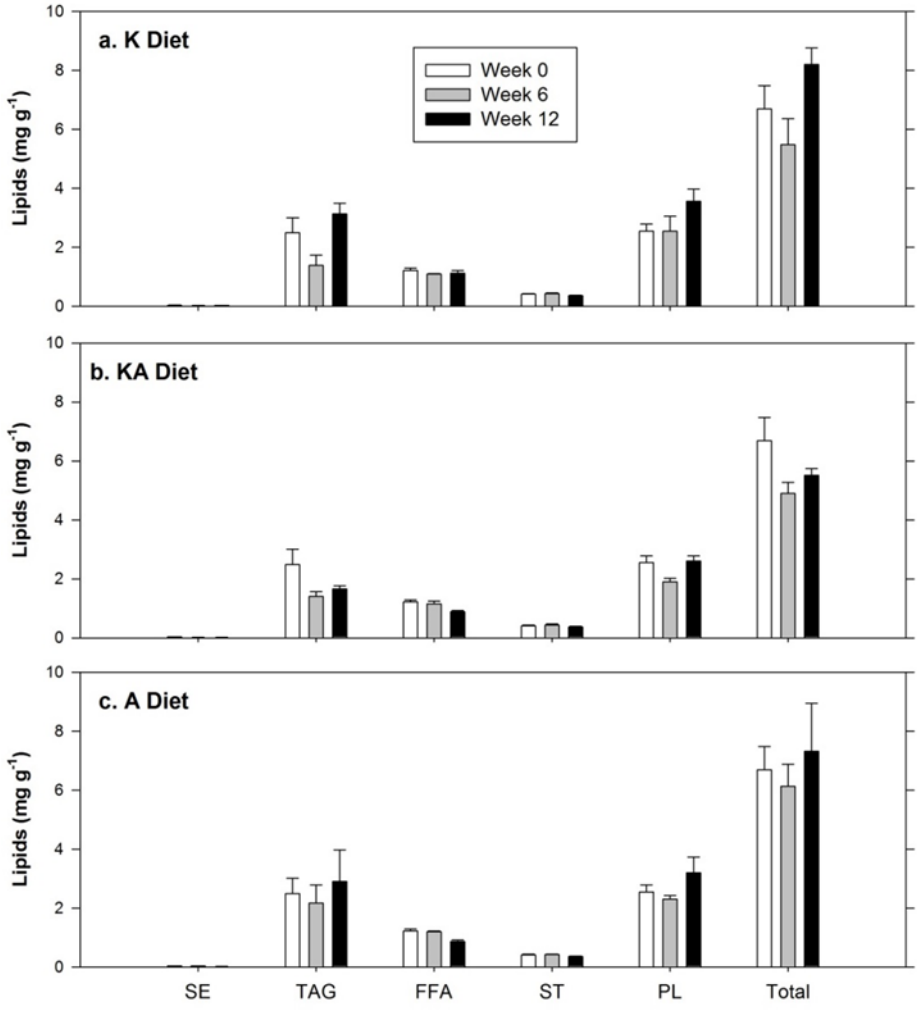


**Figure 2.6** Percent fatty acids in muscle tissue of salmon feeding on krill (K), krill and anchovy (KA), or anchovy (A) at weeks 0, 1, 2, 4, 6, 8, and 12. Week 0 baseline values are from tank averages ± standard error SE (n = 1 fish per tank) and all other time periods represent tank means ± SE (n = 3 tanks per treatment).

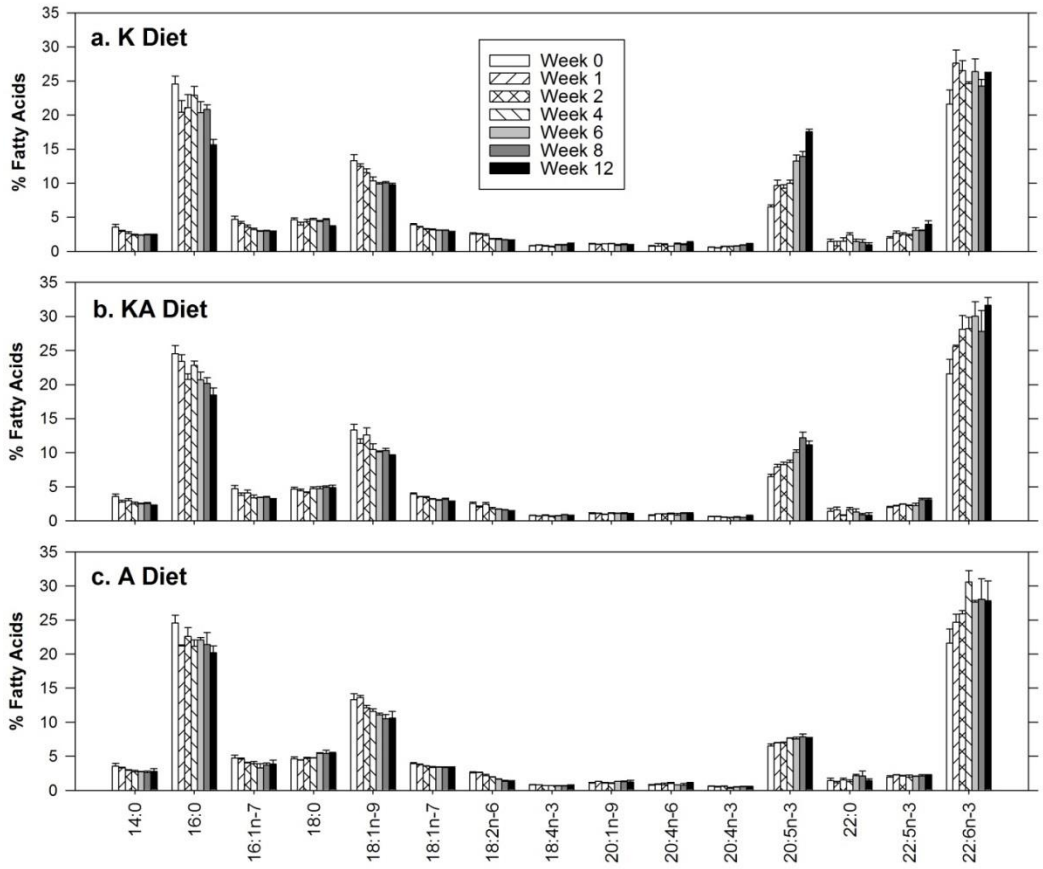


**Figure 2.7** Stable isotope values of a) carbon and b) nitrogen from muscle tissue of salmon reared on krill (K), krill and anchovy (KA), or anchovy (A) enriched diets for 12 weeks. Symbols represent tank means ± standard error (n = 3 tanks per treatment).

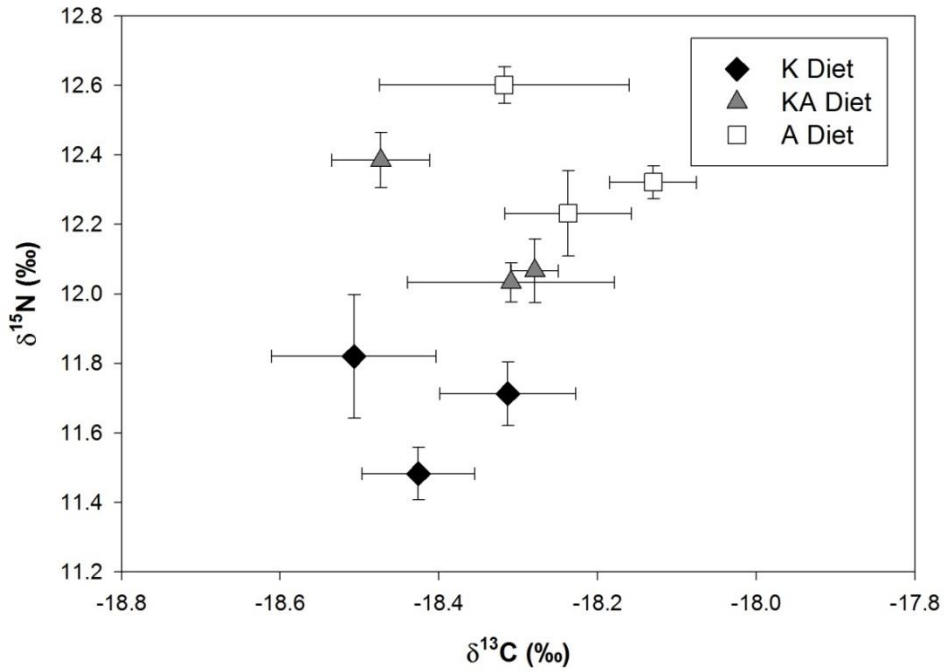


**Figure 2.8** Percent of a) eicosapentaenoic acid (EPA), b) docosahexaenoic acid (DHA), and c) ratios of DHA:EPA from muscle tissue of salmon reared on krill (K), krill and anchovy (KA), or anchovy (A) enriched diets through the 12-week feeding study. Baseline value (week 0) is an average from all tanks (n = 9 per symbol) and all other time periods represent tank means ± SE (n = 3 tanks per treatment). Lines represent the best nonlinear least squares regression model to the data. Circles to the left and right of the data represent values for pre-treatment and treatment diets, respectively.

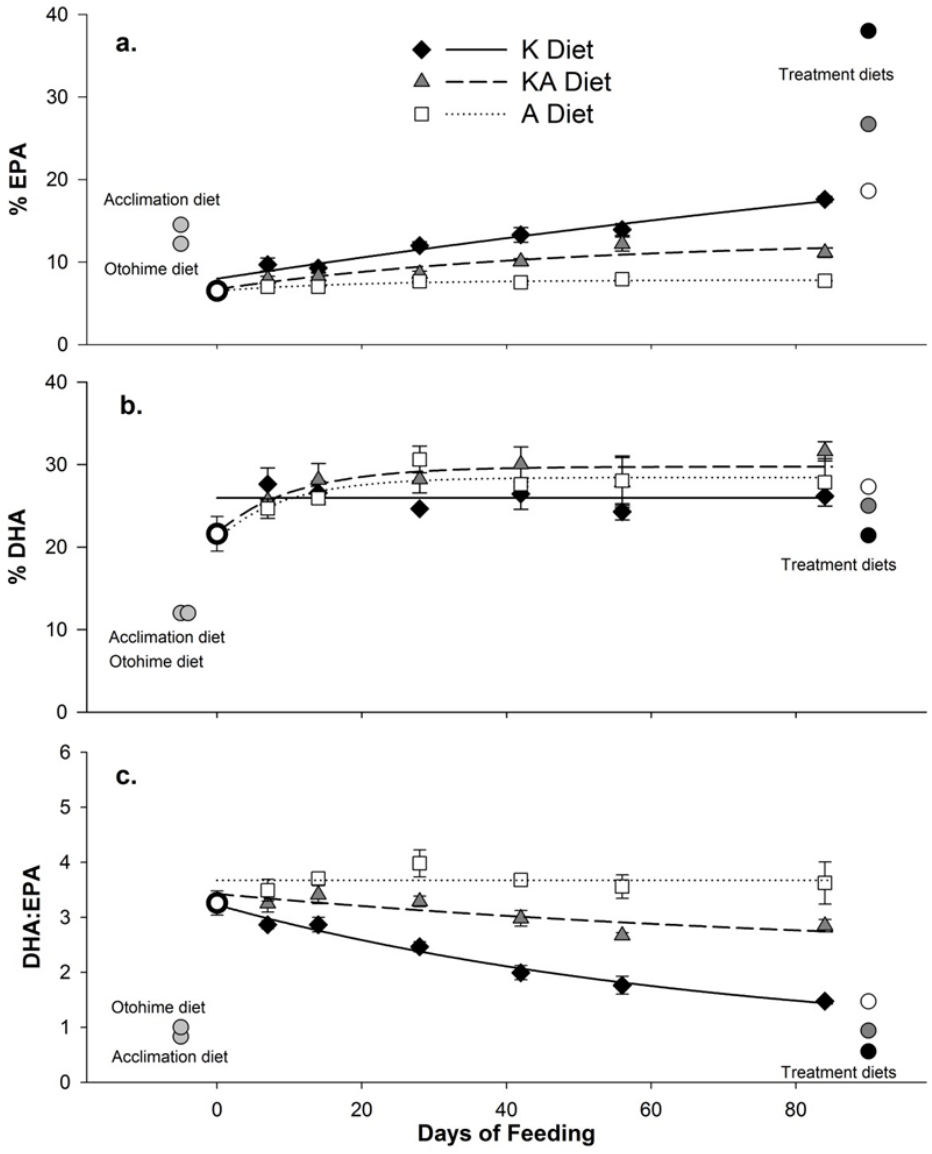


**Figure 2.9** Stable isotope values of a) carbon and b) nitrogen from muscle tissue of salmon reared on krill (K), krill and anchovy (KA), or anchovy (A) enriched diets for 12 weeks. Symbols represent tank means ± standard error (n = 3 tanks per symbol). Baseline value (day 0) is an average from all tanks (n = 9 per symbol). Lines represent the best regressions to the data. Circles to the left and right of the data represent values for pre-treatment and treatment diets, respectively.

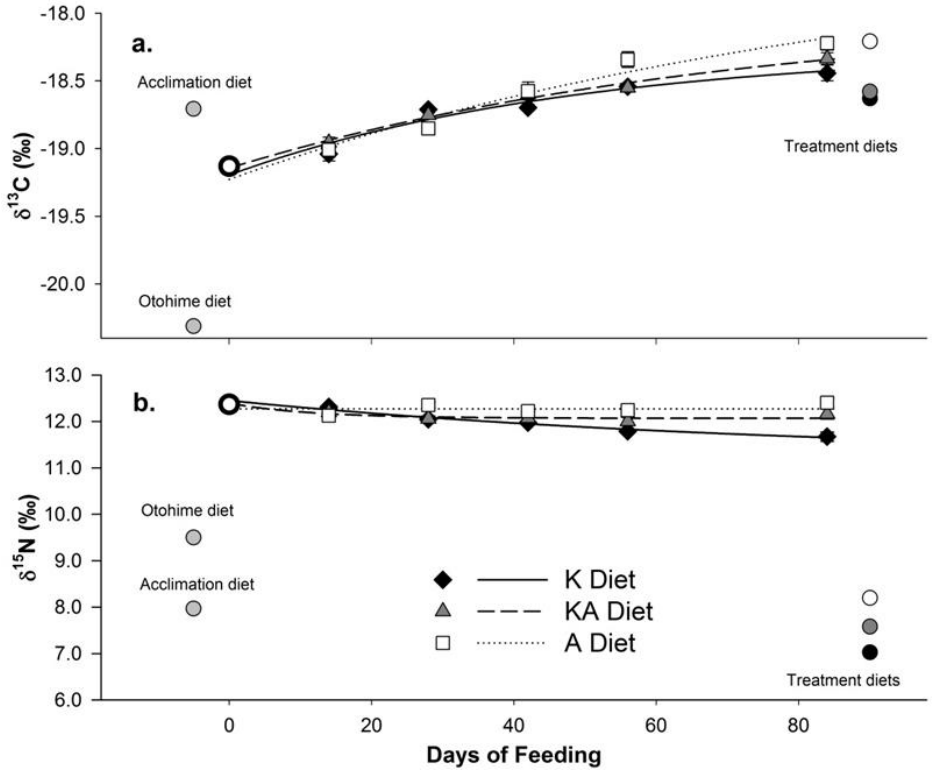


**Table 2.1** Ingredients in acclimation diet (AD), krill diet (K), krill and anchovy diet (KA), and anchovy diet (A) fed to juvenile salmon.

| **Ingredient** | **AD (g kg$^{-1}$)[a]** | **K (g kg$^{-1}$)** | **KA (g kg$^{-1}$)** | **A (g kg$^{-1}$)** |
|---|---|---|---|---|
| Otohime EP2[b] | 135.7 | 94.1 | 94.1 | 94.1 |
| Krill | 271.5 | 341.5 | 170.8 | 0.0 |
| Northern anchovy | 0.0 | 0.0 | 170.8 | 341.5 |
| Twinlab Amino Fuel[c] | 11.9 | 10.9 | 10.9 | 10.9 |
| Powdered gelatin[d] | 191.2 | 174.3 | 174.3 | 174.3 |
| Water | 382.3 | 348.5 | 348.5 | 348.5 |
| Krill oil[e] | 7.2 | 0.0 | 0.0 | 0.0 |
| EPA oil[f] | 0.0 | 25.0 | 15.2 | 6.3 |
| DHA oil[g] | 0.0 | 5.4 | 15.2 | 24.2 |
| Multivitamins[h] | 0.2 | 0.2 | 0.2 | 0.2 |

Contained: pro vitamin A, vitamin A, vitamin C, vitamin E, thiamin, riboflavin, niacin, vitamin B-6, folic acid, vitamin B12, biotin, pantothenic acid, calcium, iron, iodine, magnesium, zinc, selenium, copper, manganese, chromium, molybdenum, choline, inositol, and floragio lutein.

[a] Acclimation diet: fed for 6 weeks prior to onset of feeding experiment.
[b] Otohime EP2, extruded pellet manufactured by: Marubeni Nisshin Feed Co., Ltd., Toyko, Japan and imported by Reed Mariculture, Inc., Campbell, CA, USA. Feed contains: krill meal, fish meal, squid meal, wheat flour, potato starch, corn starch, fish oil, calcium phosphate, betaine, soy lecithin, licorice plant, and wheat germ.
[c] Amino Fuel, Twinlab Corp., American Fork, UT, USA.
[d] Knox unflavored Gelatine, Kraft Foods Global Inc., Northfield, IL, USA.
[e] MegaRed Extra Strength Omega 3 Krill Oil, Schiff Nutrition International, Inc. Salt Lake City, UT, USA.
[f] Epax Omega-3 Concentrates 6015 TG, Epax Inc., Norway AS, Ålesund, Norway.
[g] Epax Omega-3 Concentrates 1050 TG, Epax Inc., Norway AS, Ålesund, Norway.
[h] Daily One Caps without Iron, Twinlab Corp., American Fork, UT, USA.

**Table 2.2** Composition of Otohime® diet (O), acclimation diet (AD), krill diet (K), krill and anchovy diet (KA), and anchovy diet (A) fed to juvenile salmon during the experiment. Data are presented for mean ± SE stable isotopes values of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$, ‰), total lipids per wet weight (mg $g^{-1}$), lipid classes (% of total lipids), and fatty acids (FA, % of total fatty acids).

| | O | AD | K | KA | A |
|---|---|---|---|---|---|
| $\delta^{13}C$ | -20.3 ± 0.1 | -18.7 ± 0.0 | -18.6 ± 0.1 | -18.6 ± 0.1 | -18.2 ± 0.0 |
| $\delta^{15}N$ | 9.5 ± 0.0 | 8.0 ± 0.1 | 7.0 ± 0.0 | 7.6 ± 0.0 | 8.2 ± 0.3 |
| Lipids | 118.1 ± 3.1 | 10.0 ± 2.5 | 20.6 ± 0.1 | 26.1 ± 1.2 | 20.7 ± 3.4 |
| Steryl esters | 0.2 ± 0.2 | 0.0 ± 0.0 | 0.0 ± 0.0 | 0.1 ± 0.1 | 0.2 ± 0.2 |
| Triacylglycerols | 65.2 ± 0.9 | 55.7 ± 0.5 | 40.9 ± 0.3 | 44.0 ± 6.6 | 31.7 ± 3.3 |
| Free FAs | 1.8 ± 0.0 | 11.2 ± 1.8 | 7.5 ± 0.0 | 6.9 ± 1.1 | 12.4 ± 7.1 |
| Sterols | 2.1 ± 0.1 | 8.4 ± 0.4 | 5.6 ± 0.6 | 2.6 ± 0.8 | 4.8 ± 2.6 |
| Polar lipids | 30.8 ± 0.9 | 24.7 ± 1.7 | 46.1 ± 0.3 | 46.4 ± 8.3 | 50.9 ± 6.2 |
| 14:0 | 6.5 ± 0.1 | 7.5 ± 0.2 | 2.9 ± 0.1 | 3.1 ± 0.1 | 3.6 ± 0.0 |
| 16:0 | 18.8 ± 0.1 | 21.3 ± 0.5 | 9.7 ± 0.5 | 10.2 ± 0.2 | 12.1 ± 0.0 |
| 18:0 | 3.1 ± 0.0 | 3.2 ± 0.0 | 2.2 ± 0.2 | 3.0 ± 0.0 | 4.1 ± 0.1 |
| ∑SFA[1] | 30.5 ± 0.3 | 33.1 ± 0.7 | 15.9 ± 0.6 | 17.8 ± 0.3 | 21.6 ± 0.3 |
| 16:1n-7 | 5.8 ± 0.0 | 6.2 ± 0.1 | 3.0 ± 0.1 | 3.7 ± 0.0 | 4.6 ± 0.1 |
| 18:1-n-7 | 4.1 ± 0.0 | 5.1 ± 0.1 | 2.7 ± 0.2 | 2.7 ± 0.0 | 3.1 ± 0.0 |
| 18:1n-9 | 14.0 ± 0.1 | 14.3 ± 0.3 | 8.6 ± 0.6 | 8.4 ± 0.1 | 9.6 ± 0.1 |
| 20:1n-9 | 1.7 ± 0.0 | 0.8 ± 0.8 | 0.6 ± 0.6 | 0.0 ± 0.0 | 0.0 ± 0.0 |
| 20:1n-11 | 1.7 ± 0.0 | 1.5 ± 0.1 | 0.5 ± 0.5 | 1.5 ± 0.0 | 2.0 ± 0.1 |
| ∑MUFA[2] | 32.5 ± 0.1 | 29.1 ± 0.1 | 16.2 ± 0.6 | 17.6 ± 0.2 | 20.9 ± 0.1 |
| 16:2n-4 | 1.4 ± 0.0 | 1.4 ± 0.0 | 0.9 ± 0.1 | 0.9 ± 0.0 | 0.9 ± 0.0 |
| 18:3n-3 (ALA) | 0.9 ± 0.0 | 1.0 ± 0.0 | 0.9 ± 0.0 | 0.7 ± 0.0 | 0.6 ± 0.0 |
| 18:4n-3 | 2.0 ± 0.0 | 2.6 ± 0.0 | 1.2 ± 1.2 | 1.9 ± 0.0 | 1.6 ± 0.0 |
| 20:4n-3 | 0.6 ± 0.0 | 0.0 ± 0.0 | 1.6 ± 0.1 | 1.1 ± 0.0 | 0.8 ± 0.0 |
| 20:4n-6 (ARA) | 0.8 ± 0.0 | 0.8 ± 0.0 | 1.2 ± 1.2 | 2.0 ± 0.0 | 0.9 ± 0.9 |
| 20:5n-3 (EPA) | 12.2 ± 0.1 | 14.5 ± 0.3 | 38.0 ± 1.6 | 26.7 ± 0.5 | 18.6 ± 0.2 |
| 22:5n-3 | 1.4 ± 0.0 | 1.2 ± 0.0 | 1.1 ± 1.1 | 2.3 ± 0.0 | 2.3 ± 0.0 |
| 22:5n-6 | 0.3 ± 0.0 | 0.0 ± 0.0 | 0.4 ± 0.4 | 1.2 ± 0.0 | 1.5 ± 0.1 |
| 22:6n-3 (DHA) | 12.0 ± 0.2 | 12.0 ± 0.3 | 21.4 ± 1.2 | 25.0 ± 0.4 | 27.3 ± 0.5 |
| ∑PUFA[3] | 36.4 ± 0.3 | 36.7 ± 0.6 | 67.5 ± 1.3 | 64.2 ± 0.5 | 56.9 ± 0.3 |
| DHA:EPA | 1.0 ± 0.0 | 0.8 ± 0.0 | 0.6 ± 0.0 | 0.9 ± 0.0 | 1.5 ± 0.0 |

[1] Also contains <1% of i-15:0, ai15:0, 15:0, i16:0, ai16:0, i17:0, ai17:0, 17:0, 19:0, 20:0, 21:0

[2] Also contains <1% of 14:1, 16:1n-5, 16:1n-9, 16:1n-11, 17:1, 18:1n-5, 18:1n-6, 20:1n-7, 20:1n-9, 22:1n-9, 24:1n-9

[3] Also contains <1% of 16:3n-4, 16:4n-1, 16:4n-3, 18:2n-4, 18:3n-4, 18:4n-1, 20:3n-3, 20:3n-6, 20:4n-6, 21:5n-3, 22:5n-6

**Table 2.3** Parameter estimates (± SE) for nonlinear regressions of fatty acids (eicosapentaenoic acid [EPA], docosahexaenoic acid [DHA], and DHA:EPA) versus days feeding. Average turnover (half-life, in days) and days to reach equilibrium include the range calculated from the confidence interval of *b*. Average values are presented for data that did not vary through time.

| | $Y_0$ | *a* | *b* | **Turnover (*ln2/b*)** | **Equilibrium (*1/b*)** |
|---|---|---|---|---|---|
| **EPA** | | | | | |
| K | 7.97 ± 0.67 | 29.40 ± 39.41 | 0.005 ± 0.01 | 151 (57–∞) | 218 (83–∞) |
| KA | 6.71 ± 0.70 | 5.94 ± 1.61 | 0.02 ± 0.01 | 32 (19–102) | 46 (27–147) |
| A | 6.52 ± 0.25 | 1.31 ± 0.25 | 0.05 ± 0.02 | 14 (9–28) | 20 (13–40) |
| **DHA** | | | | | |
| K | 25.95 ± 0.53 | - | - | - | - |
| KA | 21.82 ± 2.92 | 7.91 ± 2.94 | 0.09 ± 0.06 | 7 (4–24) | 11 (6–35) |
| A | 21.09 ± 2.97 | 7.35 ± 3.01 | 0.10 ± 0.08 | 7 (4–25) | 10 (6–36) |
| **DHA:EPA** | | | | | |
| K | 3.22 ± 0.12 | -2.54 ± 0.63 | 0.01 ± 0.01 | 48 (32–91) | 69 (47–131) |
| KA | 3.42 ± 0.15 | -1.16 ± 1.54 | 0.01 ± 0.02 | 66 (21–∞) | 95 (30–∞) |
| A | 3.67 ± 0.09 | - | - | - | - |

**Table 2.4** Parameter estimates (± SE) for nonlinear regressions of carbon and nitrogen stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) versus days feeding. Average turnover (half-life, in days ) and days to reach equilibrium include the range calculated from the confidence interval of *b*. Average values are presented for data that did not vary through time.

| | $Y_0$ | *a* | *b* | **Turnover (*ln2/b*)** | **Equilibrium (*1/b*)** |
|---|---|---|---|---|---|
| **$\delta^{13}C$** | | | | | |
| K | -19.19 ± 0.08 | 0.93 ± 0.15 | 0.02 ± 0.01 | 34 (24–57) | 48 (34–83) |
| KA | -19.14 ± 0.05 | 1.16 ± 0.20 | 0.01 ± 0.005 | 49 (37–75) | 71 (53–109) |
| A | -19.23 ± 0.08 | 1.78 ± 0.68 | 0.01 ± 0.01 | 66 (40–182) | 95 (58–263) |
| **$\delta^{15}N$** | | | | | |
| K | 12.45 ± 0.08 | -1.21 ± 0.42 | 0.01 ± 0.01 | 54 (33–154) | 78 (48–222) |
| KA | 12.39 ± 0.13 | -0.32 ± 0.14 | 0.09 ± 0.07 | 8 (5–40) | 12 (7–58) |
| A | 12.27 ± 0.04 | - | - | - | - |

CHAPTER 3

# ONTOGENETIC SHIFTS IN THE DIETS OF JUVENILE CHINOOK SALMON: NEW INSIGHT FROM STABLE ISOTOPES AND FATTY ACIDS

Marisa N. C. Litz, Jessica A. Miller, Louise A. Copeman, David J. Teel, Laurie A. Weitkamp, Elizabeth A. Daly, and Andrew M. Claiborne

*Environmental Biology of Fishes*
Online ISSN: 1573-5133
doi: 10.1007/s10641-016-0542-5

ABSTRACT

Variations in marine prey availability and nutritional quality can affect juvenile salmon growth and survival during early ocean residence. Salmon growth, and hence survival, may be related to the onset of piscivory, but there is limited knowledge on the interplay between the prey field, environment, and salmon ontogeny. Subyearling Chinook salmon (*Oncorhynchus tshawytscha*) and their potential prey were sampled in coastal waters off Willapa Bay, USA to explore this issue. Three seasonal prey assemblages were identified, occurring in spring (May), early summer (June – July), and late summer (August – September). The onset of piscivory, based on salmon stomach contents, fatty acids, and stable isotopes occurred later in 2011 compared to 2012, and coincided with the appearance of northern anchovy (*Engraulis mordax*). Salmon fork length (FL) and carbon isotope values ($\delta^{13}C$) increased with a fatty acid biomarker for marine phytoplankton and decreased with a freshwater marker, indicating dietary carbon sources changed as salmon emigrated from the Columbia River. Salmon FL also increased with nitrogen isotope ratios ($\delta^{15}N$), trophic position, and a fatty acid marker for piscivory – a consequence of the ontogenetic shift in diet to fish. Salmon grew faster and obtained larger size and condition by September 2011 compared to 2012, which was related to inter-annual differences in ocean conditions and the duration over which northern anchovy were available. Our results support the idea that juvenile salmon growth depends on the onset and duration of piscivory, suggesting both of these factors may be important components of lifetime growth and fitness.

## INTRODUCTION

The occurrence of ontogenetic, or size-related, shifts in diet or habitat are prevalent in nature and important in shaping species interactions and community structure (Werner and Gilliam 1984). Pacific salmon (*Oncorhynchus* spp.) populations undergo ontogenetic shifts in both diet and habitat as they migrate from freshwater to saltwater, and research suggests that year class strength is determined during this critical period (Pearcy 1992; Beamish et al. 2004; Pearcy and McKinnell 2007). A suite of environmental factors during early marine residence (e.g. physical conditions, plankton and predator abundance) have recently been shown to correlate with salmon survival (Burke et al. 2013; Miller et al. 2013; 2014), but identifying specific mechanisms that account for juvenile salmon mortality in the ocean remains a challenge. Because predation pressure and selective mortality may be higher in smaller or slower growing fish, rapid growth may provide a survival advantage during ontogeny (Zabel and Williams 2002; Claiborne et al. 2011; Duffy and Beauchamp 2011). Rapid growth may reduce the potential pool of competitors, predators, and pathogens, as well as provide sufficient energetic stores needed to survive the first winter at sea (Beamish and Mahnken 2001).

Across several taxa of fish that become piscivorous during ontogeny, many experience dramatic increases in growth following the onset of piscivory (i.e. when fish become mostly piscivorous; see reviews by Juanes 1994; Mittelbach and Persson 1998). Variations in the timing of the onset of piscivory are related to predator size, prey availability, and environmental variability (Juanes et al. 2002; Hansen et al. 2013). Bigger juveniles have larger gape widths, more developed jaw structures, larger reaction distances, better visual acuity, and swim faster than smaller conspecifics. Collectively,

these attributes allow fish of a certain size expand their trophic niche. Predator and prey phenologies may also determine the onset of piscivory (Juanes 1994). Predators and prey respond differently to environmental cues across species and life stages. For example, anomalously high temperatures that shift the timing of predator migration (Anderson et al. 2013) may lead to temporal or spatial mismatches between predator and prey (Cushing 1972) and advance or delay the onset of piscivory.

For juvenile Chinook salmon (*Oncorhynchus tshawytscha*), whose diets during early marine residence have been extensively studied (Peterson et al. 1982; Emmett et al. 1986; Brodeur et al. 2007), there is clear support for an ontogenetic shift from invertebrate and terrestrial insect prey to piscivory of larval and young-of-the-year (YOY) marine fishes (Brodeur 1991; Daly et al. 2009; Duffy et al. 2010). Despite this, quantitative estimates of potential prey fields, relationships between prey community and environmental variables, information on the timing and size at the onset of piscivory, and the effects of prey quality on salmon growth remain understudied (but see Schabetsberger et al. 2003; Brodeur et al. 2011; Wells et al. 2012). Juvenile salmon size and survival are related to climate across broad scales (Beamish and Bouillon 1993; Mantua et al. 1997) and expected to increase when conditions during the first few months of ocean residence are favorable (i.e. during cool, productive, upwelling conditions) and when lipid-rich prey are plentiful (Peterson et al. 2014). Therefore the onset of piscivory might occur earlier when ocean conditions are favorable.

Tracking ontogenetic shifts in diet from salmon stomach contents alone has its inherent limitations. While providing considerable taxonomic resolution, observations are temporally limited to the most recent meal, and interpretations based on quantitative

measures can be biased by differences in digestion rates (Rindorf and Lewy 2011). A more informative approach combines stomach content analysis with chemical analyses of trophic biomarkers from lipids (fatty acids) and stable isotopes. Fatty acids and bulk stable isotopes of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) measured in the muscle tissue of consumers reflect diet integrated over weeks to months (Fry 2006; Copeman et al. 2016; Vander Zanden et al. 2015). While carbon isotopes and some fatty acid biomarkers generally reflect sources of primary production (Peterson and Fry 1987; Budge and Parrish 1998; Parrish 2013), nitrogen isotopes and other fatty acid biomarkers vary with nutrient source and consumer trophic position (Post 2002; El-Sabaawi et al. 2009; Daly et al. 2010). When combined, stomach content and trophic biomarker analyses provide a more robust method for recent (weeks to months) diet reconstruction than either method alone. The goal of our study was to identify and evaluate the timing and size at the onset of piscivory in a population of juvenile Chinook salmon using a combination of field sampling of potential prey with measurements of salmon size, growth, stomach contents, stable isotopes, and fatty acids. We defined the onset of piscivory as the timing or size when salmon consumed more fish prey by wet weight than any other prey category.

Our study was divided into three parts. First, we characterized seasonal and annual variations in the salmon prey field by sampling potential prey over two years and identifying environmental variables associated with prey community composition. Next, we developed metrics to account for variation in juvenile salmon size, growth, and body condition. For this analysis, we selected an abundant stock group of upper Columbia summer-fall Chinook salmon (UCSF) that was repeatedly sampled through time and identified using genetics. Subyearlings from the UCSF stock group have been detected

exiting the Columbia River from May through November, with abundance peaking in July (Weitkamp et al. 2015). Because UCSF subyearlings remain concentrated nearshore along the Oregon and Washington coasts during their first few months at sea (Fisher et al. 2014; Teel et al. 2015) this stock group is ideal for a longitudinal foraging study. Lastly, we evaluated ontogenetic changes in salmon diet using direct observations (stomach content analysis), stable isotopes, and fatty acids. In response to the ontogenetic shift in habitat from freshwater to saltwater, we expected changes in salmon carbon stable isotopes and phytoplankton fatty acid biomarkers, indicating changes in the carbon pool at the base of the food web. We hypothesized that the onset of piscivory would be related to the availability of marine fish prey and that piscivorous salmon would be larger, in better condition, and grow faster than salmon feeding on invertebrates. Compared to invertebrate feeders, we also expected that piscivores would have higher stable nitrogen isotope and fatty acid marker values related to trophic position but that there would be a lag of at least a month between consumption of fish prey and expression of diet in consumer tissues (Copeman et al. 2013; Heady and Moore 2013; Vander Zanden et al. 2015). This is the first study to quantify seasonality in the salmon prey field using a trawling method designed to sample micronekton upon which juvenile salmon feed. It is also the first study to present information on ontogenetic shifts in juvenile Chinook salmon diets using an integrative approach that combines stomach content, stable isotopes and fatty acid analyses.

## METHODS

### *Field collections*

We sampled two stations located off Willapa Bay, Washington, USA (46º 40’ N) a total of 52 times during monthly cruises from late-May through late-September 2011 and 2012 (Fig 3.1). Each station was sampled 2 – 4 times per cruise. The first station was located 9 nautical miles (nm) offshore (16.7 km) and the second station was located 14 nm (26.0 km) offshore. Sampling occurred during daylight hours when juvenile salmon feed (Brodeur et al. 2011). There was no cruise in June 2012 due to difficulties chartering a vessel. We collected animals used in this study under Scientific Research Permit 1410 issued to the Northwest Fisheries Science Center under the authority of Section 10(a)(1)(A) of the Endangered Species Act, Scientific Taking Permit 17203 issued by Oregon Department of Fish and Wildlife, and Washington State Scientific Collection Permit 12-128.

We fished for salmon and their potential prey by deploying a 264 Nordic rope trawl (NET Systems Bainbridge Island, Washington) for 15 minutes at an average speed of 5.7 km $hr^{-1}$ from the chartered commercial fishing vessel *F/V Miss Sue*. The trawl had variable mesh sizes (162.6 cm at the mouth to 8.9 cm at the cod end), with a 6.1 m long, 0.3 cm knotless liner sewn into the cod end. This gear has been used to successfully sample micronekton at mid-water (30 m) depths (Phillips et al. 2009) and was the type of gear recommended by Brodeur et al. (2011) to best sample all potential salmon prey types. We recorded GPS locations at the start and end of each haul and estimated volume swept ($m^3$) by multiplying distance trawled (m) by the mouth area of the net (336 $m^2$). Hydrographic information was collected to within 5 m from the bottom by deploying a Seabird SBE 25 conductivity, temperature, and depth (CTD) profiler at each station. The CTD recorded water temperature (°C), salinity (psu), density (kg $m^{-3}$), turbidity (mg $m^{-}$

$^{3}$), fluorescence (mg $m^{-3}$), dissolved oxygen concentration (ml $l^{-1}$), and dissolved oxygen saturation (%).

*Analysis of the prey field*

All potential prey items collected in the trawl were sorted by size (<80 mm total length; TL and <3.0 g), frozen, and transported back to the laboratory. Up to 30 individuals per taxon and station were measured (nearest mm) and weighed (nearest 0.01 g). Prey field biomass estimates were calculated for each prey type and station by dividing the total mass of the prey by the volume of water sampled by the trawl net, standardized to µg $m^{-3}$ by multiplying by 1,000, and averaged by cruise.

Size at and timing of ocean entry varies considerably for populations of salmon originating from the Columbia River basin (Weitkamp et al. 2015). Development of the prey field is also highly variable and dependent on environmental conditions, thus contributing to potential variability in the prey field juvenile salmon first encounter. We tested for seasonal variation in the salmon prey field by conducting ecological analyses on the community structure of catch data. Data were evaluated using nonparametric multi-response permutation procedures (Mielke and Berry 2001) and nonmetric multidimensional scaling (NMS; Kruskal 1964) with the Sørensen distance measure in the statistical package PC-ORD v. 6.07 (MjM Software Design). Because we were interested in seasonality of the prey field, we used nonparametric multi-response permutation tests to test the hypothesis of no difference in prey field community by month across years. We used NMS to ordinate sample units (biomass by haul) in species space to identify sample unit clusters with similar prey field community compositions.

Biomass estimates were normalized using a generalized logarithmic transformation [$\log(x + x_{min}) - \log(x_{min})$] to reduce bias from overly abundant species and to account for zero truncation in the data (McCune and Grace 2002).

In NMS, the most dissimilar samples are farthest apart and the most similar samples closest together. To measure the success of the prey community ordination, we calculated a stress value from 250 runs of real data starting from a random configuration (Mather 1976). Monte Carlo simulations were conducted with an additional 250 runs of randomized data which were then compared to the real data. Statistical significance ($\alpha = 0.05$) was calculated as the proportion of randomized runs with stress less than or equal to the observed stress.

Indicators of the physical ocean environment such as temperature and salinity are related to salmon recruitment (Peterson et al. 2014). We hypothesized that coastal ocean environmental variables would also be related to the salmon prey community so we evaluated associations between prey community NMS ordinations and the physical environment with correlation analyses using *in situ* measurements of 1 m sea surface temperature (SST), salinity, turbidity, fluorescence (a proxy for chlorophyll-*a* concentration), and dissolved oxygen concentration collected by the CTD. We also selected two of the regional physical variables that positively correlate with Chinook salmon adult returns (Miller et al. 2013; Burke et al. 2013), Columbia River plume volume (www.stccmop.org) and coastal upwelling (www.pfeg.noaa.gov), for inclusion in the analysis. We obtained estimates of the three-dimensional volume ($km^3$) of the Columbia River plume (salinity cutoff 28 PSU) using simulation database DB31 of the "Virtual Columbia River" modeling system generated by the Center for Coastal Margin

Observation and Prediction (Zhang and Baptista 2008). For upwelling, we used indices from daily averages of offshore Ekman transport driven by geostrophic wind stress between 45°N and 48°N and 125°W.

*Analysis of juvenile salmon*

We transported juvenile salmon frozen at sea back to the laboratory where they were identified to species, measured for fork length (FL; nearest mm), and weighed (nearest 0.1 g). To estimate genetic stock of origin, we extracted fin clips from 288 juvenile Chinook salmon and genotyped them at 13 microsatellite DNA loci following Teel et al. (2015). Salmon were assigned to stock groups using a standardized genetic database (Seeb et al. 2007), the likelihood model of Rannala and Mountain (1997), and the program ONCOR (Kalinowski et al. 2007). Based on genetic information, we assigned 61% (n = 175) of juvenile Chinook salmon to the UCSF genetic stock group with mean ± standard error (SE) probability of assignment of 89.1 ± 1.0%. Our analysis focused on subyearlings (age-0; 96% of UCSF fish), which we classified by length (Weitkamp et al. 2015): ≤120 mm FL in May (0% of catch), ≤140 mm FL in June (1% of catch), ≤180 mm FL in July (49% of catch), ≤210 mm FL in August (21% of catch), and ≤250 mm FL in September (25% of catch). Of these fish, 40% had an adipose fin clip, passive integrated transponder (PIT), or coded wire tag (CWT), indicating likely hatchery origin. The UCSF stock group is composed of fish originating in main-stem and tributary sources east of the Cascade Mountains, although both hatchery and natural production of the stock also occurs in the mid-Columbia River (Miller et al. 2013; Teel et al. 2014).

To evaluate salmon size, we compared FL and mass by month between 2011 and 2012 using Student's t-tests. We developed a condition index for UCSF subyearlings using residuals from the linear regression of ln-transformed FL and mass ($r^2 = 0.99$, $p < 0.001$; Jakob et al. 1996; Brodeur et al. 2004), and compared condition by month within years using analysis of variance (ANOVA) followed by Tukey's Honestly Significant Difference (HSD). We increased the sample size of UCSF subyearlings used for size, growth, and condition calculations from 168 to 518 by including salmon from two other studies that used the same genetic and life history identification methods. The first study sampled UCSF subyearlings (n = 201) as they exited the Columbia River (Weitkamp et al. 2015). The second study sampled salmon (n = 149) in coastal waters from central Oregon to northern Washington (Teel et al. 2015). We included only individuals that were collected May through September in 2011 and 2012 from the mouth of the Columbia River north along the shelf to Willapa Bay. Inclusion of these additional samples did not change our results but increased statistical power to detect differences in size, growth, and condition by sampling period.

Monthly estimates of early ocean growth ($G_L$ in mm $d^{-1}$) in UCSF subyearlings were calculated from differences in FL between ocean and estuary-caught individuals, assuming a uniform size and time of entry for each month:

$$G_L = \frac{(L_o - L_e)}{(t_o - t_e)},$$

where $L_o$ is individual FL at capture in the ocean at time $t_o$ and $L_e$ is the mean monthly FL at capture in the estuary the prior month at mean time $t_e$. We also estimated specific growth rates (SGR in % body weight [BW] $d^{-1}$) from changes in salmon weight as:

$$SGR = \frac{(ln[W_o] - ln[W_e])}{(t_o - t_e)} \times 100,$$

where $W_0$ is individual mass at capture in the ocean at time $t_o$ and $W_e$ is the mean mass at capture in the estuary the prior month at mean time $t_e$. Even though we did not know which month the fish entered the ocean, we considered growth estimates to be valid based on evidence that abundances of UCSF subyearlings exiting the estuary are normally distributed around June and August (Weitkamp et al. 2015) and observations that average estuary residence times for this stock are low (<1 week, Claiborne et al. 2014). We compared monthly estimates of $G_L$ and SGR between years using t-tests.

*Dietary analysis and comparison with the prey field*

An integrative approach for assessing salmon foraging ecology includes stomach content analysis conducted alongside salmon stable isotope and fatty acid analyses. We identified stomach contents from a subsample of 229 UCSF subyearlings collected in the lower estuary and ocean from June through September in both years. Prey items were identified to the lowest possible taxa under a dissecting scope following methods described in Brodeur et al. (2007) and taxonomic identification guides (Matrese et al. 1989; Carlton 2007). To quantify stomach contents, we weighed the entire stomach

contents and individual prey items (nearest 0.001 g), enumerated all of the prey, and measured the total length of up to 10 prey per taxon per stomach (nearest mm).

To standardize stomach fullness, we calculated mean stomach fullness as a percent of total body weight:

$$Fullness\ (\%) = \frac{stomach\ content\ weight\ (g)}{total\ fish\ weight\ (g)\ -\ stomach\ content\ weight\ (g)} \times 100.$$

We defined stomachs as empty when fullness <0.05% according to Weitkamp and Sturdevant (2008). Stomach fullness was compared by month within years using ANOVA followed by Tukey HSD tests. To visually represent diet composition, prey taxa were grouped into 14 categories that contributed ≥2% of salmon diets by weight: nonfood (e.g. Plantae), insects (Insecta), pteropods (Pteropoda), cladocerans (Cladocera), ostracods (Ostracoda), copepods (Copepoda), isopods (Isopoda), amphipods (Amphipoda), mysids (Mysidacea), krill (Euphausiidae), shrimp larvae (Pandalidae), crab larvae (*Metacarcinus magister* and *Cancer productus* zoea and megalopae), YOY northern anchovy (*Engraulis mordax*; hereafter referred to as anchovy), and unidentified fish (Osteichthyes). Average size at the onset of piscivory was compared between years using t-tests.

*Stable isotope and lipid analysis*

To address ontogenetic changes in diet, we subsampled (n = 29, 3 – 6 fish per month) UCSF subyearlings for bulk stable isotopes of nitrogen and carbon, total lipids,

and fatty acids. For isotopes, we sampled dorsal muscle tissue with skin removed from the right side just under the dorsal fin (average = 0.32 g wet weight). For lipids, we sampled dorsal muscle from the left side (average = 0.54 g wet weight). In addition, we processed a representative sample of Dungeness crab megalopae collected from May through July in each year (n = 5 – 6 per year) for nitrogen stable isotopes. This was done to establish a trophic baseline to estimate salmon trophic position as megalopae are primary consumers and the salmon prey item with the lowest trophic position as determined by Miller et al. (2010). We also measured fatty acids from a subsample of invertebrate prey (n = 32) and fish prey (n = 144) collected from May through September in each year to develop a piscivory biomarker based on fatty acid differences between these two main prey types.

We processed bulk stable isotopes of carbon and nitrogen at Oregon State University (College of Earth, Ocean, and Atmospheric Sciences Stable Isotope Laboratory). Dried tissue was ground into a fine powder and 1.0 ± 0.1 mg of powder packed into a tin capsule. Prepared samples and international standards (USGS40, ANU Sucrose, and IAEA-N2) were combusted at > 1000 °C using a Carlo Erba NA1500 elemental analyzer. The resulting $CO_2$ and $N_2$ were measured by continuous-flow mass spectrometry using a DeltaPlus isotope ratio mass spectrometer. Stable isotopes of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) were expressed in the delta notation:

$$Stable\ Isotopes = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000\ ‰,$$

where *R* is $^{15}N:^{14}N$ or $^{13}C:^{12}C$. Instrument error was ± 0.1‰ for carbon and ± 0.2‰ for nitrogen. Because no samples had atomic C:N ratios >3.5, they were not lipid-corrected as suggested by Post et al. (2007).

We converted all $\delta^{15}N$ values to trophic position (TP) using the notation of Post (2002):

$$TP = \lambda + \frac{\delta^{15}N_{salmon} - \delta^{15}N_{base}}{\Delta_n},$$

where λ is the trophic position of Dungeness crab megalopae used to establish the $\delta^{15}N_{base}$ relative to $\delta^{15}N_{salmon}$, and $\Delta_n$ ($\Delta\delta^{15}N$) is the enrichment in $\delta^{15}N$ per trophic level. For $\Delta\delta^{15}N$ we used the value of 3.4‰ per trophic level from Post (2002). The $\delta^{15}N_{base}$ in this case was estimated each year from the average $\delta^{15}N$ value determined for Dungeness crab megalopae sampled in 2011 ($\delta^{15}N$ = 10.3 ± 0.3 SE) and 2012 ($\delta^{15}N$ = 10.2 ± 0.6 SE) and setting λ = 2.1 according to Miller et al. (2010). We assumed a one month lag between consumption of prey and expression of trophic position in tissues of the consumer based on the turnover model of Vander Zanden et al. (2015).

We extracted lipids in chloroform and methanol according to Parrish (1999) using a modified Folch procedure (Folch et al. 1957). To calculate fatty acid concentration (μg $mg^{-1}$), a constant amount of internal standard (23:0) was added to each sample. We prepared fatty acid methyl esters (FAME) by transesterification using sulfuric acid according to Budge et al. (2006) and analyzed FAME on an HP 7890 GC FID equipped with an autosampler and a DB wax+ GC column (Agilent Technologies, Inc., USA)

according to Copeman et al. (2016). The column temperature began at 65 °C for 0.5 min and was increased to 195 °C (40 °C $min^{-1}$), held for 15 min then increased again (2 °C $min^{-1}$) to a final temperature of 220 °C. Final temperature was held for 1 min. The carrier gas was hydrogen, flowing at a rate of 2 ml $min^{-1}$. Injector temperature was set at 250 °C and the detector temperature was constant at 250 °C. We identified peaks using retention times based upon Supelco standards (37 component FAME, BAME, PUFA 1, and PUFA 3). We used Nu-Check Prep GLC 487 quantitative fatty acid mixed standard to develop correction factors for individual fatty acids and integrated chromatograms using Chem Station (version A.01.02, Agilent).

*Analysis of trophic markers*

Fatty acids and stable isotopes integrate information about dietary history over a period of weeks to months (Fry 2006; Copeman et al. 2016; Vander Zanden et al. 2015). We used correlation analyses to compare salmon stable isotopes and fatty acids to assess their coherence as trophic biomarkers. Trophic biomarkers were selected *a priori* from existing literature (Table 3.1). The piscivory marker (the ratio of docosahexaenoic acid to eicosapentaenoic acid, DHA:EPA) was selected based on initial observations by Daly et al. (2010) that fish prey contains higher proportions of DHA relative to EPA than invertebrate prey and later confirmed by fatty analysis of prey items collected in this study (fish prey DHA:EPA = 1.6 ± 0.1 SE and invertebrate prey = 0.9 ± 0.1 SE). To evaluate the relationship between environmental variability and salmon foraging ecology, we used regression analysis to estimate the relative importance of biological and physical factors in explaining variation in trophic position. Explanatory variables included

measures of salmon size (FL and condition), measures of prey availability (proportion of fish in the diet and anchovy biomass), and environmental conditions measured in the coastal environment (SST, fluorescence, upwelling, and Columbia River plume volume). We lagged all explanatory variables except FL by one month to account for tissue turnover and conducted all statistical analyses using R (R Core Team 2015).

## RESULTS

### *Salmon prey field*

During the two years of our study, we captured 22,661 potential juvenile salmon prey items representing 47 taxa (Appendix A). Species richness was highest in May, with 22 taxa collected in each of 2011 and 2012, but on average, biomass estimates were lower in May (53.1 ± 26.3 μg $m^{-3}$) compared to other months. Lowest diversity (3 taxa) occurred in August 2012, but average biomass estimates were highest (2,585 μg $m^{-3}$) during this sampling period because of large catches of anchovy, an important prey for subyearling Chinook salmon in the California Current (Brodeur 1991; Daly et al. 2009; MacFarlane 2010). In fact, during both years of the study, highest prey biomass estimates coincided with large catches of anchovy, although the timing of peak anchovy biomass differed between years. In 2011, the highest average anchovy biomass estimates occurred in September (342 μg $m^{-3}$), whereas the highest anchovy biomass estimates in 2012 occurred in August (2,577 μg $m^{-3}$). Over the whole study, average prey biomass estimates were lowest in September 2012 (1.8 μg $m^{-3}$). Interestingly, this was just one month after biomass estimates peaked for the study. Average anchovy biomass estimates

in September 2012 were >450 times lower than they were in September 2011, representing a clear shift in prey phenology between the two years.

As expected, the prey field community transitioned throughout the sampling season as the coastal environment varied. Results of the multi-response permutation procedure comparing community composition revealed significant differences in the prey field by month ($p < 0.001$). Pairwise comparisons showed there was no difference in the prey field community between June and July or between August and September over the entire sampling period (both with $p > 0.100$), which justified combining months into 3 seasons over both years of the study (spring = May, early summer = June and July, and late summer = August and September). A diverse, but low biomass community of invertebrate prey and YOY fishes (osmerids, flatfishes, and other groundfish in their pelagic phase) occurred in spring and early summer, which transitioned into a community dominated by anchovy by late summer.

The NMS ordination that best described the prey field dataset had three dimensions, Monte Carlo $p < 0.001$ and medium stress (12.5), suggesting little risk of drawing false inferences (Fig 3.2, Table 3.2). The ordination represented 86.6% of the variation in the prey community. Axis 1 accounted for 55.5% of the variation and was positively associated with Dungeness crab megalopae, smelt (Osmeridae), Pacific sanddab (*Citharichthys sordidus*), slender sole (*Lyopsetta exilis*), and sand sole (*Psettichthys melanosticus*) during spring (May), when Columbia River plume volume was highest. Axis 1 was negatively associated with anchovy during late summer (August and September), when SST and fluorescence values were highest, indicating high productivity. Axis 2 accounted for 15.3% of the variation and separated coastal

downwelling from upwelling conditions. Axis 3 accounted for 15.8% of the variation and was positively associated with rockfish (*Sebastes* spp.), negatively associated with California market squid (*Doryteuthis opalescens*), but was not associated with any environmental variables measured.

*UCSF subyearlings*

Subyearling UCSF Chinook salmon was the most abundant genetic stock group sampled alongside the prey community from July through September in both years. We also collected juvenile Chinook salmon from 14 other genetic stock groups, as well as juvenile coho, chum (*O. keta*), and sockeye (*O. nerka*) salmon, but they were not included in this analysis. Average size of UCSF subyearlings, including salmon sampled in the two other complementary studies, ranged from 89 mm FL and 6.9 g in May to 151 mm FL and 43.2 g in September (Fig 3.3a–b). Salmon lengths (t-test, $p = 0.014$) and weights ($p = 0.002$) were significantly lower in June 2011 compared to June 2012, but were significantly larger by the end of September in 2011 compared to 2012 (length and mass both $p < 0.001$). Average early ocean growth rates were significantly ($p = 0.005$) slower from June to July in 2011 (0.4 mm $d^{-1}$) than 2012 (0.6 mm $d^{-1}$), but significantly faster ($p < 0.001$) from August to September in 2011 (1.2 mm $d^{-1}$) compared to 2012 (0.9 mm $d^{-1}$; Fig 3.3c). Average specific growth rates were also significantly ($p < 0.001$) faster from August to September 2011 (3.1% BW $d^{-1}$) compared to August to September 2012 (2.0% BW $d^{-1}$; Fig 3d). As expected, UCSF subyearlings grew fastest when anchovy were most abundant in the field and consumed. Salmon condition was also significantly higher (ANOVA and Tukey HSD, $p < 0.05$) when anchovy biomass in the

field was greatest (Fig 3.4). Across years, mean salmon condition and anchovy biomass were significantly and positively correlated ($r = 0.900$, $p = 0.015$).

*Stomach Contents*

Juvenile salmon stomach contents varied by month and year over the sampling period and reflected variations in the prey field (Fig 3.5). Of the stomachs examined, 18 were considered empty. In general, proportions of fish increased in stomachs through time, except from August to September 2012, when proportions of fish in diet (and salmon growth rate) decreased. The onset of piscivory, which we defined as when diets contained more fish than any other prey category, occurred later in 2011 (September = 62% of diet) than 2012 (August = 50% of diet). Average salmon size at the onset of piscivory (Fig 3.6) was significantly higher (t-test, $p < 0.01$) in 2011 (140 – 150 mm FL; 49% fish in diet) than in 2012 (120 – 130 mm FL; 43% fish in diet). All salmon >150 mm were completely piscivorous in 2011 whereas proportions of fish in diet decreased rather than increased in fish >130 mm FL in 2012, indicating that the onset of piscivory was related more to prey availability than predator size. Prey-sized (<80 mm TL) anchovy were caught in the trawl in August and September 2011 and from July through September 2012. Stomach fullness (% of total body weight) was significantly higher (ANOVA and Tukey HSD, $p < 0.05$) when salmon ate more anchovy (mean ± SE = 2.2 ± 0.4% in September 2011 and 2.0 ± 1.2% in August 2012), compared to when anchovy were less abundant and overall prey biomass estimates were low (0.6 ± 0.3% in September 2012).

*Salmon stable isotopes and lipids*

Salmon stable isotopes, trophic position, and fatty acids varied by month and year (Table 3.3). Correlation analyses identified significant relationships among bulk stable isotopes of carbon and nitrogen, fatty acids, and salmon size (Table 3.4, Fig 3.7 and 3.8). Values of $\delta^{13}C$, indicating carbon source at the base of the food web, were positively correlated with salmon FL ($r = 0.620$, $p < 0.001$) and a fatty acid biomarker for marine diatoms:flagellates (the ratio of all polyunsaturated fatty acids [PUFA] containing 16 carbon atoms to all PUFA containing 18 carbon atoms, $r = 0.730$, $p < 0.001$; Fig 3.7a and 3.7c). Carbon isotopes and salmon FL were both negatively correlated ($\delta^{13}C$ $r = -0.700$ and FL $r = -0.560$, both $p < 0.002$) with a fatty acid biomarker for freshwater (the sum of linolenic and linoleic fatty acids [18:3n-3+18:2n-6]; Fig 3.7b and 3.7d), indicating that the dietary carbon pools changed as salmon migrated from freshwater to saltwater. Values of $\delta^{15}N$ were positively correlated with salmon FL ($r = 0.460$, $p = 0.012$), $\delta^{13}C$ ($r = 0.690$, $p < 0.001$), and a fatty acid marker for piscivory (DHA:EPA, $r = 0.720$, $p < 0.001$; Fig 3.8), which supports the observation that salmon diet shifted from invertebrate prey to piscine prey during early ocean residence as salmon grew (Fig 3.9). Across years, salmon in September 2012 had the highest $\delta^{15}N$, trophic position, and DHA:EPA, even though they were not the largest fish sampled and were not piscivorous at the time of collection. Due to the lag between when prey is consumed and expressed in salmon isotopes and fatty acids, we assumed that salmon biochemistry in September 2012 reflected fish prey consumed in August 2012, the sampling period when anchovy were most abundant in the field and when salmon first became piscivorous.

*Models estimating trophic position*

Regression analysis of average salmon trophic position and physical and biological factors showed salmon trophic position increased from July to September from 2.5 to 2.9 in 2011 and from 2.6 to 3.0 in 2012, reflecting prey consumed from approximately June through August in both years (Table 3.3, Fig 3.9). Monthly and inter-annual variations in trophic position were best explained by differences in fluorescence (1-mo lag), Columbia River plume volume (1-mo lag), salmon FL, and proportion of fish in salmon diet (1-mo lag; Fig 3.9). These results demonstrate that all fish were transitioning from being zooplantivorous to piscivorous through time as they increased in size. An association between trophic position and the physical environment also highlights the potential role of bottom-up productivity in regulating the timing of the onset of piscivory.

## DISCUSSION

Our analyses showed that inter-annual differences in timing and size at the onset of piscivory in a population of Chinook salmon were related to prey availability. Seasonal variation in the prey field during ontogeny has broad implications for early ocean foraging success, growth, and survival in UCSF subyearlings. The composition of the prey field is also important for other populations of Columbia River salmon and steelhead (*O. mykiss*) that have stock-specific differences in their size and timing of ocean entry (Weitkamp et al. 2015). Our results that UCSF subyearlings became piscivorous at a smaller size and earlier in 2012 than 2011, but that the earlier onset of piscivory did not result in higher growth rates by the end of the sampling period in 2012, lends support to

the idea that the total duration of piscivory, not just the onset, should be considered in terms of long-term fitness and survival. A longer period of piscivory in early marine life may increase survival by increasing salmon size at the end of the first summer at sea, as suggested by the "critical size, critical period" hypothesis (Beamish and Mahnken 2001). It may also be that Chinook salmon size-at-maturity, fecundity, and fitness are related to the total duration of piscivory during marine life.

The spatial coverage of our study was limited through time therefore we do not know how representative our samples were of the prey community throughout salmon's range. We suspect that our samples represented available prey in the northern California Current as previous surveys of zooplankton (Lamb 2011) and ichthyoplankton (Auth 2011) resources concluded that community structure was homogenous north and south of the region sampled. In June 2016, NOAA Fisheries conducted a coast-wide (northern Washington to central California) survey of the salmon prey field in shelf waters using the same gear type as we did to further investigate this issue. That survey also used zooplankton net tows (bongo and Methot nets) to capture small marine invertebrate prey such as pteropods, ostracods, copepods, amphipods, and decapod larvae that our trawl gear was less effective at sampling. Future studies could also include image analysis (e.g. *in situ* ichthyoplankton imaging system [*IS*IIS], Cowen and Guigand 2008) or acoustics to provide a more complete quantitative estimate of the prey field, especially at depths greater than we sampled where salmon might feed (Brodeur et al. 2011). This type of sampling could help better understand prey patchiness as it relates to fronts and other oceanographic features (Peterson and Peterson 2008; Ainley et al. 2009; Brodeur and Morgan 2016).

Estimates of marine growth in UCSF subyearlings were based on the assumption that salmon caught in the estuary and ocean were representative of the entire population and that changes in size were due to ocean growth and not factors such as emigration, immigration, or size-selective mortality. We contend that this is a reasonable assumption as our estimates of growth (0.4 to 1.2 mm $d^{-1}$ and 0.8 to 3.1% BW $d^{-1}$) were similar to estimates calculated for this stock based on otoliths (0.8 to 1.2 mm $d^{-1}$ and 0.9 to 2.6% BW $d^{-1}$; Miller et al. 2013; Claiborne et al. 2014). We suggest that foraging and growth patterns observed in UCSF subyearlings would be similar in salmon populations with similar life histories. One example is the Snake River fall population of Chinook salmon, which was the second most abundant genetic stock group represented in our samples (14.2% of catch). Unlike the UCSF population, Snake falls are listed under the U.S. Endangered Species Act. These fish migrate to the ocean slightly earlier than UCSF subyearlings (Weitkamp et al. 2015), but have the same genetic lineage (Waples et al. 2004) and similar early marine distributions and growth rates (Teel et al. 2015; Weitkamp et al. 2015).

Combining stomach content analysis with stable isotope and fatty acid analyses is a powerful integrated approach for evaluating diet and for understanding biological processes. For example, carbon isotope values in fish, which represent primary producers at the base of the food web, can be difficult to interpret as fractionation of $\delta^{13}C$ in phytoplankton tends to vary positively with SST, cell size, and growth rate, and negatively with dissolved inorganic carbon pools ($CO_2$ and $HCO_3^-$) (Laws et al. 1995; Burkhardt et al. 1999). Combining stable isotopes with fatty acid biomarkers can help aid in $\delta^{13}C$ interpretation. The fatty acid biomarker approach is based on observations that

phytoplankton produce essential fatty acids not biosynthesized by consumers that are then deposited in consumer tissue with minimal modification (Dalsgaard et al. 2003; Budge et al. 2006; Copeman et al. 2016). Freshwater biomarkers (18:2n-3 + 18:2n-6), likely originating from the Columbia River, varied inversely with $\delta^{13}C$ and salmon FL, whereas marine phytoplankton biomarkers (16:18 PUFA) varied positively with $\delta^{13}C$ and salmon FL. These results confirm a general pattern of enrichment of $\delta^{13}C$ in salmon tissue by up to 7.5‰ associated with the ontogenetic shift in diet and habitat from freshwater to saltwater. However, it varies from other interpretations of juvenile salmon $\delta^{13}C$ that consider there to be a gradient between enriched $\delta^{13}C$ waters onshore and depleted $\delta^{13}C$ values offshore within the marine realm (Miller et al. 2008). Salmon $\delta^{13}C$ may also vary along a SST gradient with lower $\delta^{13}C$ values at lower temperatures due to higher concentrations of dissolved $CO_2$ in cooler waters (Hertz et al. 2015a), although we found no significant relationship between salmon $\delta^{13}C$ and SST ($r = 0.00$, $p = 0.99$).

Completely piscivorous fish should have a trophic position of 3.5 – 4.0, but by September our estimates for trophic position were 2.9 in 2011 and 3.0 in 2012. There are several explanations for this. The first is that piscivorous diets were not yet reflected in salmon tissue. We assumed a one month lag between a diet shift and when tissue actually equilibrates with that value, but muscle may take longer to equilibrate than other tissues (Heady and Moore 2013). Anchovy consumed in August may not have been reflected in salmon muscle by September. A two month lag would suggest that September $\delta^{15}N$ values reflected zooplanktivorous diets consumed in July. We also may have overestimated the trophic discrimination factor of 3.4‰ given that our $\delta^{15}N$ baseline values for crab megalopae were near 10‰. Recent analyses (Hussey et al. 2014; Hertz et

al. 2016) show that turnover can complicate interpretation of ontogeny in salmon. We also may have inadequately captured the trophic baseline by integrating megalopae values across season and space. A final possibility is that UCSF juveniles never became completely piscivorous, an observation supported by stomach content data and consistent with the notion that Chinook salmon are generalist foragers that feed upon a variety of prey types (Gregory and Northcote 1993).

The use of DHA:EPA as a biomarker of piscivory is based on observations that DHA is conserved in higher trophic levels in marine ecosystems (Dalsgaard et al. 2003; Parrish 2013) and found in higher concentrations in marine fish prey relative to invertebrate prey (Daly et al. 2010; this study). Increases in the DHA:EPA ratio may also indicate a decrease in juvenile salmon condition as lipid classes get utilized differently for energy under poor feeding conditions. Storage lipids (triacylglycerides) contain small amounts of DHA, but are mobilized more readily than polar lipids, which contain proportionally higher amounts of DHA. Similarly, fasting has been shown to increase $\delta^{15}N$ signatures by up to 0.5‰ in juvenile Chinook salmon (Hertz et al. 2015b). Future applications of DHA:EPA and $\delta^{15}N$ as trophic markers must consider salmon condition in addition to stomach content data, as poor feeding conditions may cause these biomarkers to increase even though no fish prey has been consumed.

Availability of anchovy prey appears to have important consequences for the onset of piscivory and growth in UCSF subyearlings. Anchovy are an abundant forage fish in the northern California Current (Litz et al. 2008) and the timing and duration over which they spawn is related to physical factors such as SST and river plume dynamics (Richardson 1973; Parnel et al. 2008). Coastal ocean conditions were similar in the two

years of our study and ecosystem indicators of ocean conditions related to salmon recruitment such as Pacific Decadal Oscillation (Mantua et al. 1997), winter SST, and copepod community structure (Peterson et al. 2014) were all considered favorable. Notably, mean volume of the Columbia River plume was 4 times larger in June 2011 (200 $km^3$) compared to June 2012 (49 $km^3$). June and July have been identified as important months for spawning anchovy that utilize plume fronts during reproduction (Richardson 1973; Auth et al. 2011). There was also a difference in the intensity of upwelling favorable winds during July of 2011 relative to 2012; wind speed cubed ([m $s^{-1}$]$^3$) was 2.4 times lower in July 2011 (50.5) compared to 2012 (122.5; www.pfeg.noaa.gov). Differences in plume size and wind strength may have contributed to inter-annual differences in the timing and magnitude of anchovy recruitment, which occurred later and persisted longer in 2011 than 2012. A less windy surface layer, as was observed in June and July 2011, is hypothesized to benefit first feeding anchovy during early life (Lasker 1978).

Yearling Chinook and coho salmon (juveniles that enter the ocean as age-1.0 fish) and juvenile steelhead originating from the Columbia River are typically larger, migrate to the ocean earlier (April-May), and become piscivorous sooner than subyearlings (Daly et al. 2014; Weitkamp et al. 2015). Marine YOY fishes may contribute as much as 50 to 90% of the mass of larger juvenile diets during spring and early summer (Brodeur et al. 2007; Daly et al. 2009), but have been previously sampled in the field with limited success (Schabetsberger et al. 2003; Brodeur et al. 2011; Brodeur and Morgan 2016). Yearling Chinook, coho, and steelhead consume smelt, rockfishes, greenlings (Hexagramidae), sculpin (Cottidae), Pacific sand lance (*Ammodytes hexapterus*), and

flatfishes (Pleuronectiformes, Brodeur et al. 2007; Daly et al. 2010; 2014). These prey items were well represented in our samples, but mainly collected in May when average biomass estimates were low (57.0 ± 26.3 µg $m^{-3}$ SE). It is currently unknown whether the observed low biomass estimates of fish prey measured in May was related to predator density, but hypotheses addressing prey limitation and predator density dependence could be further explored by comparing yearling densities, diets (including stomach fullness), condition, and composition of the prey field. Intra- and interspecific competition among outmigrating juvenile salmon is a topic that has received considerable attention in the North Pacific Ocean and Bering Sea (see Ruggerone and Nielsen 2004 for a review), but has not been extensively investigated for fish exiting the Columbia River.

Understanding variability in feeding ecology of juvenile salmon first entering the marine environment, and in particular identifying factors relating to their ontogenetic diet shift, is important for understanding future salmon survival. Chinook salmon from the UCSF population typically spend 2 – 4 years in the ocean before returning to spawn, with the majority returning after three ocean winters. Adult passage of summer and fall Chinook salmon at Priest Rapids Dam on the upper Columbia River (www.cbr.washington.edu) after three years in the ocean provides a measure of relative survival (Miller et al. 2013; Losee et al. 2014). Juveniles from the same year class as fish sampled in this study in 2011 and 2012 predominantly returned during summer and fall of 2014 and 2015. Adult returns of UCSF salmon was high in 2014 (198,341) – almost twice the ten-year average from 2004 to 2013 (111 008). Adult returns in 2015 were also unexpectedly high (167,440) despite a large developing El Niño (www.elnino.noaa.gov) and unprecedented warming in the Northeast Pacific known as the “The Blob” (Bond et

al. 2015). Hatchery production of UCSF subyearlings has been similar over the last two decades (www.fpc.org) therefore the high returns in 2014 and 2015 were not due to increased hatchery production. Because El Niño and warm ocean temperatures are typically associated with poor salmon survival (Mantua et al. 1997; Meuter et al. 2002), high returns of 2011 and 2012 outmigrants suggests that UCSF salmon may have benefitted from favorable ocean conditions and abundant anchovy prey during early ocean residence. Comparison of salmon prey, diet, trophic biomarkers, and growth during years of poor survival could be used to test this hypothesis. During a warm and unproductive outmigration year, we might expect changes in the overall composition and abundance of salmon prey, earlier or later shifts in prey phenology and the onset of piscivory, lower growth rates, condition, and adult returns. Our integrated approach that combines sampling of salmon prey with estimates of salmon growth, stomach contents, stable isotopes, and fatty acids provides a useful framework for assessing bottom-up regulatory mechanisms impacting foraging ecology during a critical period in salmon life history.

## ACKNOWLEDGEMENTS

This study was supported by the U.S. National Marine Fisheries Service, the Bonneville Power Administration, the NOAA Educational Partnership Program with Minority Serving Institutions Graduate Research and Training Scholarship Program, the Living Marine Resources Cooperative Science Center, the Oregon State University Cooperative Institute for Marine Resources Studies, and two scholarships awarded from the Hatfield Marine Science Center: a Mamie Markham Research Award and a Bill Wick Marine

Fisheries Award. Thanks to P. Bentley, S. Hinton, T. Auth, T. Britt, E. A. Hill, C. Barcélo, and the captain and crew of the *F/V Miss Sue* for their assistance collecting samples used in this study. Salmon genetics, diet, lipids, and stable isotopes were processed with laboratory assistance from K. Bosley, A. Chappell, K. Dale, D. Draper, P. Frey, K. Klink, D. Kuligowski, J. McKay, and A. Sremba. Database support provided by C. Morgan.

## LITERATURE CITED

Ainley DG, Dugger KD, Ford RG, Pierce SD, Reese DC, Brodeur RD, Tynan CT, Barth JA (2009) Association of predators and prey at frontal features in the California Current: competition, facilitation, and co-occurrence. Mar Ecol Prog Ser 389, 271–294.

Anderson, JJ, Gurarie, E, Bracis, C, Burke, BJ, Laidre, KL (2013) Modeling climate change impacts on phenology and population dynamics of migratory marine species. Ecol Model 264, 83–97.

Auth TD (2011) Analysis of the spring-fall epipelagic ichthyoplankton community in the northern California Current in 2004-2009 and its relation to environmental factors. Calif Coop Ocean Fish Invest Rep 52, 148–167.

Beamish RJ, Bouillon DR (1993) Pacific salmon production trends in relation to climate. Can J Fish Aquat Sci 50, 1002–1016.

Beamish RJ, Mahnken C (2001) A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog Oceanogr 49, 423–437.

Beamish RJ, Sweeting RM, Neville CM (2004) Improvement of juvenile Pacific salmon production in a regional ecosystem after the 1998 climatic regime shift. Trans Am Fish Soc 133, 1163–1175.

Bond NA, Cronin MF, Freeland, H, Mantua N (2015) Causes and Impacts of the 2014 Warm Anomaly in the NE Pacific. Geophys Res Lett 42, 3414–3420.

Brodeur RD (1991) Ontogenetic variations in the type and size of prey consumed by juvenile coho, *Oncorhynchus kisutch*, and chinook, *O. tshawytscha*, salmon. Environ Biol Fish 30, 303–315.

Brodeur RD, Fisher JP, Teel DJ, Emmett RL, Casillas E, Miller TW (2004) Juvenile salmonid distribution, growth, condition, origin, environmental and species associations in the northern California Current. Fish Bull 102, 25–46.

Brodeur RD, Daly EA, Sturdevant MV, Miller TW, Moss JH, Thiess ME, Trudel M, Weitkamp LA, Armstrong J, Norton EC (2007) Regional comparisons of juvenile salmon feeding in coastal marine waters off the west coast of North America. In Grimes CB, Brodeur RD, Haldorson LJ, McKinnell SM (eds) The Ecology of Juvenile Salmon in the Northeast Pacific Ocean: Regional Comparisons. American Fisheries Society, Bethesda, pp 183–203.

Brodeur RD, Daly EA, Benkwitt CE, Morgan CA, Emmett RL (2011) Catching the prey: sampling juvenile fish and invertebrate prey fields of juvenile coho and Chinook Salmon during their early marine residence. Fish Res 108, 65–73.

Brodeur RD, Morgan CA (2016) Influence of a coastal riverine plume on the cross-shelf variability in hydrography, zooplankton, and juvenile salmon diets. Estuar Coasts 39, 1183–1198.

Budge SM, Parrish CC (1998) Lipid biogeochemistry of plankton, settling matter, and sediments in Trinity Bay, Newfoundland. II. Fatty acids. Org Geochem 29, 1547–1559.

Budge SM, Iverson SJ, Koopman HN (2006) Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. Mar. Mamm Sci 22, 759–801.

Burke BJ, Peterson WT, Beckman BR, Morgan CA, Daly EA, Litz MNC (2013) Multivariate models of adult Pacific salmon returns. PLoS ONE 8(1), e54134.

Burkhardt S, Riebesell U, Zondervan I (1999). Effects of growth rate, $CO_2$ concentration, and cell size on the stable carbon isotope fractionation in marine phytoplankton. Geochim Cosmochim Acta 63, 3729–3741.

Carlton JT (ed) (2007) The Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon. Fourth Edition. University of California Press, Berkeley.

Claiborne AM, Fisher JP, Hayes SA, Emmett RL (2011) Size at release, size-selective mortality, and age of maturity of Willamette River hatchery yearling Chinook Salmon. Trans Am Fish Soc 140, 1135–1144.

Claiborne AM, Miller JA, Weitkamp LA, Teel DJ (2014) Evidence for selective mortality in marine environments: the role of fish migration size, timing, and production type. Mar Ecol Prog Ser 515, 187–202.

Copeman LA, Parrish CC Gregory RS, Jamieson RE, Wells J, Whiticar MJ (2009) Fatty acid biomarkers in coldwater eelgrass meadows: elevated terrestrial input to the food web of age-0 Atlantic cod *Gadus morhua*. Mar Ecol Prog Ser 386, 237–251.

Copeman LA, Laurel BJ, Parrish CC (2013) Effect of temperature and tissue type on fatty acid signatures of two species of North pacific juvenile gadids: A laboratory feeding study. J Exp Mar Biol Ecol 448, 188–196.

Copeman LA, Laurel BJ, Boswell KM, Sremba AL, Klinck K, Heintz RA, Vollenweider JJ, Helser TE, Spencer ML (2016) Ontogenetic and spatial variability in trophic biomarkers of juvenile saffron cod (*Eleginus gracilis*) from the Beaufort, Chukchi and Bering Seas. Polar Biol 39, 1109–1126.

Cowen RK, Guigand CM (2008) *In situ* ichthyoplankton imaging system (*IS*IIS): system design and preliminary results. Limnol Oceanogr-Meth 6, 126–132.

Cushing DH (1972) The production cycle and the numbers of marine fish. Symp Zool Soc Lond 29, 213–232.

Dalsgaard J, St. John MA, Kattner G, Müller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46, 225–340.

Daly EA, Brodeur RD, Weitkamp LA (2009) Ontogenetic shifts in diets of juvenile and subadult coho and Chinook Salmon in coastal marine waters: Important for marine survival? Trans Am Fish Soc 138, 1420–1438.

Daly EA, Benkwitt CE, Brodeur RD, Litz MNC, Copeman LA (2010) Fatty acid profiles of juvenile salmon indicate prey selection strategies in coastal marine waters. Mar Biol 157, 1975–1987.

Daly EA, Scheurer JA, Brodeur RD, Weitkamp LA, Beckman BR, Miller JA (2014) Juvenile steelhead distribution, migration, feeding, and growth in the Columbia River estuary, plume, and coastal waters. Mar Coast Fish 6, 62–80.

Duffy EJ, Beauchamp DA, Sweeting RM, Beamish RJ, Brennan JS (2010) Ontogenetic diet shifts of juvenile Chinook Salmon in nearshore and offshore habitats of Puget Sound. Trans Am Fish Soc 139, 803–823.

Duffy EJ, Beauchamp DA (2011) Rapid growth in the early marine period improves marine survival of Puget Sound Chinook Salmon. Can J Fish Aquat Sci 68, 232–240.

El-Sabaawi R, Dower JF, Kainz M, Mazumder A (2009) Characterizing dietary variability and trophic positions of coastal calanoid copepods: insight from stable isotopes and fatty acids. Mar Biol 156, 225–237.

Emmett RL, Miller DR, Blahn TH (1986) Food of juvenile Chinook, *Oncorhynchus tshawytscha*, and coho, *O. kisutch*, salmon off the northern Oregon and southern Washington coasts, May–September 1980. Calif Fish Game 72, 38–46.

Fisher JP, Weitkamp LA, Teel DJ, Hinton SA, Trudel M, Morris JFT, Theiss ME, Sweeting RM, Orsi JA, Farley Jr EV (2014) Early ocean dispersal patterns of Columbia River Chinook and Coho Salmon. Trans Am Fish Soc 143, 252–272.

Folch J, Lees M, Stanley GHS (1957) A simple method for the isolation and purification of total lipid from animal tissues. J Biol Chem 226, 497–509.

Fry B (2006) Stable Isotope Ecology. Springer, New York.

Gregory RS, Northcote TG (1993) Surface, planktonic, and benthic foraging by juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. Can J Fish Aquat Sci 50, 233–240.

Heady WN, Moore JW (2013) Tissue turnover and stable isotope clocks to quantify resource shifts in anadromous rainbow trout. Oecologia 172, 21–34.

Hertz E, Trudel M, Brodeur RD, Daly EA, Eisner L, Farley Jr EV, Harding JA, MacFarlane RB, Mazumder S, Moss JH, Murphy JM, Mazumder A (2015a) Continental-scale variability in the feeding ecology of juvenile Chinook Salmon along the coastal Northeast Pacific Ocean. Mar Ecol Prog Ser 537, 247–263.

Hertz E, Trudel M, Cox MK, Mazumder A (2015b) Effects of fasting and nutritional restriction on the isotopic ratios of nitrogen and carbon: a meta-analysis. Ecol Evol 8, 4829–4839.

Hertz E, Trudel M, El-Sabaawi R, Tucker S, Dower JF, Beachum TD, Edwards AM, Mazumder A (2016) Hitting the moving target: modelling ontogenetic shifts with stable isotopes reveals the importance of isotopic turnover. J An Ecol 85, 681–691.

Hussey NE, MacNeil MA, McMeans BC, Olin JA, Dudley SFJ, Cliff G, Wintner SP, Fennessy ST, Fisk AT (2014) Rescaling the trophic structure of marine food webs. Ecol Lett 17, 239–250.

Jakob EM, Marshall SD, Uetz GW (1996) Estimating fitness: a comparison of body condition indices. Oikos 77, 61–67.

Juanes F (1994) What determines prey size selectivity in piscivorous fishes? In Stouder DJ, Fresh KL, Feller RJ (eds) Theory and Application in Fish Feeding Ecology. University of South Carolina Press, Columbia, pp 79–100.

Juanes F, Buckel JA, Scharf FS (2002) Feeding ecology of piscivorous fishes. In Hart PJB, Reynolds JB (eds) Handbook of Fish Biology and Fisheries, Volume 1: Fish Biology. Blackwell Scientific Publications, Oxford, pp 267–283.

Kalinowski ST, Manlove KR, Taper ML (2007) ONCOR: a computer program for genetic stock identification. Montana State University, Bozeman.

Kruskal JB (1964) Nonmetric multidimensional scaling: a numerical method. Psychometrika 29, 115–129.

Lamb J (2011) Comparing the hydrography and copepod community structure of the continental shelf ecosystems of Washington and Oregon, USA from 1998 to 2009: Can a single transect serve as an index of ocean conditions over a broader area? MS thesis, Oregon State University, Corvallis.

Lasker R (1978) The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp P-V Reun Cons Int Explo Mer 173, 212–230.

Laws EA, Popp BN, Bidigare RR, Kennicutt MC, Macko SA (1995) Dependence of phytoplankton carbon isotopic composition on growth rate and $[CO_2]_{aq}$: theoretical considerations and experimental results. Geochim Cosmochim Acta 59, 1131–1138.

Litz MNC, Emmett RL, Heppell SS, Brodeur RD (2008) Ecology and distribution of the northern subpopulation of northern anchovy (*Engraulis mordax*) off the U.S. west coast. Calif Coop Ocean Fish Invest Rep 49, 167–182.

Losee J, Miller JA, Peterson WT, Teel DJ, Jacobson KC (2014) Influence of ocean ecosystem variation on trophic interactions and survival of juvenile coho and Chinook Salmon. Can J Fish Aquat Sci 71, 1747–1757.

MacFarlane RB (2010) Energy dynamics and growth of Chinook Salmon (*Oncorhynchus tshawytscha*) from the Central Valley of California during the estuarine phase and first ocean year. Can J Fish Aquat Sci 67, 1549–1565.

Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. Bull Am Meteorol Soc 78, 1069–1079.

Mather PM (1976) Computational Methods of Multivariate Analysis in Physical Geography. J.Wiley and Sons, London.

Matarese AC, Kendall Jr AW, Blood DM, Vinter BM (1989) Laboratory guide to early life history stages of northeast Pacific fishes. NOAA Technical Report NMFS 80.

McCune B, Grace JB (2002) Analysis of Ecological Communities. MjM Software Design, Gleneden Beach.

Meuter FJ, Peterman RM, Pyper BJ (2002) Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. Can J Fish Aquat Sci 59, 456–463.

Mielke Jr PW, Berry KJ (2001) Permutation Methods: A Distance Function Approach. Springer, New York.

Miller TW, Brodeur RD, Rau G (2008) Carbon stable isotopes reveal relative contribution of shelf-slope production to the northern California Current pelagic community. Limnol Oceanogr 53, 1493–1503.

Miller TW, Brodeur RD, Rau G, Omori K (2010) Prey dominance shapes trophic structure of the northern California Current pelagic food web: evidence from stable isotopes and diet analysis. Mar Ecol Prog Ser 420, 15–26.

Miller JA, Teel DJ, Baptista A, Morgan CA (2013) Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook Salmon (*Oncorhynchus tshawytscha*). Can J Fish Aquat Sci 70, 617–629.

Miller JA, Teel DJ, Peterson WT, Baptista AM (2014) Assessing the relative importance of local and regional processes on the survival of a threatened salmon population PLoS ONE 9, e99814.

Mittelbach GG, Persson L (1998) The ontogeny of piscivory and its ecological consequences. Can J Fish Aquat Sci 55, 1454–1465.

Parnel MM, Emmett RL, Brodeur RD (2008) Ichthyoplankton community in the Columbia River plume off Oregon: effects of fluctuating oceanographic conditions. Fish Bull 106, 161–173.

Parrish CC (1999) Determination of total lipids, lipid classes and fatty acids in aquatic samples. In Arts MT, Wainmann BC (eds) Lipids in Freshwater Ecosystems. Springer, New York, pp 4–20.

Parrish CC (2013) Lipids in marine cosystems. ISRN Oceanography 2013 Article ID 604045, 16 pp.

Pearcy WG (1992) Ocean Ecology of North Pacific Salmonids. Washington Sea Grant Program University of Washington Press, Seattle.

Pearcy WG, McKinnell SM (2007) The ocean ecology of salmon in the northeast Pacific Ocean – an abridged history. In Grimes CB, Brodeur RD, Halderson LJ, McKinnell SM

(eds) The Ecology of Juvenile Salmon in the Northeast Pacific Ocean: Regional Comparisons. American Fisheries Society, Bethesda, pp 7–30.

Peterson WT, Brodeur RD, Pearcy WG (1982) Food habits of juvenile salmon in the Oregon coastal zone, June 1979. Fish Bull 80, 841–851.

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18, 293–320.

Peterson JO, Peterson WT (2008) Influence of the Columbia River plume (USA) on the vertical and horizontal distribution of mesozooplankton over the Washington and Oregon shelf. ICES J Mar Sci 65, 477–483.

Peterson WT, Fisher JL, Peterson JO, Morgan CA, Burke BJ, Fresh KL (2014) Applied fisheries oceanography: Ecosystem indicators of ocean conditions inform fisheries management in the California Current. Oceanography 27, 80–89.

Phillips AJ, Brodeur RD, Suntsov AV (2009) Micronekton community structure in the epipelagic zone of the northern California Current upwelling system. Prog Oceanogr 80, 74–92.

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703–718.

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods, and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152, 179–189.

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org/.

Rannala B, Mountain JL (1997) Detecting immigration by using multilocus genotypes. P Natl Acad Sci USA 94, 9197–9201.

Richardson S (1973) Abundance and distribution of larval fishes in waters off Oregon, May-October 1969, with special emphasis on the northern anchovy, *Engraulis mordax*. Fish Bull 71, 697–711.

Rindorf A, Lewy P (2011) Bias in estimating food consumption of fish by stomach-content analysis. Can J Fish Aquat Sci 61, 2487–2498.

Ruggerone GT, Nielsen JL (2004) Evidence for competitive dominance of Pink salmon (*Oncorhynchus gorbuscha*) over other Salmonids in the North Pacific Ocean. Rev Fish Biol Fish 14, 371–390.

Schabetsberger R, Morgan CA, Brodeur RD, Potts CL, Peterson WT, Emmett RL (2003) Prey selectivity and diel feeding chronology of juvenile Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Columbia River plume. Fish Oceanogr 12, 523–540.

Seeb LW, Antonovich A, Banks MA, Beachem TD, Bellinger, MR, Blankenshipp, SM, Campbell, MR, Decovich, NA, Garza, JC, Guthrie III, CM, Lundrigan, TA, Moran, P, Narum, SR, Stephanson, JJ, Supernault, KJ, Teel, DJ, Templin, WD, Wenburg, JK, Young, SF, Smith, CT (2007) Development of a standardized DNA database for Chinook Salmon. Fisheries 32, 540–549.

Teel, DJ, Bottom, DL, Hinton, SA, Kuligowski, DR, McCabe, GT, McNatt, R, Roegner, GC, Stamatiou, LA, Simenstad, CA (2014) Genetic identification of Chinook Salmon in the Columbia River estuary: Stock-specific distributions of juveniles in shallow tidal and freshwater habitats. N Am J Fish Man 34, 621–641.

Teel DJ, Burke BJ, Kuligowski DR, Morgan CA, Van Doornik DM (2015) Genetic identification of Chinook Salmon: stock-specific distributions of juveniles along the Washington and Oregon coasts. Mar Coast Fish 7, 274–300.

Vander Zanden MJ, Rasmussen JB (1999) Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. Ecology 80, 1395–1404.

Vander Zanden MJ, Clayton MK, Moody EK, Solomon CT, Weidel BC (2015) Stable isotope turnover and half-life in animal tissues: a literature synthesis. PLoS ONE 10, e0116182.

Waples RS, Teel DJ, Myers J, Marshall A (2004) Life history divergence in Chinook Salmon: historic contingency and parallel evolution. Evolution 58, 386–403.

Weitkamp LA, Sturdevant MV (2008) Food habits and marine survival of juvenile Chinook and coho salmon from marine waters of Southeast Alaska. Fish Oceanogr 17, 380–395.

Weitkamp LA, Teel DJ, Liermann M, Hinton SA, Van Doornik DM, Bentley PJ (2015) Stock-specific size and timing at ocean entry of Columbia River juvenile Chinook Salmon and steelhead: implications for early ocean growth. Mar Coast Fish 7, 370–392.

Wells BK, Santora JA, Field JC, MacFarlane RB, Marinovic BB, Sydeman WJ (2012) Population dynamics of Chinook salmon *Oncorhynchus tshawytscha* relative to prey availability in the central California coastal region. Mar Ecol Prog Ser 457, 125–137.

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Syst 15, 393–425.

Zabel RW, Williams JG (2002) Selective mortality in Chinook Salmon: what is the role of human disturbance? Ecol Appl 12, 173–183.

Zhang YL, Baptista AM (2008) SELFE: A semi-implicit Eulerian-Lagrangian finite-element model for cross-scale ocean circulation. Ocean Model 21, 71–96.

**Figure 3.1** Map of study area showing the two stations repeatedly sampled on the continental shelf off of Willapa Bay, Washington from May through September in 2011 and 2012.

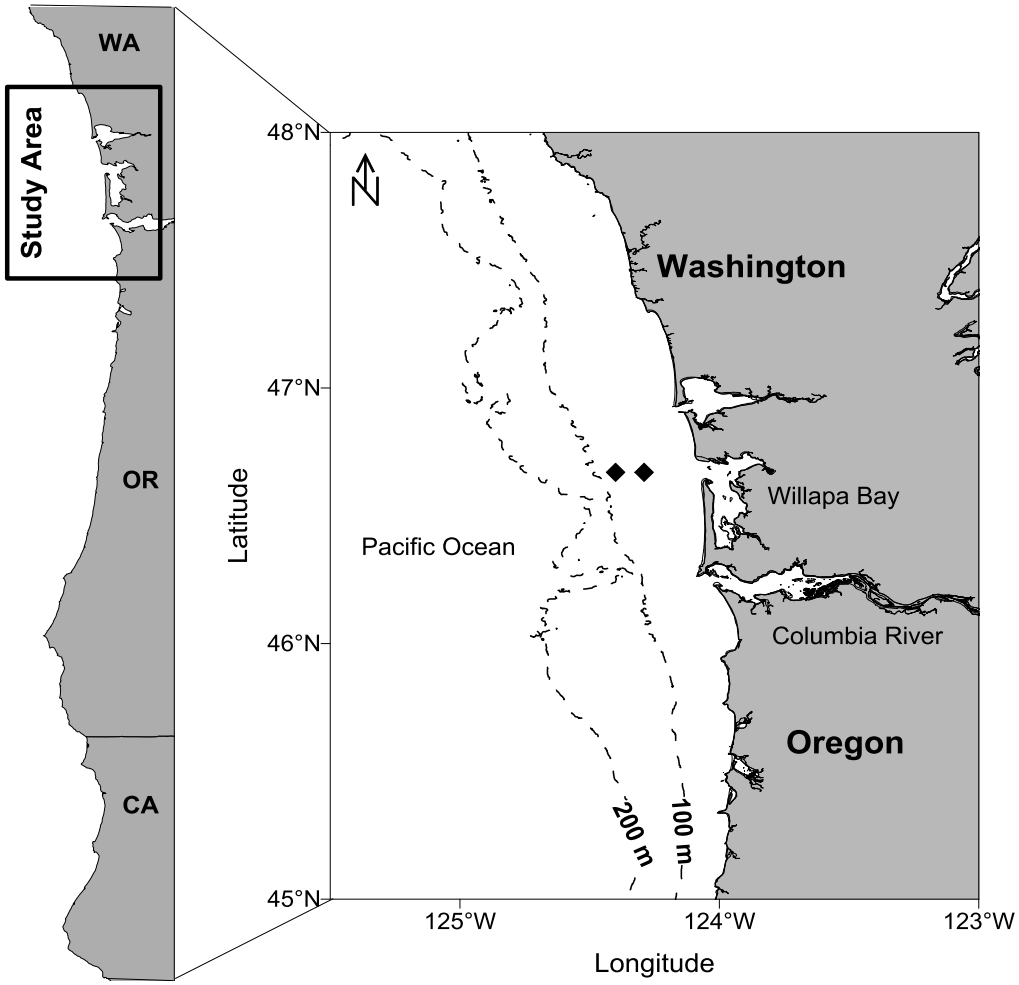


**Figure 3.2** Results of nonmetric multidimensional scaling analysis where each point represents the log-transformed biomass (µg $m^{-3}$) of invertebrate and marine fish prey sampled by haul and plotted in species space from May through September 2011 and 2012; top plots show joint plots of environmental variables (cut-off $r^2$ = 0.30 for inclusion) for a) axes 1-2, and b) axes 1-3; bottom plots show joint plots of species (cut-off $r^2$ = 0.30 for inclusion) for c) axes 1-2, and d) axes 1-3 (symbols are based on categorical groupings for season: spring = May, denoted by a filled black triangle, early summer = June-July, denoted by a grey circle, and late summer = August-September, denoted by an open square); abbreviations are 1 m sea surface temperature (SST), Columbia River plume volume (CR plume; $km^3$), and unidentified (unid).

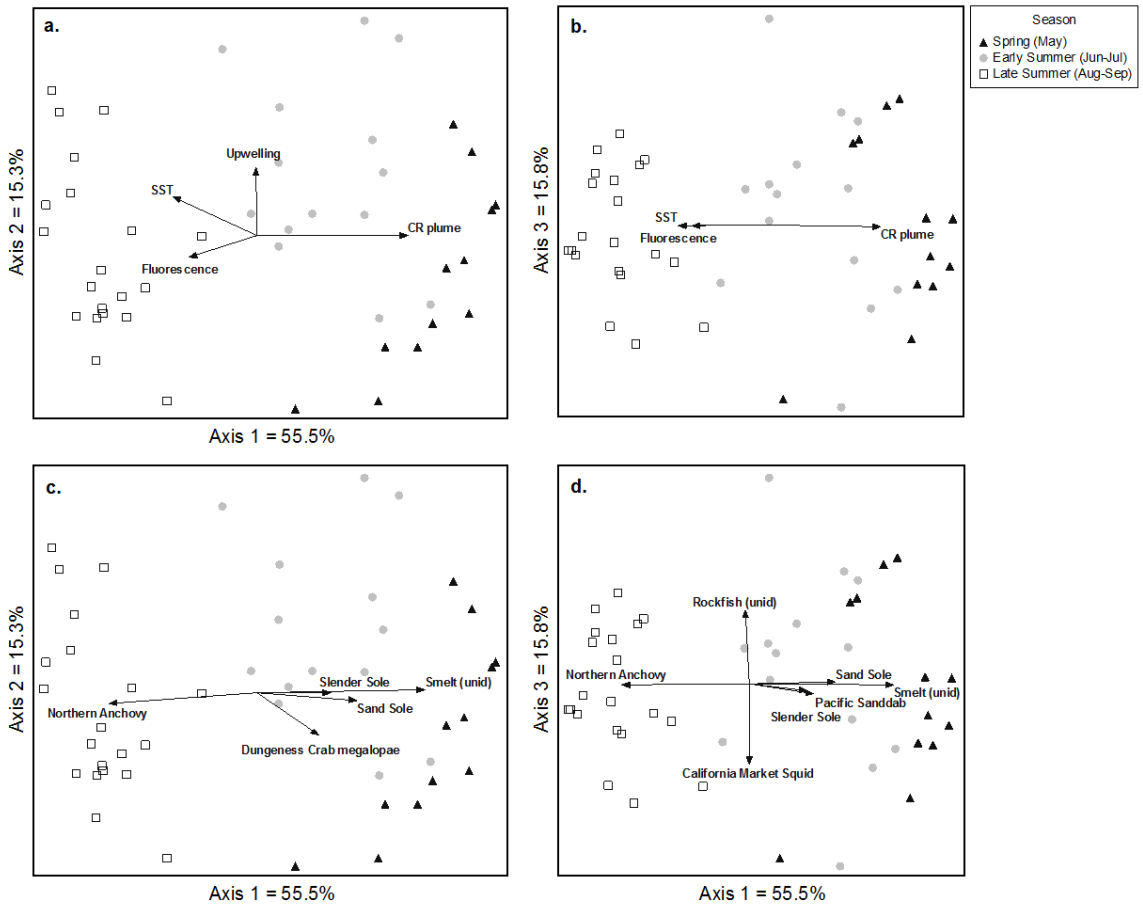


**Figure 3.3** Plots of average ± SE a) fork length b) mass, c) growth rates, and d) specific growth rates of subyearling Chinook salmon (*Oncorhynchus tshawytscha*) assigned to the upper Columbia summer-fall genetic stock group in 2011 and 2012 (*indicates significance [Student's t-test, $p < 0.05$]).

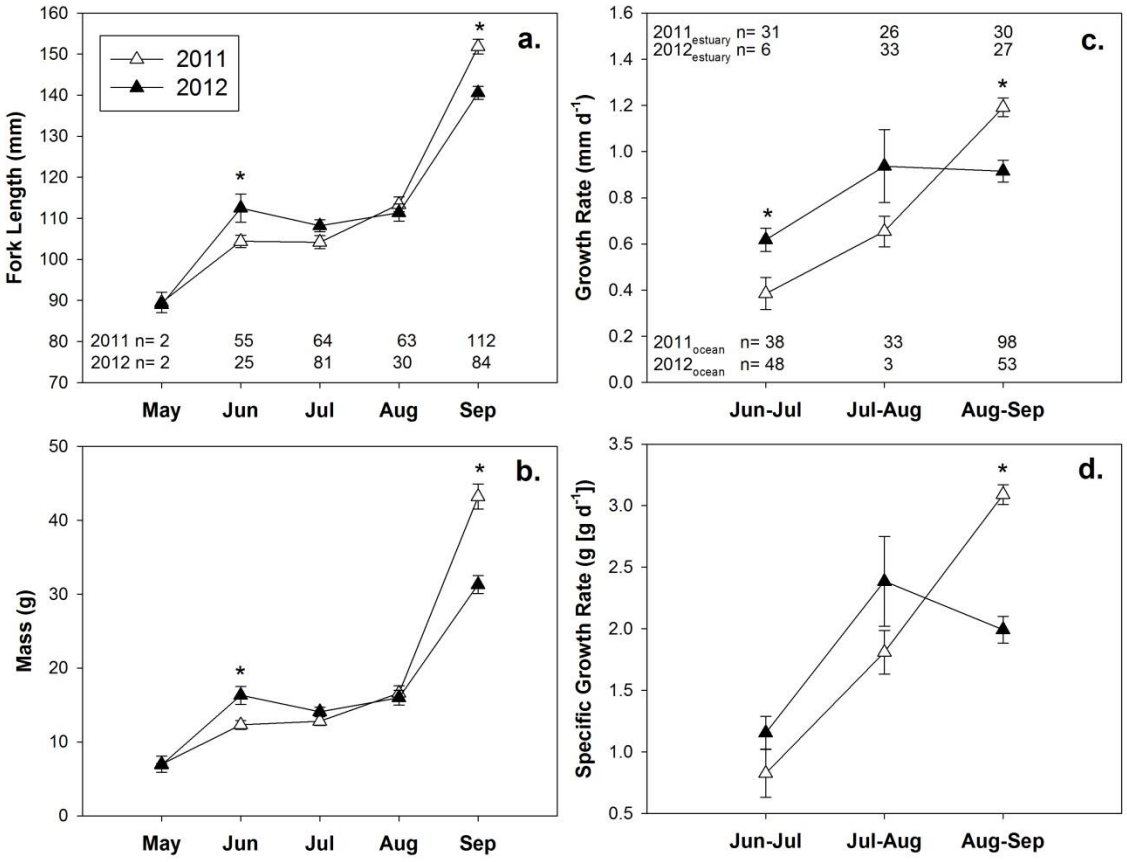


**Figure 3.4** Scatterplots with separate scales on the y-axis for monthly mean ± SE condition of subyearling Chinook salmon (*Oncorhynchus tshawytscha*) assigned to the upper Columbia summer-fall genetic stock group (filled triangles) and mean ± SE biomass of northern anchovy (*Engraulis mordax*) measured in net tows (open circles) sampled July through September in a) 2011 and b) 2012 (different subscripts indicate months when salmon condition varied significantly [ANOVA and Tukey HSD; $p < 0.05$]).

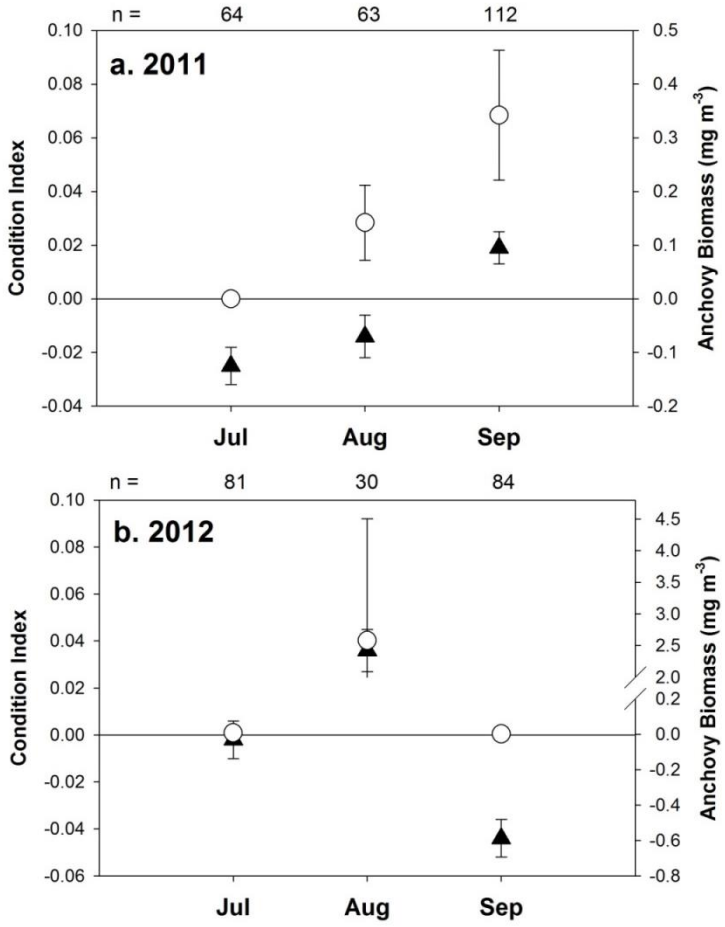


**Figure 3.5** Average percent biomass of potential prey measured from June through September in a) 2011 and b) 2012, and diet composition presented as percent wet mass of prey eaten by subyearling Chinook salmon (*Oncorhynchus tshawytscha*) in c) 2011 (n = 125) and d) 2012 (n = 104; fish prey indicated by colored bars, invertebrate prey indicated by black and white bars).

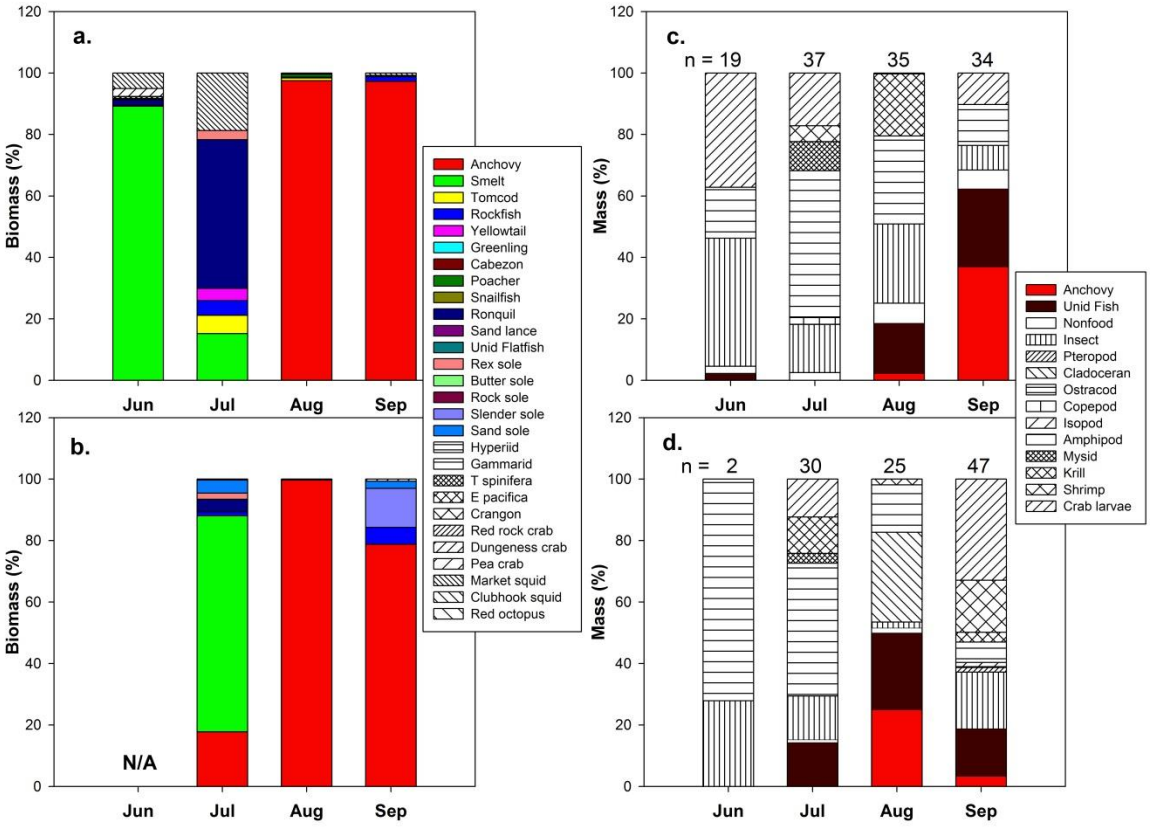


**Figure 3.6** Salmon diet composition presented as percent of wet mass of prey by length category in a) 2011 (n = 125) and b) 2012 (n = 104; fish prey indicated by colored bars, invertebrate prey indicated by black and white bars).

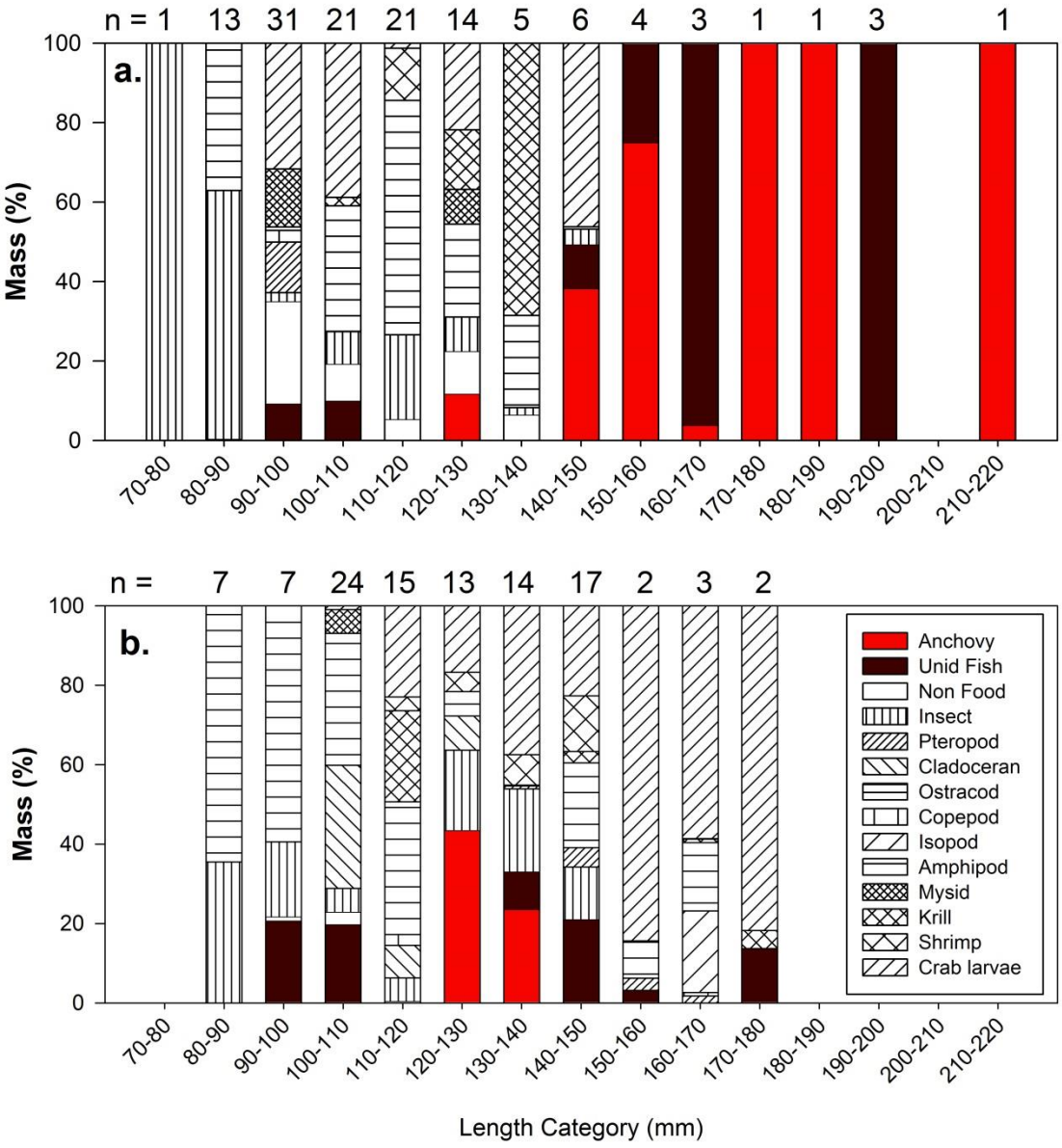


**Figure 3.7** Correlations between subyearling Chinook salmon (*Oncorhynchus tshawytscha*) carbon stable isotope values ($\delta^{13}C$), fatty acids biomarkers (based on percent total fatty acids), and size: a) the relationship between diatom to flagellate markers indicated by the ratio of all polyunsaturated fatty acids (PUFA) containing 16 carbon atoms to all PUFA containing 18 carbon atoms and $\delta^{13}C$, b) the relationship between freshwater markers indicated by the sum of linolenic acid (18:3n-3) and linoleic acid (18:2n-6) and $\delta^{13}C$, c) the relationship between salmon fork length (FL) and 16:18 PUFA, and d) the relationship between salmon FL and 18:3n-3+18:2n-6 (symbols are based on categorical groupings for year and month: 2011 = filled symbols, 2012 = open symbols; July values are denoted by a triangle, August by a square, and September by a circle).

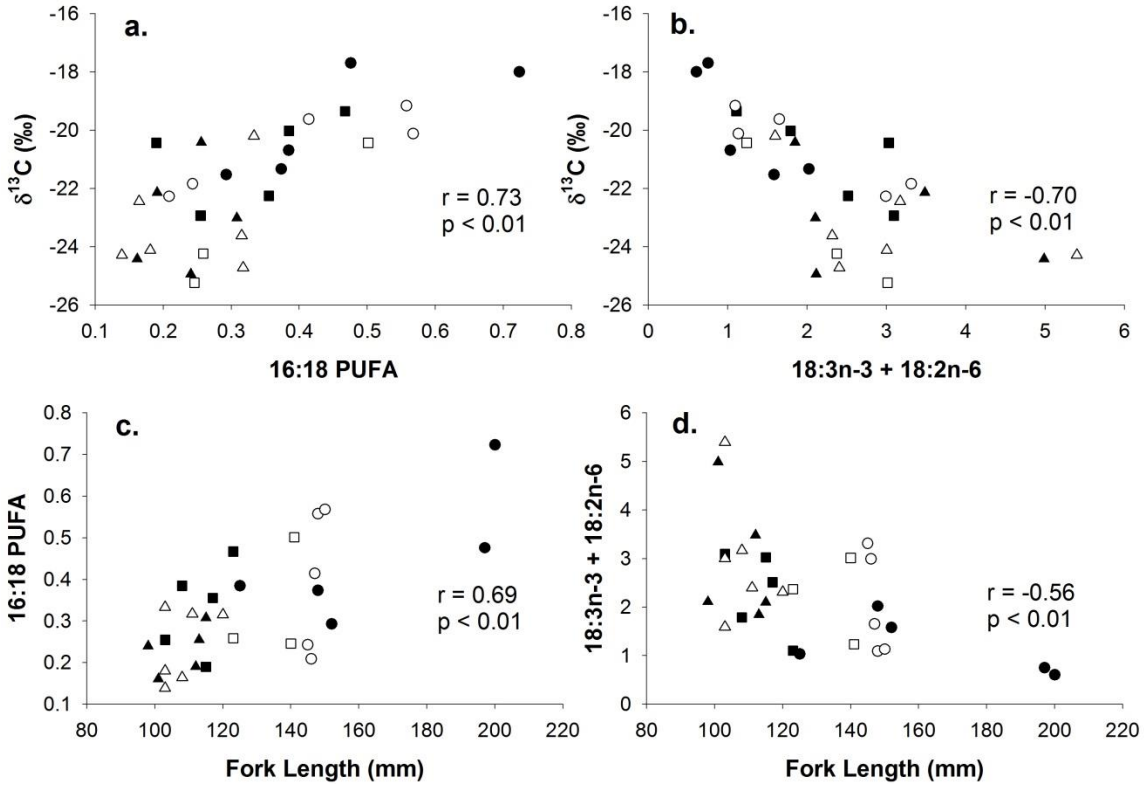


**Figure 3.8** Correlations between subyearling Chinook salmon (*Oncorhynchus tshawytscha*) stable isotope values, fatty acid biomarkers (based on percent of total fatty acids), and size: a) the relationship between carbon and nitrogen stable isotope values ($\delta^{13}C$ and $\delta^{15}N$), b) the relationship between the ratio of docosahexaenoic acid to eicosapentaenoic acid (DHA:EPA) and $\delta^{15}N$, (c) the relationship between salmon fork length (FL) and $\delta^{15}N$, and d) the relationship between salmon FL and DHA:EPA (symbols are based on categorical groupings for year and month: 2011 = filled symbols, 2012 = open symbols; July values are denoted by a triangle, August by a square, and September by a circle).

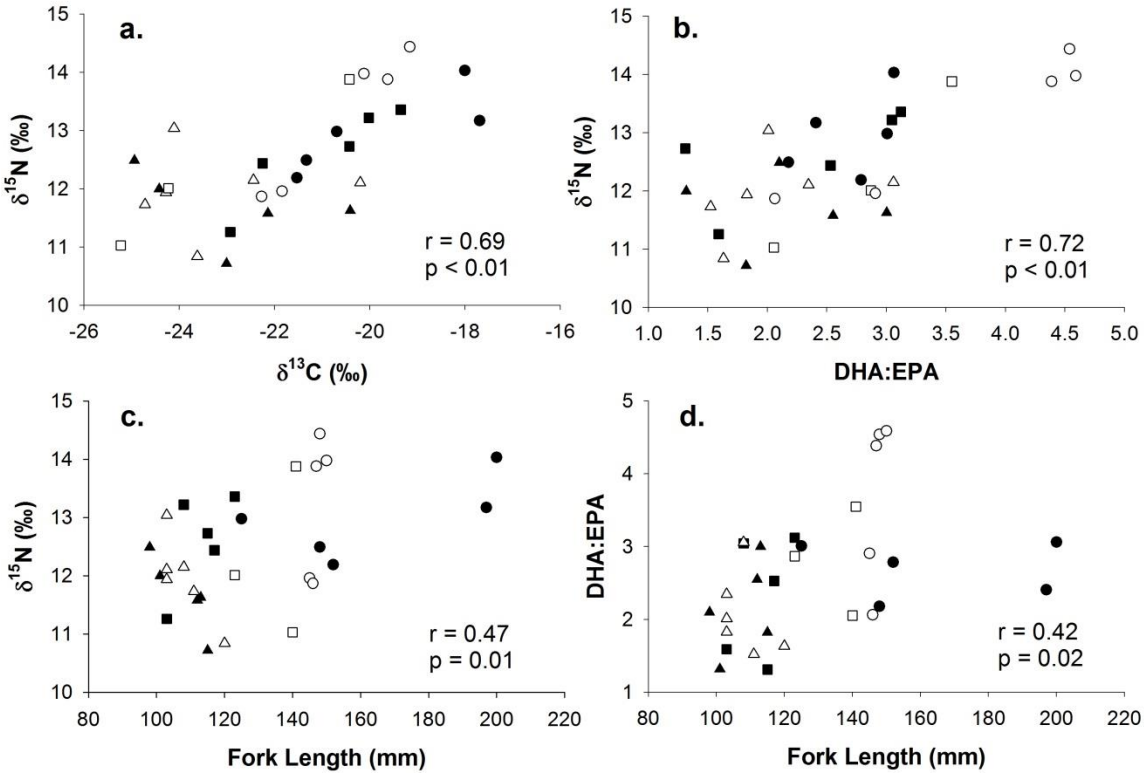


**Figure 3.9** Associations between mean ± SE subyearling Chinook salmon (*Oncorhynchus tshawytscha*) trophic position and a) fluorescence (1-mo lag), b) Columbia River plume volume (1-mo lag), c) salmon fork length, d) proportion of fish measured in salmon diet (1-mo lag), e) biomass of juvenile northern anchovy (*Engraulis mordax*) measured in the field (1-mo lag), and f) salmon condition (1-mo lag).

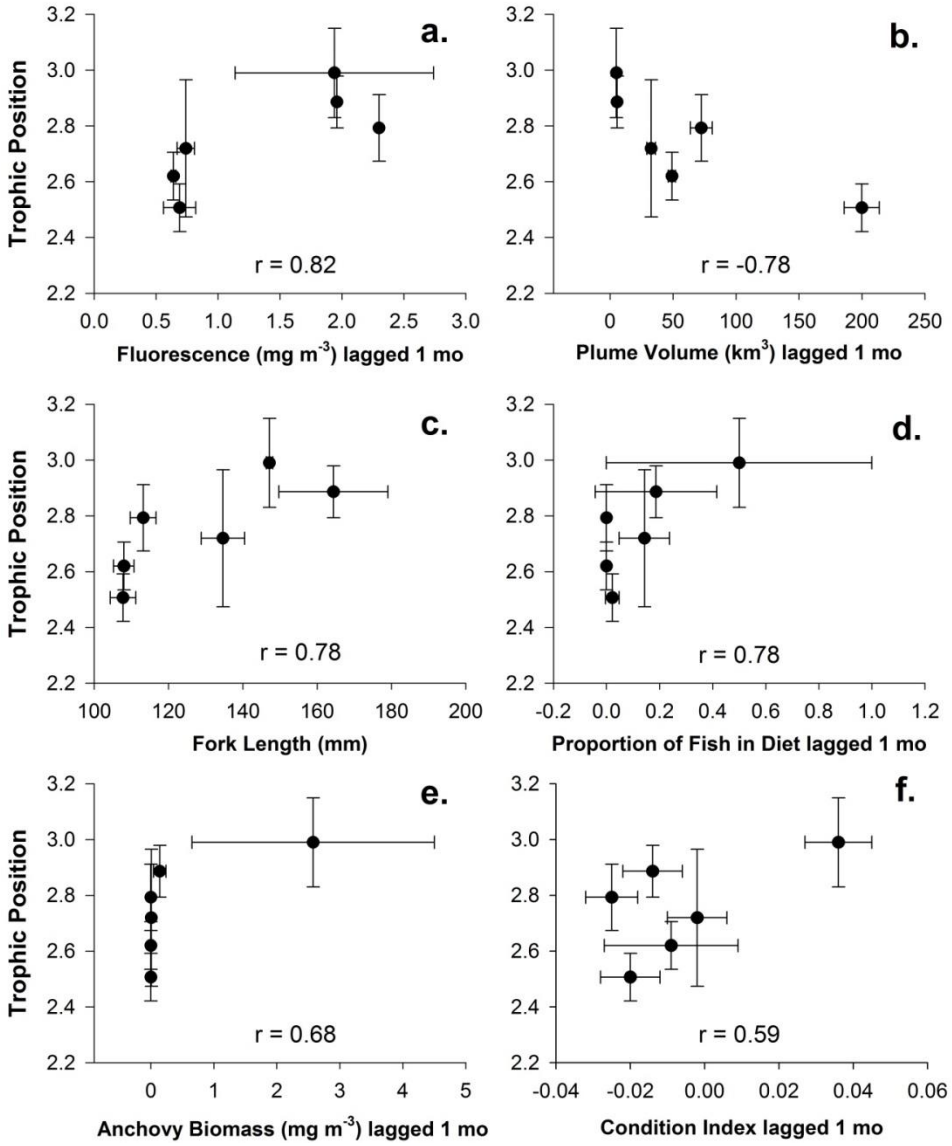


**Table 3.1** Summary of trophic biomarkers analyzed in this study, including stable isotopes of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) and fatty acid biomarkers (based on percent of total fatty acids).

| Biomarker | Indicator Type | Reference |
|---|---|---|
| $\delta^{13}C$ | Carbon source | Peterson and Fry 1987 |
| $\delta^{15}N$ | Trophic position | Vander Zanden and Rassmussen 1999 |
| 18:3n-3+18:2n-6 | Freshwater/Nearshore | Budge and Parrish 1998; Copeman et al. 2009 |
| 16:18 PUFA[a] | Diatoms:Flagellates | Budge and Parrish 1998 |
| DHA:EPA[b] | Piscivory | Daly et al. 2010; this study |

[a] Proportion of marine diatoms to flagellates indicated by the ratio of all polyunsaturated fatty acids (PUFA) containing 16 carbon atoms to all PUFA containing 18 carbon atoms

[b] Piscivory indicated by the ratio of docosahexaenoic acid (DHA; 22:6n-3) to eicosapentaenoic acid (EPA; 20:5n-3)

**Table 3.2** Pearson's correlation coefficients for associations between nonmetric multidimensional scaling ordination axes and environmental variables or species ($R^2$ >0.30 in **bold**).

| | | Axis 1 | Axis 2 | Axis 3 |
|---|---|---|---|---|
| **Environmental variables** | | | | |
| Sea surface (1 m) temperature (°C) | | **-0.61** | 0.41 | -0.07 |
| Fluorescence (mg $m^{-3}$) | | **-0.55** | -0.31 | -0.06 |
| Columbia River plume volume ($km^3$) | | **0.82** | -0.02 | -0.09 |
| Upwelling index | | -0.06 | **0.55** | 0.01 |
| **Species** | **Scientific Name** | | | |
| Dungeness crab larvae | *Metacarcinus magister* | **0.53** | -0.43 | 0.23 |
| California market squid | *Doryteuthis opalescens* | -0.01 | -0.35 | **-0.65** |
| Northern anchovy | *Engraulis mordax* | **-0.81** | -0.22 | -0.05 |
| Smelt (unidentified) | Osmeridae | **0.86** | 0.12 | -0.07 |
| Rockfish (unidentified) | *Sebastes* spp. | -0.13 | -0.53 | **0.62** |
| Pacific sanddab | *Citharichthys sordidus* | **0.55** | 0.12 | -0.19 |
| Slender sole | *Lyopsetta exilis* | **0.57** | -0.01 | -0.23 |
| Sand sole | *Psettichthys melanostictus* | **0.67** | -0.19 | 0.09 |

**Table 3.3** Average ± SE subyearling Chinook salmon (*Oncorhynchus tshawytscha*) fork length (FL), mass, stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$, ‰), total fatty acids expressed as the amount per dry weight of each sample, percent fatty acids comprising >1% of total fatty acids, and biomarker* values for fatty acids from 29 samples collected July through September 2011 and 2012. We assumed a one month lag between diet and expression of diet in salmon biochemistry.

| | Jul 2011 | Aug 2011 | Sep 2011 | Jul 2012 | Aug 2012 | Sep 2012 |
|---|---|---|---|---|---|---|
| **Size** | | | | | | |
| FL (mm) | 107.8 ± 3.5 | 113.2 ± 3.5 | 164.4 ± 14.7 | 108.0 ± 2.8 | 134.7 ± 5.8 | 147.2 ± 0.9 |
| Mass (g) | 13.5 ± 1.3 | 16.6 ± 1.5 | 58.5 ± 15.2 | 13.9 ± 0.9 | 27.3 ± 3.4 | 34.5 ± 1.6 |
| **Stable Isotopes** | | | | | | |
| $\delta^{13}C$ | -23.0 ± 0.8 | -21.0 ± 0.7 | -19.8 ± 0.8 | -23.2 ± 0.6 | -23.3 ± 1.5 | -20.6 ± 0.6 |
| $\delta^{15}N$ | 11.7 ± 0.3 | 12.6 ± 0.4 | 13.0 ± 0.3 | 12.0 ± 0.3 | 12.3 ± 0.8 | 13.2 ± 0.5 |
| Trophic position | 2.5 ± 0.1 | 2.8 ± 0.1 | 2.9 ± 0.1 | 2.6 ± 0.1 | 2.7 ± 0.2 | 3.0 ± 0.2 |
| **Fatty Acids** | | | | | | |
| Total fatty acids (μg $g^{-1}$) | 10.1 ± 1.0 | 11.6 ± 2.1 | 11.4 ± 1.3 | 15.5 ± 1.7 | 16.7 ± 1.0 | 15.5 ± 1.7 |
| **Percent Fatty Acids** | | | | | | |
| 14:0 | 1.1 ± 0.2 | 1.9 ± 0.2 | 1.2 ± 0.1 | 1.5 ± 0.2 | 1.7 ± 0.1 | 1.5 ± 0.2 |
| 16:0 | 23.2 ± 2.1 | 26.9 ± 2.5 | 27.4 ± 2.1 | 23.7 ± 0.6 | 21.0 ± 1.2 | 23.3 ± 0.9 |
| 18:0 | 6.8 ± 1.0 | 6.6 ± 1.1 | 4.8 ± 0.3 | 6.8 ± 0.4 | 5.2 ± 0.3 | 5.1 ± 0.3 |
| 22:0 | 1.6 ± 0.4 | 1.0 ± 0.7 | 0.8 ± 0.4 | 1.3 ± 0.7 | 0.7 ± 0.7 | 1.6 ± 0.7 |
| ∑SFA[a] | 34.8 ± 0.24 | 34.8 ± 0.29 | 34.8 ± 0.19 | 34.8 ± 0.14 | 34.8 ± 0.16 | 34.8 ± 0.14 |
| 16:1n-7 | 2.2 ± 0.3 | 3.3 ± 0.6 | 2.0 ± 0.4 | 3.3 ± 0.5 | 2.3 ± 0.2 | 2.2 ± 0.4 |
| 18:1n-9 | 6.3 ± 0.5 | 6.6 ± 0.8 | 6.0 ± 0.3 | 7.4 ± 0.4 | 7.1 ± 0.4 | 9.2 ± 1.0 |
| 18:1n-7 | 3.2 ± 0.3 | 3.2 ± 0.2 | 2.4 ± 0.6 | 3.5 ± 0.2 | 2.4 ± 0.1 | 2.4 ± 0.2 |
| ∑MUFA[b] | 14.5 ± 0.1 | 17.8 ± 0.2 | 13.2 ± 0.1 | 17.7 ± 0.1 | 14.1 ± 0.1 | 17.2 ± 0.2 |
| 18:2n-6 | 1.6 ± 0.2 | 1.3 ± 0.1 | 0.6 ± 0.1 | 1.6 ± 0.2 | 1.1 ± 0.1 | 1.1 ± 0.2 |
| 18:3n-3 | 1.3 ± 0.4 | 1.0 ± 0.2 | 0.6 ± 0.2 | 1.4 ± 0.4 | 1.2 ± 0.4 | 1.0 ± 0.3 |

**Table 3.3** (Continued)

| | Jul 2011 | Aug 2011 | Sep 2011 | Jul 2012 | Aug 2012 | Sep 2012 |
|---|---|---|---|---|---|---|
| **Percent Fatty Acids** | | | | | | |
| 20:4n-6 | 2.4 ± 0.4 | 1.4 ± 0.2 | 1.3 ± 0.2 | 2.2 ± 0.3 | 2.0 ± 0.5 | 1.3 ± 0.3 |
| 20:5n-3 | 11.4 ± 0.3 | 10.3 ± 1.1 | 11.7 ± 0.8 | 11.5 ± 0.6 | 11.7 ± 0.6 | 8.9 ± 0.8 |
| 22:5n-3 | 3.9 ± 0.3 | 3.0 ± 0.3 | 3.1 ± 0.5 | 3.6 ± 0.2 | 4.0 ± 0.5 | 2.9 ± 0.2 |
| 22:6n-3 | 24.4 ± 2.8 | 23.3 ± 3.5 | 31.1 ± 2.4 | 23.4 ± 1.8 | 32.7 ± 4.2 | 31.4 ± 2.9 |
| ∑PUFA[c] | 50.6 ± 0.2 | 43.6 ± 0.2 | 51.1 ± 0.2 | 47.2 ± 0.1 | 50.6 ± 0.2 | 49.3 ± 0.2 |
| **Fatty Acid Biomarkers** | | | | | | |
| 16:18 PUFA | 0.2 ± 0.0 | 0.4 ± 0.1 | 0.5 ± 0.1 | 0.3 ± 0.0 | 0.3 ± 0.1 | 0.4 ± 0.1 |
| 18:3n-3 + 18:2n-6 | 2.9 ± 0.6 | 2.3 ± 0.4 | 1.2 ± 0.3 | 3.0 ± 0.5 | 2.2 ± 0.5 | 2.0 ± 0.5 |
| DHA:EPA | 2.2 ± 0.3 | 2.3 ± 0.4 | 2.7 ± 0.2 | 2.1 ± 0.2 | 2.8 ± 0.4 | 3.7 ± 0.5 |
| **Sample size (n = )** | 5 | 5 | 5 | 6 | 3 | 5 |

[*]See Table 3.1 for explanation of trophic biomarkers
[a]Also contains < 1% of i-15:0, ai15:0, 15:0, i16:0, ai16:0, i17:0, ai17:0, 17:0, 19:0, 20:0, 21:0, 24:0
[b]Also contains < 1% of 14:1, 15:1, 16:1n-5, 17:1, 18:1n-11, 18:1n-6, 18:1n-5, 20:1n-9, 20:1n-11, 20:1n-7, 22:1n-11, 22:1n-9, 22:1n-7, 24:1
[c]Also contains < 1% of 16:2n-4, 16:3n-4, 16:4n-3, 16:4n-1, 18:2n-4, 18:3n-6, 18:3n-4, 18:4n-3, 18:4n-1, 20:2a, 20:2b, 20:2n-6, 20:3n-6, 20:3n-6, 20:3n-3, 20:4n-3, 21:5n-3, 22:4n-6, 22:5n-6, 22:4n-3

**Table 3.4** Significant ($p < 0.05$) Pearson's correlation coefficients for comparisons between carbon and nitrogen stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) and fatty acid biomarkers[a] from 29 subyearling Chinook salmon (*Oncorhynchus tshawytscha*) muscle tissue samples collected July through September 2011 and 2012 (strongest correlations in **bold**).

| **Biomarker** | $\delta^{13}C$ | $\delta^{15}N$ | 18:3n-3 + 18:2n-6 | 16:18 PUFA | DHA:EPA |
|---|---|---|---|---|---|
| $\delta^{13}C$ | 1.00 | | | | |
| $\delta^{15}N$ | 0.69 | 1.00 | | | |
| 18:3n-3 + 18:2n-6 | **-0.70** | -0.56 | 1.00 | | |
| 16:18 PUFA | **0.73** | 0.72 | -0.82 | 1.00 | |
| DHA:EPA | 0.60 | **0.72** | -0.58 | 0.64 | 1.00 |

[a] See Table 3.1 for explanation of trophic biomarkers

CHAPTER 4

# ENERGY DYNAMICS OF SUBYEARLING CHINOOK SALMON REVEAL THE IMPORTANCE OF PISCIVORY TO SHORT-TERM GROWTH DURING EARLY MARINE RESIDENCE

Marisa N. C. Litz, Jessica A. Miller, Richard D. Brodeur, Elizabeth A. Daly, Laurie A. Weitkamp, and Adam G. Hansen

*Fisheries Oceanography*
Online ISSN: 1365-2419
In prep

ABSTRACT

Variation in prey quantity and quality can influence growth and survival of marine predators, including anadromous fish that migrate from freshwater systems. The objective of this study was to quantify the relative importance of prey quantity, prey quality, and temperature to variation in seasonal growth rates of subyearling Chinook salmon (*Oncorhynchus tshawytscha*) following freshwater emigration. To address this objective, a population of Chinook salmon was repeatedly sampled from June – September over two years in the lower Columbia River estuary and in coastal waters off Oregon and Washington. Subyearlings from the same population were also reared under laboratory conditions. Using a bioenergetics model evaluated in the laboratory, we found that growth rate variability in the field was associated most with differences in northern anchovy (*Engraulis mordax*) consumption and less with variation in diet energy density or ocean temperature. Highest growth rates occurred in months when anchovy biomass was highest, and the timing of peak anchovy biomass varied by year. Our results confirm a general pattern among juvenile Chinook salmon occurring from Alaska to California, that feeding rates contribute most to growth rate variation during early marine residence, although dominant prey types may vary by ecosystem. In the California Current, faster growth appears to be associated with the availability of age-0 marine fishes. Monitoring the seasonal development of the prey field and identifying environmental drivers influencing prey quantity and quality may help better understand linkages between oceanographic variability and salmon growth and survival.

INTRODUCTION

Given the highly dynamic, three-dimensional, and large spatial scale of marine ecosystems, interactions between predators and prey can be incredibly complex (Steele 1991; Lima 1998; Hunsicker et al. 2011). Environmental variability, which can influence the timing, abundance, availability, or quality of prey, can impact feeding success, growth, behavior, and survival of the predator (Österblom et al. 2008). Among fish populations, a match/mismatch between prey resources and consumers during critical life stages has been recognized as a potential mechanism influencing survival to adulthood for over a century (Hjort 1914; Cushing 1990; Houde 2008). Trophic interactions in marine environments can be measured directly, by quantitatively sampling predator diets, but this approach is limited temporally to the last meal, and predator-prey relationships can change over time. A more informative approach is longitudinal sampling of predator and prey, which can clarify the consequences of prey variability on predator consumption through time. Understanding how energy is transferred between predator and prey through time also leads to better estimates of the predator's growth.

A potential critical period in the life history of Pacific salmon (*Oncorhynchus* spp.) and steelhead (*O. mykiss*), hereafter referred to as "salmonids", has been identified as the early marine phase following freshwater emigration, when mortality rates are exceptionally high and variable (Hartt 1980; Pearcy 1992; Pearcy and McKinnell 2007). There is some evidence that mortality may be size-selective during this time, especially in juvenile life history types that migrate to sea as age-0 fish, or subyearlings (Neilson and Geen 1986; Miller et al. 2013; Woodson et al. 2013). Other studies have demonstrated a relationship between early marine growth and subsequent adult survival (Duffy and Beauchamp 2011; Tomaro et al. 2012). Larger size and faster growth are attributes

expected to benefit juvenile salmonids through the first few months of ocean entry when predation rates are high as well as through the first ocean winter when prey abundances may decrease and fish may starve (Beamish and Mahnken 2001).

During the early marine phase, some juvenile salmonids, namely Chinook (*O. tshawytscha*), and coho (*O. kisutch*) salmon, undergo an ontogenetic shift in diet when invertebrate prey is gradually replaced by marine fish prey, with piscivorous salmonids typically larger than those that feed primarily on invertebrates (Brodeur 1991; Schabetsberger et al. 2003; Daly et al. 2009). The size and timing of freshwater emigration varies by species and stock group (Weitkamp et al. 2015), therefore stocks are likely to encounter different prey fields. Previous studies indicate that a higher proportion of juveniles surviving to return as adults have an earlier date of marine entry than other members of their cohort (Scheurell et al. 2009), and that this may be related to earlier peaks in nearshore productivity that impact trophic interactions (Chittendon et al. 2010). Because seasonal variability in the prey field will affect growth and survival rates of juvenile salmonids differently depending on their timing of ocean entry, understanding seasonal variability in the prey field may help fisheries ecologists to better predict future adult returns. Prey resources are expected to vary seasonally based on upwelling intensity and other nearshore oceanographic processes, hence monitoring of the prey field can help illustrate the mechanistic linkages between the environment and the prey community and serve as an early indicator of salmon growth and survival.

Currently, the biomass of ichthyoplankton sampled biweekly from January through March in bongo nets at five stations along the Newport Hydrographic (NH) line off Newport, Oregon, USA (44° 39’ N), are used to estimate potential prey resources

available to salmonids following freshwater emigration two to three months later (Daly et al. 2013). Winter ichthyoplankton biomass is one of several indicators of ocean conditions that relate to the recruitment of salmonids in the California Current (Burke et al. 2013; Peterson et al. 2014). This indicator is correlated with adult returns of yearling migrant populations, because yearlings tend to enter the ocean during the spring or early summer. Subyearlings typically migrate from freshwater later than yearlings, and the winter ichthyoplankton biomass indicator performs less well for these populations. The indicator has also been criticized because of the temporal lag between when ichthyoplankton is measured (winter) and when salmonids enter the ocean (spring and summer), during which time environmental forces may render the prey unavailable. Concurrent sampling of subyearling salmon and their prey provides an alternative sampling strategy for direct measurements of predator (size, abundance, diet, etc.) and prey (composition, availability) that is more insightful in trying to elucidate predator-prey interactions.

The objective of this study was to explore energy dynamics in a population of subyearling Chinook salmon originating from the Columbia River basin, Pacific Northwest, USA, to better understand how juvenile growth is related to temporal variation in the prey field. To address this objective, we used a bioenergetics model validated in the laboratory prior to applying it to field observations to estimate consumption and feeding rates over two years. We then conducted a sensitivity analysis to determine whether salmon growth was most affected by observed variations in feeding rate, prey energy density, or temperature, constrained by field observations. Previous bioenergetics models indicate that juvenile salmon growth is most sensitive to changes in

feeding rate or prey energy density when ocean temperatures range from about 8 – 18° C (Trudel et al. 2002; Beauchamp et al. 2007). Our goal was to determine if the variability in juvenile salmon growth rates during their initial summer reflected changes in prey availability or quality. This work provides novel insight into the seasonal energy dynamics of subyearlings and their prey during early marine residence and identifies factors affecting variation in growth that can be used to guide management efforts to support early marine growth and survival of salmonid populations.

## METHODS

We conducted our analysis of growth and energy dynamics on upper Columbia summer-fall (UCSF) subyearling Chinook salmon using a bioenergetics model. Salmon from this population spawn in main-stem and tributary habitats east of the Cascade Mountains, with hatchery and natural production occurring in both the mid- and upper-Columbia River (Miller et al. 2013; Teel et al. 2014). Subyearlings from the UCSF stock group enter the ocean throughout the summer, peaking in July (Weitkamp et al. 2015), but remain concentrated nearshore along the Oregon and Washington coasts during their first few months at sea (Fisher et al. 2014; Teel et al. 2015). The protracted ocean entry period, along with the limited ocean dispersal by this group during the critical period make UCSF subyearlings a suitable stock group for a longitudinal study of early marine diet and growth.

### *Bioenergetics Model*

Bioenergetics models are an important tool for examining the effects of environmental variability on Pacific salmon populations and have successfully been used to model subyearling Chinook salmon energy dynamics in the ocean in many regions (MacFarlane 2010; Marin Jarrin 2012; Gamble 2016). The model is based on the principle of thermodynamics (Kleiber 1975) and contains mass-dependent functions for maximum daily consumption and metabolism, temperature-dependent functions for maximum daily consumption and metabolism (basal respiration and activity), and a temperature- and ration-dependent function for waste (Beauchamp 2009). Bioenergetics models can account for changing thermal and food conditions explicitly and are valuable analytical tools for isolating and evaluating the relative contribution of different factors (e.g. food quality, prey availability, and temperature) on growth during different life stages.

To investigate the energy dynamics of UCSF subyearlings, we used the Wisconsin bioenergetics model (Hanson et al. 1997) parameterized for Chinook salmon (Stewart and Ibarra 1991) and coded to run in the R statistical package (R Core Team 2015). The Wisconsin bioenergetics model operates on a daily time step, enabling simulations to account for changing conditions at fine temporal resolution. We first used the model to predict consumption based on growth observed in the laboratory and then used the model to predict growth based on total laboratory consumption. Error was evaluated as the percent difference from observed and modeled growth and consumption. Next, we fit the model to observed growth in the field to calculate consumption and feeding rate over three months in two years. Each simulation lasted approximately one month. Finally, to evaluate the relative importance of prey quantity, prey quality, and

environmental variability on growth observed across months and years, we conducted a sensitivity analysis to quantify the response of growth to observed variation in feeding rate, prey energy density, and temperature. Because the thermal environment experienced by subyearlings was ≤17 °C across all simulations, we did not adjust for the upper temperature-dependent consumption equation of Thornton and Lessem (1978) as suggested by Plumb and Moffitt (2015).

*Laboratory rearing of subyearlings*

To evaluate performance of the bioenergetics model in juvenile Chinook salmon, subyearlings from the UCSF group were obtained from Priest Rapids Hatchery in May 2013 and transported to the Hatfield Marine Science Center in Newport, Oregon. A total of 80 fish were transferred to a 568-L round aquaculture tank with a constant current speed of 0.2 m $s^{-1}$, a continuous flow of charcoal-filtered freshwater (mean = 14.9 ± 0.1 °C standard error SE), and air supply. Salmon were allowed to acclimate for 4 weeks before being gradually introduced to seawater from Yaquina Bay, Oregon, over 1 week. Seawater was sand filtered to 50 µm and sterilized using ultraviolet light before entering the lab. Temperature, salinity, and dissolved oxygen were measured daily. Throughout the duration of the experiment, temperature averaged 12.1 ± 0.4 °C, salinity was 32.4 ± 0.2 PSU, and dissolved oxygen concentrations were 7.2 ± 0.4 ml $L^{-1}$.

To determine growth of laboratory-reared fish, all salmon were measured for fork length (FL, mm) and mass (g) at the start of the study in late June and at the end of weeks 4, 8, and 12 in late July, August, and September. At the start of the experiment, seven fish were inserted with a passive integrated transponder (PIT) tag to track individual growth

for comparison with tank-averaged growth. Specific growth rates (SGR, g, % body weight [BW] $d^{-1}$) were calculated from the difference between initial and final mass according to the following formula:

$$SGR = \frac{(\ln[W_f] - ln[W_i])}{(t_f - t_i)} \times 100,$$

where $W_f$ is final mass at time $t_f$ and $W_i$ is initial mass at $t_i$. To measure consumption, a maintenance diet of commercial hatchery feed (Otohime Fish Diet® extruded pellets; 11.8% lipid and 13,709 J $g^{-1}$ by wet weight) was offered once daily at 2% of the total fish weight in the tank based on size measurements. Fish were observed until all food was consumed, which typically took <2 min. Ration was adjusted weekly between measurements by assuming an approximate increase of 1.5% BW $d^{-1}$ according to the temperature-dependent growth formula of Iwama and Tautz (1981).

Chinook salmon energy density is a required input into the Wisconsin bioenergetics model (Hanson et al. 1997) and is typically estimated from an allometric relationship between size and energy density determined for adults (Stewart and Ibarra 1991). However, as noted by Trudel et al. (2005), this relationship tends to overestimate juvenile salmon energy density, and can result in model error. To evaluate this issue, we compared model output using salmon energy densities estimated both by the Stewart and Ibarra (1991) method and by using juvenile data to estimate energy density. For the latter, we fit a regression model based on 44 measurements of juvenile Chinook salmon mass

and energy density collected in summer off southern British Columbia (Trudel et al. 2005) that had the following form:

$$ED = 1.76w + 4218.54,$$

where ED is salmon energy density (J $g^{-1}$) and *w* is the wet mass (g) of the salmon. The model had an $R^2$ value of 0.46 and $p < 0.01$.

To evaluate error in the bioenergetics model, we ran simulations to estimate the change in mass (Δ g) and total consumption (g) in individual PIT-tagged fish and the tank average over three months. For each 4-week period between measurements, percent error was calculated from the difference between observed and modeled output. For each simulation, we compared results using both methods for calculating salmon energy density (Stewart and Ibarra 1991; Trudel et al. 2005). Error in growth and consumption was compared for both methods with one-way analysis of variance (ANOVA) after an arcsine square root transformation to ensure assumptions of normality and equal variance were met.

*Field Collections*

Juvenile salmon were collected in three separate surveys (Teel et al. 2015; Weitkamp et al. 2015; Litz et al. in press) conducted in coastal waters from June through September 2011 and 2012 (Fig 4.1). Sampling occurred from the lower Columbia River estuary north to Willapa Bay, Washington. We also collected potential salmon prey in 36 surface trawls from July through September in each year using a 264 Nordic rope trawl

(NET Systems, Bainbridge Island, Washington) with 3-mm mesh in the cod end (Litz et al. in press). Juvenile salmon used in the study (n = 514) were assigned to the UCSF genetic stock based on genotyping of 13 microsatellite DNA loci following Teel et al. (2015) and classified as subyearlings based on FL (Weitkamp et al. 2015; Litz et al. in press).

*Salmon ocean growth rates and diet composition*

Monthly estimates of ocean growth from June through September 2011 and 2012 were calculated from mean differences in mass between salmon sampled in the estuary from June through August of each year and in the ocean from July through September. For these measurements, mean size and time of capture were organized by month for estuary and ocean surveys separately and SGR determined from the difference between mean estuary size and time and mean ocean size and time the following month (Weitkamp et al. 2015; Litz et al. in press).

Stomach contents were measured in 208 UCSF subyearlings from July – September in 2011 and 2012 using methods described by Brodeur et al. (2007) and are presented in Litz et al. (in press). For this analysis, we assumed stomach contents represented prey consumed over the previous month (i.e. stomach contents measured in July 2011 represented diet from June – July 2011). Stomach fullness was determined as the percent of stomach weight relative to whole fish weight minus the stomach (Weitkamp and Sturdevant 2008). Prey taxa that contributed ≥2% of salmon diets by weight were grouped into 13 categories that included insects (Insecta), pteropods (Pteropoda), cladocerans (Cladocera), ostracods (Ostracoda), copepods (Copepoda),

isopods (Isopoda), amphipods (Amphipoda), mysids (Mysidacea), krill (Euphausiidae), shrimp larvae (Pandalidae), crab larvae (*Metacarcinus magister* and *Cancer* spp. zoea and megalopae), northern anchovy (*Engraulis mordax*), and unidentified fish (Osteichthyes). Stomach contents were averaged and presented as the proportion of total stomach content wet mass, excluding unidentified digested material or non-food items (Fig 4.2; Appendix Table B1).

To determine prey energy density, we relied on measurements obtained from the literature, as well as proximate analysis of prey samples caught concurrently with the salmon (Appendix Table B2). For this analysis, we measured percent water, lipids, and nitrogen (N) in each prey sample based on wet mass. Water content of samples was measured by drying samples in an oven at 60 °C for 48 h. Lipids were extracted in chloroform and methanol according to Copeman et al. (2016), and % N was determined using mass spectrometry (Litz et al. in press). For calculation of the % protein in each sample, the % N was multiplied by a conversion factor of 5.8 (Gnaiger and Bitterlich 1984; Clarke et al. 1992; Doyle et al. 2007). Carbohydrate fraction, which is often a negligible (<2%) component of prey (Lawson et al. 1998), was determined from the remainder. Quantities of lipid, protein, and carbohydrates were expressed in joules (J) based on published energy equivalents (Schmidt-Nielsen 1997), with lipid equal to 39,300 J $g^{-1}$, protein equal to 17,800 J $g^{-1}$, and carbohydrates equal to 17,600 J $g^{-1}$. For these measurements, indigestible fractions of lipid, protein, and carbohydrates were assumed to be 15%, 10%, and 60%, respectively based on Sklan et al. (2004).

*Thermal environment*

The thermal environment experienced by UCSF subyearlings from late June through late September 2011 and 2012 was estimated from daily measurements of SST collected by four buoys in coastal waters from the mouth of the Columbia River to Grays Harbor, Washington. The buoys were station 46243 (Clatsop Spit, Oregon; 46°12' N, 124°7' W), station 46029 (Columbia River Bar 20 nautical miles west of Columbia River Mouth; 46°9' N, 124°30' W), station 46248 (Astoria Canyon, Oregon; 46°8' N, 124°38' W), and station 46211 (Grays Harbor, Washington; 46°51' N, 124°14' W), and data were obtained from the National Data Buoy Center (http://www.ndbc.noaa.gov/). Daily averages from the four stations were compiled for input into the bioenergetics model (Appendix Fig B1). We assumed that surface waters reflected the thermal environment experienced by subyearlings in the coastal ocean even though juvenile salmon may migrate vertically into cooler water during part of the day (Emmett et al. 2004). To further investigate this issue, we compared buoy data with surface (1 m) and vertically-integrated (1 to 15 m) temperatures measured *in situ* with a Seabird SBE 25 conductivity, temperature, and depth (CTD) profiler at 13 stations sampled 81 times along the Columbia River and Willapa Bay transects from June – September 2011 and 2012. We found that the average difference between CTD and buoy SST was 0.3 °C, indicating strong coherence between these two datasets. We also found that on average, surface temperatures were 1.5 °C warmer than the vertically integrated temperatures. However, given that temperature-dependent growth varies little within the range of temperatures we measured (9.9 – 15.9 °C; Beauchamp 2009), we considered these differences to be negligible.

*Bioenergetics models*

Bioenergetics model simulations to estimate consumption and feeding rate in field-caught salmon were run from June – July, July – August, and August – September of each year. For each period, we relied on empirical measurements of growth, diet proportions, diet energy densities, and temperature to calculate total consumption (g), average daily consumption (g $d^{-1}$, J $d^{-1}$, and % BW $d^{-1}$), and feeding rate (proportion [*p*] of the maximum theoretical daily consumption rate [$C_{max}$]). Aggregate diet energy densities were calculated for each month by multiplying diet proportions with prey energy densities and indigestible fractions summed across all prey types. The number of crab larvae and anchovy consumed per day was calculated by dividing average daily consumption (g $d^{-1}$) of these prey types by their average mass. Average mass was determined from 66 field-caught crab larvae and 557 anchovy collected from July – September 2011 and 2012.

To evaluate the effects of piscivory on juvenile Chinook salmon growth, we compared specific growth rates, biomass of potential prey, diet energy densities, diet proportions, and feeding rates during periods when fish comprised ≥50% of the diet (August – September 2011 and July – August 2012) with periods when subyearlings fed mostly on invertebrates (June – July 2011 and 2012, July – August 2011, and August – September 2012) using one-way ANOVA. For these comparisons, prey biomass data were ln-transformed and all other proportions were arcsine square root transformed prior to analysis.

To quantify the effects of diet energy density, feeding rate, and temperature on subyearling Chinook salmon growth, we conducted a sensitivity analysis constrained by

field observations made in 2011 and 2012. Across years, we determined minimum, average, and maximum diet energy densities (2,894, 3,257, and 3,394 J $g^{-1}$), feeding rates (44%, 66%, and 92% of $C_{max}$), and temperatures (9.9, 13.6, and 15.9 °C), then ran 135 four-week simulations of growth in UCSF subyearlings with starting masses of 5, 10, 15, 20, and 25 g, by changing one variable across the range at a time. The starting weights represented the observed range in salmon mass upon ocean entry from June through August. Across simulations, minimum and maximum values corresponded with a decrease (increase) in diet energy density of 11% (4%), feeding rate of 33% (39%), and temperature of 27% (17%) relative to average conditions.

We expected that initial mass may have an effect on specific growth rate. To test for this, we compared percent change in growth relative to average conditions by mass across all simulations using one-way ANOVA. Next, to determine if increasing or decreasing diet energy density, feeding rate, and temperature to maximum and minimum values had an effect on growth relative to average conditions, we used one-sample t-tests to evaluate if the percent change in growth varied significantly from zero. Finally, to determine which factor contributed most to growth rate variability, we used ANOVA followed by Tukey post-hoc tests to compare growth responses at the maximum and minimum values for diet energy density, feeding rate, and temperature. For this analysis, we included all size classes and arcsine square root transformed the growth data.

## RESULTS

### *Evaluation of bioenergetics model*

Subyearling Chinook salmon from the UCSF group increased in mass in the laboratory from an average of 9.8 g in June to 21.8 g in September (Fig 4.3a). There were no significant differences between the average mass of PIT-tagged fish and the average mass of all fish in the tank over the course of the experiment (ANOVA, $F = 0.003$, $p = 0.96$). Therefore, we used the average mass of all fish measured each month to calculate growth. Specific growth rates (g, % BW $d^{-1}$) increased from 0.85 to 1.14 over the three months. When fit to growth, the bioenergetics model overestimated consumption by 13.2 ± 0.8% SE if adult values were used to estimate salmon energy density. Model error was only 0.70 ± 0.8% SE using juvenile values. Error in consumption was significantly higher (ANOVA, $F = 27.64$ $p = 0.006$) using the adult method compared to the juvenile method. When fit to consumption, growth was underestimated by 5.7 ± 0.3% SE if adult values were used to estimate salmon energy density, whereas growth was only underestimated by 0.4 ± 0.3% SE using juvenile values. Error in growth using the adult method was also significantly (ANOVA, $F = 19.9$ $p = 0.01$) greater than error using the juvenile method. Given that model error was <1% for both growth and consumption based on the juvenile salmon energy density estimates, we used the juvenile method for all further simulations.

*Field data*

Individual size variation of UCSF subyearling Chinook salmon sampled in the field in 2011 and 2012 was high, ranging from 4.9 g in June to 118.8 g in September (Fig 4.3b–c), yielding mean specific growth rates that varied from 0.97 to 3.22% BW $d^{-1}$ among months (Table 4.1). Although variable, similar growth estimates (0.90 to 2.60% BW $d^{-1}$) were found in UCSF subyearlings using otoliths from 1998 – 2008 (Miller et al.

2013) and from 2010 – 2011 (Claiborne et al. 2014). Growth was significantly faster (ANOVA $F = 8.0$ $p = 0.049$) from August to September 2011 (3.22% BW $d^{-1}$) and July to August 2012 (2.43% BW $d^{-1}$), when salmon were piscivorous compared to when they fed mostly on invertebrates (Fig 4.4a). Prey biomass was >350 µg $m^{-3}$ during periods of piscivory and was also significantly higher (ANOVA $F = 7.3$, $p = 0.05$) compared to months when salmon consumed mostly invertebrates (Fig 4.4b). Anchovy comprised >97% of the total prey biomass when growth was fastest (Litz et al. in press).

Salmon diets contained significantly (ANOVA $F = 29.3$ $p = 0.01$) more invertebrates by wet mass in July of both years and during August 2011 and September 2012, and significantly (ANOVA $F = 29.1$ $p = 0.01$) more fish in September 2011 and August 2012. The proportion of fish in salmon stomachs varied by year, but was highest (≥0.50) in September 2011 and August 2012, and decreased to <0.20 in September 2012, presumably as anchovy became unavailable (Litz et al. in press).

We used stomach content data and prey energy densities to aggregate diet energy densities by month for bioenergetics model simulations. Seasonal and inter-annual variation in prey size and lipid content resulted in differences in prey energy densities, particularly for crab larvae and anchovy. We found crab larvae to be the most energetically dense prey, ranging from 3,295 to 5,027 J $g^{-1}$ and anchovy to be the least energetically dense prey, ranging from 2,345 to 3,257 J $g^{-1}$. Despite this, overall diet energy densities were similar across months and years (2,894 to 3,394 J $g^{-1}$; Fig 4.4c). We found that diet energy densities did not significantly vary (ANOVA, $F = 1.6$, $p = 0.28$) during periods when salmon were mostly piscivorous (fish represented ≥50% of the diet) compared to when they fed mostly on invertebrates, indicating that differences in

growth were probably not due to differences in prey quality, but differences in prey availability.

The thermal environment experienced by UCSF subyearlings ranged from 9.9 to 15.9 °C across years. Within-year variability in SST reflected northwesterly wind patterns typical of the northern California Current in summer when upwelling and relaxation events fluctuate over periods of days to weeks (Hickey and Banas 2003). Juvenile salmon temperature-dependent growth rates tend to vary little within the range of temperatures experienced by salmon in this study (Beauchamp 2009).

*Bioenergetics models*

By fitting bioenergetics models to salmon growth measured in the field from June – July, July – August, and August – September 2011 and 2012, we determined that UCSF subyearlings consumed, on average, between 0.77 and 2.52 g $d^{-1}$, equivalent to 2,814 and 9,071 J $d^{-1}$, and 6.0 and 10.6% BW $d^{-1}$ (Fig 4.4d–f). Feeding rates were significantly higher (ANOVA $F = 16.9$, $p = 0.01$) when salmon were piscivorous, which occurred from August to September 2011 (92% of $C_{max}$), and from July to August 2012 (82% of $C_{max}$; Fig 4.4g), compared to when they were feeding mostly on invertebrates. The lowest feeding rates occurred during July of both years, when salmon consumed mostly amphipods (44 – 49% of diet by wet mass) and fed at rates ≤50% of $C_{max}$. To illustrate the potential difference in foraging costs between feeding on fish compared to invertebrates, model simulations indicated that salmon consumed 1 – 2 anchovy per day when anchovy comprised >30% of diet by wet mass (August – September 2011), and 25

– 26 crab larvae when crab comprised a similar amount of the diet (August – September 2012; Table 4.2).

*Sensitivity analysis*

Simulated specific growth rates varied 18-fold in response to observed variation in feeding rate (min = 44%, average = 66%, max = 92% $C_{max}$), diet energy density (2,894, 3,257, 3,394 J g–1), temperature (9.8, 13.6, 15.9 °C), and starting weight (5 – 25 g) (Fig 4.5). Within simulations, there were no differences in specific growth rates by initial salmon mass (ANOVA, $F = 0.02$, $p = 0.99$). Across simulations, specific growth rates ranged from -0.04 to 4.76% BW $d^{-1}$ (average = 1.75% BW $d^{-1}$). Negative growth (-0.04% BW $d^{-1}$) was only determined from one simulation for salmon with an initial mass of 25 g feeding on the lowest quality diet (2,894 J $g^{-1}$), at the lowest feeding rate (44% of $C_{max}$), and the highest temperature (15.9 °C). Fastest growth (4.76% BW $d^{-1}$) was calculated for salmon with an initial mass of 5 g feeding for 4 weeks on the highest quality prey (3,394 J $g^{-1}$), at the highest feeding rate (92% of $C_{max}$), and average temperature (13.6 °C).

Increasing or decreasing diet energy density, feeding rate, and temperature to the minimum or maximum observed values significantly changed growth rates relative to average conditions (t-tests, $p < 0.01$). The factor that contributed most to growth rate variability across all simulations was feeding rate, and the factor that contributed least was diet energy density (Table 4.3). The percent change in growth relative to average conditions was significantly greater (ANOVA $F = 819.8$, $p < 0.01$) at the maximum feeding rate (42.1% ± 3.0 SE) than at maximum diet energy density or maximum

temperature (Tukey HSD $p < 0.01$). Growth rate change was also significantly lower (ANOVA $F = 52.1$, $p < 0.01$) at the minimum feeding rate (29.7% ± 1.6 SE) compared to minimum diet energy density of minimum temperature (Tukey HSD $p < 0.01$).

## DISCUSSION

Results from two years of field data and bioenergetics model simulations indicate that subyearling Chinook growth during the early marine period is driven most by feeding rate, not prey quality (in terms of energy density) or temperature (given the range observed), and that there appears to be tight coupling between feeding rate and prey availability. The finding that variation in feeding rate results in the most growth variation has previously been reported for subyearlings off Oregon (Marin Jarrin 2012) and in Puget Sound (Gamble 2016), but neither of those studies quantified prey availability. In coastal waters off Washington, we found that anchovy of certain sizes allow subyearlings to achieve high feeding rates, and consequently, high daily consumption rates, when their biomass is high (Litz et al. in press). The dominance of anchovy as a prey species for subyearlings in the northern California Current over multiple years (1998 – 2012) was recently demonstrated (Dale et al. 2017). Anchovy also makes up a large proportion of the adult Chinook diet (Thayer et al. 2014) indicating that the availability of this prey type is important during all life stages.

Growth of UCSF subyearlings was calculated from mean differences between estuary- and ocean-caught individuals, assuming a mean size and date of ocean entry. We identified three potential sources of bias in these growth estimates. First, we did not account for immigration or emigration. Previous work showed that UCSF subyearlings in

the estuary are normally distributed around June and August (Weitkamp et al. 2015), and average estuarine residence times are <1 week (Claiborne et al. 2014), therefore size at capture in the estuary is probably a decent approximation of size at ocean entry. Second, it is possible that our growth estimates included subyearlings that had been in the ocean longer than others, leading to potential growth overestimation. We attempted to minimize this bias by narrowing the spatial range of salmon used in the study to those sampled between the Columbia River and Willapa Bay under the assumption that individuals closest to the river mouth had arrived in the ocean sooner than individuals farther north and south. Subyearlings from the UCSF population sampled in the ocean further north and south from where we sampled (n = 214) and not included in this study, were on average 24 g heavier by September in both years, meaning they could have been in the ocean longer. They also may have been larger because of less competition for food north and south of where we sampled, but we do not have the data to address this hypothesis. Finally, we did not account for size-selective mortality, which, if occurring, could also lead to growth overestimation if smaller individuals were being removed from the population in the ocean at a higher rate. Extensive sampling effort throughout estuarine, nearshore, and offshore habitats at high temporal resolution for multiple stocks of Chinook (tracked via coded wire tags) in four large watersheds of Puget Sound found limited evidence of size-selective mortality over the May – August period (Gamble 2016). In a separate analysis, Claiborne et al. (2014) also found no evidence for size-selective mortality in UCSF subyearlings in coastal waters during the outmigrating years of 2010 and 2011.

Our results found that UCSF subyearlings feeding mostly on anchovy had average ocean growth rates and feeding rates that were 2-fold faster than subyearlings feeding mostly on invertebrates, and piscivorous salmon were consuming prey at >80% of their daily digestive capacity. Piscivorous bull trout (*Salvelinus confluentus*) have been shown to exceed their maximum consumption rates over short periods when fish prey availability is high (Furey et al. 2016), and it has been suggested that binge-feeding on fish prey may be an adaptive response by salmonids to capitalize on patchy prey resources and maximize growth during vulnerable life history phases (Armstrong and Schindler 2011). High feeding rates during prey pulses, and the subsequent increase in growth, may be one way juvenile salmon reduce their vulnerability through smaller size stages, consistent with the "stage-duration" hypothesis, which is the idea that fast-growing fish require less time to transit through stages when they are most vulnerable to predators (Houde 2008).

We expected that the quality of marine fish prey would exceed invertebrate prey but found that anchovy were not a more favorable prey item in terms of energy density than crab larvae and were surprised to see that if invertebrates like crab larvae are abundant enough for subyearlings to feed on at high rates, salmon can achieve the same amount of growth as if feeding on anchovy at a high rate. In Puget Sound, subyearling Chinook salmon grew and survived better in years when they were able to feed on crab larvae at relatively high rates (Gamble 2016). High marine survival (12.5%) of juvenile coho salmon (*O. kisutch*) feeding intensely on crab larvae has also been documented in Southeast Alaska (Weitkamp and Sturdevant 2008). Chinook salmon are generalist predators (Gregory and Northcote 1993), and better understanding of the energetic trade-

offs of pursuing, capturing, handling, and digesting various prey types relative to their overall biomass could help determine whether highly abundant but low quality prey offer more to growth potential than less abundant high quality prey.

Previous results showed that subyearlings may revert back to feeding on invertebrates in fall after becoming mostly piscivorous and that this does not negatively impact growth (Litz et al. in press). In fact, salmon grew at 2.11% BW $d^{-1}$ from August to September 2012 (the third fastest growth rate measured during the study) while feeding mostly on invertebrates after previously feeding on anchovy. The availability of invertebrates as alternative prey may be important for growth and survival during fall and the first winter at sea (Wells et al. 2012; Dale et al. 2017), although few studies have sampled marine diets during this time period. In one instance where data are available in winter, Hertz et al. (in press) found that Chinook salmon supplemented their mostly fish diet by consuming more krill than amphipods during the winter compared to fall, suggesting that the abundance and distribution of krill may be important as a winter prey resource. Alternatively, if overwinter survival of subyearlings depends on a critical size attained by fall, as indicated by the "critical size, critical period" hypothesis (Beamish and Mahnken 2001), perhaps an earlier onset of piscivory offsets future energetic deficits by allowing subyearlings to invest more heavily in growth when fish prey are available.

Adult survival of UCSF subyearlings that entered the ocean in 2011 and 2012 and returned three years later to Priest Rapids Dam was relatively high (>165,000 salmon in each year) compared to the 50-year mean (54,110). High survival of UCSF subyearlings has been shown to be negatively related to September body condition (i.e. subyearlings with lower condition in September survive at higher rates compared to years when

September condition is higher) based on length-weight residuals (Miller et al. 2013). Interestingly, subyearlings also tend to consume proportionally more invertebrates in September during years when survival is higher (Dale et al. 2017). Two explanations have been offered to explain these counterintuitive observations (Miller et al. 2013). First, competition for resources may be greater during years of higher survival, resulting in poorer body condition in September. Second, size selective-mortality may occur in years of poor survival, which are typically warm ocean years when piscivorous predators are abundant (Emmett et al. 2006). We offer a third alternative based on observations from 2011 and 2012 – subyearlings may have higher survival in years when anchovy prey occurs earlier than average. In these years, faster growth through July and August may accelerate fish through a phase when they are most vulnerable to predation, and abundant anchovy could serve as an alternative prey species for other predators and buffer juvenile salmon from predation.

Larval anchovy are typically encountered in our study area from May through October, with peaks in June and July (Auth 2011). During El Niño periods, peak larval anchovy abundance may occur slightly earlier (May), presumably in response to warmer ocean temperatures (Auth et al. 2015). Interestingly, in 2015 and 2016, three years after this study was conducted, larval anchovy and Pacific sardine (*Sardinops sagax*) were reported up to three months earlier than previously (1971 – 2010) observed in this region (Auth, unpublished data). Anomalous ocean conditions were observed in the North Pacific throughout 2014 and 2015, with unprecedented warming of surface waters due to a resilient ridge of high pressure that led to SST anomalies that exceeded three standard

deviations (~3 °C), followed by a large El Niño (Bond et al. 2015; Di Lorenzo and Mantua 2016).

Climate change has the potential to influence interactions between Pacific salmon and their prey in the California Current ecosystem in unpredictable ways (Wainwright and Weitkamp 2013). Advances in the phenology of anchovy, which has been incrementally occurring in the southern California Current at a rate of 3 days per decade (Asch 2015) is one way in which a temporal mismatch between predator and prey develops (Both et al. 2009; Yang et al. 2009). Warmer temperatures are likely to affect the composition and distributional range of predators and prey, and increased acidification and hypoxia are likely to impact vital rates of other prey species including crustaceans, calcifying pteropods, and benthic amphipods. Biological productivity may increase but be delayed based on projections on the delayed timing and increased intensity of upwelling as a result of climate change (Rykaczewski et al. 2015), and this may impact prey availability and prey transport into or away from shelf waters where salmon typically feed. Continued monitoring of the prey field is one way to better understand mechanistic links between oceanographic variability and prey availability and make predictions about future prey fields and their impacts on salmon growth and survival.

Changes in the timing of available prey may affect some stocks that leave freshwater at later dates than other stocks and ultimately affect their marine survival (Chittenden et al. 2010). For example, earlier spawning by anchovy may lead to temporal mismatches that are greater for subyearlings than yearling salmon because subyearlings migrate to sea later and at a smaller size than yearlings (Weitkamp et al. 2015). There

may be hatchery/wild differences as well, as it has been shown that hatchery subyearlings may have higher mortality than natural fish (Claiborne et al. 2014). Smaller piscivorous fish may delay the switch to piscivory because they are gape-limited (Juanes 1994), and if anchovy spawn earlier, and are a larger size when salmon first encounter them in the ocean, smaller fish may be more gape-limited than larger, earlier migrating fish.

Our analysis determined that the Wisconsin bioenergetics model, when salmon energy densities were corrected to reflect more reasonable juvenile values, accurately predicted growth and consumption of subyearling Chinook salmon reared at low rations in the laboratory with less than one percent error. This result highlights the importance of validating bioenergetics models in the laboratory prior to applying them to field observations, and for using caution when borrowing bioenergetics parameters from other species or life history stages (Hansen et al. 1993; Ney 1993; Chipps and Wahl 2008). Mathematical errors stemming from incorrect estimates of fish energy density have been recognized in bioenergetics models for some time (Trudel et al. 2005; Madenjian et al. 2012; Canale and Breck 2013), especially for juvenile Chinook salmon, whose oxygen consumption rates likely differ from adults (Trudel and Welch 2005). Differences in activity may also result from differences in oceanographic currents among years, which could influence ocean growth and migration rates (Burke et al. 2016). Laboratory validation may help to identify systematic error in bioenergetics models, even though consumption rates and activity may differ considerably between the laboratory and the field (Madenjian et al. 2004).

Results from multiple bioenergetics modeling studies on the feeding ecology and growth of Chinook salmon, from Southeast Alaska (Weitkamp 2004), to the central coast

of California (MacFarlane 2010), including different parts of the Salish Sea (Gamble 2016), surf zones and estuaries in Oregon (Marin Jarrin 2012), and coastal waters of the Pacific Northwest (Brodeur et al. 1992; Beauchamp 2009), consistently point towards the importance of high prey availability and high feeding rates for salmon growth and survival across a wide range of temperatures, especially for subyearlings. We found fastest growth occurred when feeding rates on anchovy were highest. Our results contribute to a broader knowledge base on the foraging plasticity of subyearling Chinook salmon that is emerging from work examining energy dynamics during early marine residence across ecosystems. Dominant prey types may vary seasonally, inter-annually, and across different ecosystems, but if the feeding rate on that prey type is high enough, subyearling growth rates should increase.

There are key opportunities to address the limited information on prey densities and predator feeding levels in the field. In the coastal marine waters of the northern California Current examined by this study, anchovy appears to be the dominant prey type. In British Columbia, Pacific herring (*Clupea pallasii*) appears to be the dominant forage (Hertz et al. 2015), whereas for Puget Sound and Southeast Alaska, crab larvae seem particularly important, at least during the early marine phase. Young-of-the-year rockfish (*Sebastes* spp.), crab larvae, and krill dominate the prey field in central California (Wells et al. 2016). Synchronized sampling of juvenile salmon and their prey relative to ocean conditions is required to better understand relationships between size and timing of freshwater emigration and prey availability, so that we may better predict early marine growth and survival.

ACKNOWLEDGEMENTS

This work would not have been possible without support from the U.S. National Marine Fisheries Service, the Bonneville Power Administration, and the NOAA Educational Partnership Program Graduate Research and Training Scholarship Program. Chinook salmon used in this study came from Priest Rapids Hatchery, operated by the Washington Department of Fish and Wildlife with funds from Grant County Public Utility District and the U.S. Army Corps of Engineers. Field and laboratory samples were processed with help from A. Claiborne, T. Britt, T. Auth, E. A. Hill, C. Barceló, J. Porquez, A. Barry, L. Tomaro, T. Murphy, E. Fedewa, D. Teel, D. Kuligowski, J. McKay, A. Sremba, K. Klink, and the captain and crew of the *F/V* Miss Sue. This study was conducted with approval from Oregon State University's Institutional Animal Care and Use Committee under Animal Care and Use Protocol 4430.

LITERATURE CITED

Armstrong JB and Schindler DE (2011) Excess digestive capacity in predators reflects a life of feast and famine. Nature 476, 84–87.

Asch RG (2015) Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. Proc Nat Acad Sci USA112, E4065–E4074.

Auth TD (2011) Analysis of the spring-fall epipelagic ichthyoplankton community in the northern California Current in 2004-2009 and its relation to environmental factors. Calif Coop Oceanic Fish Invest Rep 52, 148–167.

Auth TD, Brodeur RD, Peterson JO (2015) Anomalous ichthyoplankton distributions and concentrations in the northern California Current during the 2010 El Niño and La Niña events. Prog Oceanogr 137, 103–120.

Beamish RJ, Mahnken C (2001) A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog Oceanogr 49, 423–437.

Beauchamp DA, Cross AD, Armstrong JL, Myers KW, Moss JH, Boldt JL, Haldorson LJ (2007) Bioenergetic responses by Pacific salmon to climate change and ecosystem variation N Pac Anadr Fish Comm Bull 4, 247–269.

Beauchamp DA (2009) Bioenergetic ontogeny: linking climate and mass-specific feeding to life-cycle growth and survival of salmon Am Fish Soc Symp 70, 1–19.

Boldt JL, Haldorson LJ (2002) A bioenergetics approach to estimating consumption of zooplankton by juvenile pink salmon in Prince William Sound, Alaska. Alaska Fish Res Bull 9, 111–127.

Bond NA, Cronin MF, Freeland, H, Mantua N (2015) Causes and Impacts of the 2014 Warm Anomaly in the NE Pacific. Geophys Res Lett 42, 3414–3420.

Both C, van Asch M, Bijlsma RG, Burg Van Den AB, Visser ME (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptions? J Anim Ecol 78, 73–83.

Brodeur RD (1991) Ontogenetic variations in the type and size of prey consumed by juvenile coho, *Oncorhynchus kisutch*, and chinook, *O. tshawytscha*, salmon. Environ Biol Fish 30, 303–315.

Brodeur RD, Francis RC, Pearcy WG (1992) Food consumption of juvenile coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) on the continental shelf off Washington and Oregon. Can J Fish Aquat Sci 49, 1670–1685.

Brodeur RD, Daly EA, Sturdevant MV, Miller TW, Moss JH, Thiess ME, Trudel M, Weitkamp LA, Armstrong J, Norton EC (2007) Regional comparisons of juvenile salmon feeding in coastal marine waters off the west coast of North America. In Grimes CB, Brodeur RD, Haldorson LJ, McKinnell SM (eds) The Ecology of Juvenile Salmon in the Northeast Pacific Ocean: Regional Comparisons. American Fisheries Society, Bethesda, pp 183–203.

Burke BJ, Peterson WT, Beckman BR, Morgan CA, Daly EA, Litz MNC (2013) Multivariate models of adult Pacific salmon returns. PLoS ONE 8(1), e54134.

Burke BJ, Anderson JJ, Miller JA, Tomaro L, Teel DJ, Banas NS, Baptista AM (2016) Estimating behavior in a black box: how coastal oceanographic dynamics influence yearling Chinook salmon marine growth and migration behaviors. Environ Biol Fish, 99, 671–686.

Canale RP, Breck JE (2013) Comments on proper (and improper) solutions of bioenergetics equations for modeling fish growth. Aquaculture 404-405, 41–46.

Chipps SR, Wahl DH (2008) Bioenergetics modeling in the 21st century: reviewing new insights and revisiting old constraints. Trans Am Fish Soc 137, 298–313.

Chittenden CM, Jensen JLA, Ewart D, Anderson S, Balfry S, Downey E, Eaves A, Saksia S, Smith B, Vincent S, Welch D, McKinley RS (2010) Recent salmon declines: A result of lost feeding opportunities due to bad timing? PLoS ONE 5(8), e12423.

Claiborne AM, Miller JA, Weitkamp LA, Teel DJ (2014) Evidence for selective mortality in marine environments: the role of fish migration size, timing, and production type Mar Ecol Prog Ser 515:187–202.

Clarke A, Holmes LJ, Gore DJ (1992) Proximate and elemental composition of gelatinous zooplankton from the southern-Ocean. J Exp Mar Biol Ecol 155, 55–68.

Copeman LA, Laurel BJ, Boswell KM, Sremba AL, Klinck K, Heintz RA, Vollenweider JJ, Helser TE, Spencer ML (2016) Ontogenetic and spatial variability in trophic biomarkers of juvenile saffron cod (*Eleginus gracilis*) from the Beaufort, Chukchi and Bering Seas. Polar Biol 39, 1109–1126.

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26, 249-293.

Dale, KE, Daly EA, Brodeur RD (2017) Interannual variability in the feeding and condition of subyearling Chinook salmon off Oregon and Washington in relation to fluctuating ocean conditions. Fish Oceanogr 26, 1–16.

Daly EA, Brodeur RD, Weitkamp LA (2009) Ontogenetic shifts in diets of juvenile and subadult coho and Chinook Salmon in coastal marine waters: Important for marine survival? Trans Am Fish Soc 138:1420–1438.

Daly EA, Auth TA, Brodeur RD, Peterson WT (2013) Winter ichthyoplankton biomass as a predictor of early summer prey fields and survival of juvenile salmon in the northern California Current. Mar Ecol Prog Ser 484, 203–217.

Di Lorenzo E, Mantua M (2016) Multi-year persistence of the 2014/2015 North Pacific marine heatwave. Nat Clim Change 6, 1042–1047.

Doyle TK, Houghton JDR, McDevitt R, Davenport J, Hays G (2007) The energy density of jellyfish: estimates from bomb-calorimetry and proximate-composition. J Exp Mar Biol Ecol 343, 239–252.

Duffy EJ, Beauchamp DA (2011) Rapid growth in the early marine period improves marine survival of Puget Sound Chinook Salmon. Can J Fish Aquat Sci 68:232–240.

Emmett RL, Brodeur RD, Orton PM (2004) The vertical distribution of juvenile salmon

(*Oncorhynchus* spp.) and associated fishes in the Columbia River plume Fish Oceanogr 13, 392–402.

Emmett RL, Krutzikowsky GK, Bentley P (2006) Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998–2003: Relationship to oceanographic conditions, forage fishes, and juvenile salmonids. Prog Oceanogr 68, 1–26.

Fisher JP, Weitkamp LA, Teel DJ, Hinton SA, Trudel M, Morris JFT, Theiss ME, Sweeting RM, Orsi JA, Farley Jr EV (2014) Early ocean dispersal patterns of Columbia River Chinook and Coho Salmon. Trans Am Fish Soc 143, 252–272.

Furey NB, Hinch SG, Mesa MG Beauchamp DA (2016) Piscivorous fish exhibit temperature-influenced binge feeding during an annual prey pulse. J Anim Ecol 85, 1307–1317.

Gamble MM (2016) Size-selective mortality and environmental factors affecting early marine growth during marine life stages of sub-yearling Chinook salmon in Puget Sound, Washington. MS Thesis, University of Washington, Seattle.

Gnaiger E, Bitterlich G (1984) Proximate biochemical composition and caloric content calculated from elemental CHN analysis – a stoichiometric concept. Oecologia 62, 289–298.

Gregory RS, Northcote TG (1993) Surface, planktonic, and benthic foraging by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. Can J Fish Aquat Sci 50, 233–240.

Hansen MJ, Boisclair D, Brandt SB, Hewett SW (1993) Applications of bioenergetics models to fish ecology and management – where do we go from here? Trans Am Fish Soc 122, 1019–1030.

Hanson PC, Johnson TB, Schindler DE, Kitchell JF (1997) Fish Bioenergetics 3.0 for Windows. Center for Limnology, University of Wisconsin-Madison and the University of Wisconsin Sea Grant Institute. WISCU-T-97–001.

Hartt AC (1980) Juvenile salmonids in the oceanic ecosystem—the first critical summer. In McNeil WJ, Himsworth DC (eds) Salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis, pp 25–57.

Hertz E, Trudel M, Brodeur RD, Daly EA, Eisner L, Farley Jr EV, Harding JA, MacFarlane RB, Mazumder S, Moss JH, Murphy JM, Mazumder A (2015) Continental-scale variability in the feeding ecology of juvenile Chinook Salmon along the coastal Northeast Pacific Ocean. Mar Ecol Prog Ser 537, 247–263.

Hertz E, Trudel M, Tucker S Beacham TD, Mazumder A (in press) Overwinter shifts in the feeding ecology of juvenile Chinook salmon. ICES J Mar Sci doi:10.1093/icesjms/fsw140.

Hickey, B.M., Banas, N. 2003. Oceanography of the Pacific Northwest coastal ocean and estuaries with application to coastal ecosystems. Estuaries, 26, 1010–1031.

Hjort J (1914) Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Reun. Cons. Int. Explo. Mer 20, 1–228.

Houde ED (2008) Emerging from Hjort's shadow. J Northw Atl Fish Sci 41, 53–70.

Hunsicker ME, Ciannelli L, Bailey KM, Buckel JA, White JW, Link JS, Essington TE, Gaichas S, Anderson TW, Brodeur RD, Chan KS, Chen K, Englund G, Frank KT, Fritas V, Hixon MA, Hurst T, Johnson DW, Kitchell JF Reese D, Rose GA, Sjodin H, Sydeman WJ, van der Veer HW, Vollset K, Zador S (2011) Functional responses and scaling in predator-prey interactions of marine fishes: contemporary issues and emerging concepts. Ecol Lett 14, 1288–1299.

Iwama GK, Tautz AF (1981) A simple growth model for salmonids in hatcheries. Can J Fish Aquat Sci 38, 649–656.

Juanes F (1994) What determines prey size selectivity in piscivorous fishes? In Stouder DJ, Fresh KL, Feller RJ (eds) Theory and Application in Fish Feeding Ecology. University of South Carolina Press, Columbia, pp 79–100.

Kleiber M (1975) The Fire of Life: An Introduction to Animal Energetics. RE Krieger Publ, Huntington, New York.

Lawson JW, Magalhães AM, Miller EH (1998) Important prey species of marine vertebrate predators in the northwest Atlantic: proximate composition and energy density. Mar Ecol Prog. Ser 164, 13–20.

Lima SL (1998) Nonlethal effects in the ecology of predator-prey interactions. BioScience 48, 25–34.

Litz MNC, Miller JA, Copeman LA, Teel DJ, Weitkamp LA, Daly EA, Claiborne AM (in press) Ontogenetic shifts in diets of juvenile salmon: new insight from stable isotopes and fatty acids. Environ Biol Fish doi:10.1007/s10641-016-0542-5.

MacFarlane RB (2010) Energy dynamics and growth of Chinook Salmon (*Oncorhynchus tshawytscha*) from the Central Valley of California during the estuarine phase and first ocean year. Can J Fish Aquat Sci 67, 1549–1565.

Madenjian CP, O'Connor DV, Cheryak SM, Rediske RR, O'Keefe JP (2004) Evaluation

of a Chinook salmon (*Oncorhynchus tshawytscha*) bioenergetics model. Can J Fish Aquat Sci 61, 627–635.

Madenjian CP, David SR, Pothaven SA (2012) Effects of activity and energy budget balancing algorithm on laboratory performance of a fish bioenergetics model. Trans Am Fish Soc 141, 1328–1337.

Marin Jarrin J (2012) Sandy Beach Surf Zones: What is their Role in the Early Life History of Juvenile Chinook Salmon (*Oncorhynchus tshawytscha*)? PhD Dissertation, Oregon State University, Corvallis.

Miller JA, Teel DJ, Baptista A, Morgan CA (2013) Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook Salmon (*Oncorhynchus tshawytscha*). Can J Fish Aquat Sci 70, 617–629.

Neilson JD, Geen GH (1986) First-year growth rate of Sixes River Chinook salmon as inferred from otoliths: effects on mortality and age at maturity. Trans Am Fish Soc 115, 28–33.

Ney JJ (1993) Bioenergetics modeling today – growing pains on the cutting edge. Trans Am Fish Soc 122, 736–748.

Österblom H, Olsson O, Blencker T, Furness RW (2008) Junk-food in marine ecosystems. Oikos 117, 967–977.

Pearcy WG (1992) Ocean ecology of North Pacific salmonids. Washington Sea Grant Program University of Washington Press, Seattle.

Pearcy WG, McKinnell SM (2007) The ocean ecology of salmon in the northeast Pacific Ocean – an abridged history. In Grimes CB, Brodeur RD, Halderson LJ, McKinnell SM (eds) The Ecology of Juvenile Salmon in the Northeast Pacific Ocean: Regional Comparisons. American Fisheries Society, Bethesda, pp 7–30.

Peterson WT, Fisher JL, Peterson JO, Morgan CA, Burke BJ, Fresh KL (2014) Applied fisheries oceanography: Ecosystem indicators of ocean conditions inform fisheries management in the California Current. Oceanography 27, 80–89.

Plumb JM, Moffitt CM (2015) Re-estimating temperature-dependent consumption parameters in bioenergetics models for juvenile Chinook salmon. Trans Am Fish Soc 144, 323–330.

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org/.

Rykaczewski RR, Dunne JP, Sydeman WJ, García-Reyes M, black BA, Bograd SJ

(2015) Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern boundary currents through the 21st century. Geophys Res Lett 42, 6424–6431.

Schabetsberger R, Morgan CA, Brodeur RD, Potts CL, Peterson WT, Emmett RL (2003) Prey selectivity and diel feeding chronology of juvenile Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Columbia River plume. Fish Oceanogr 12, 523–540.

Scheuerell MD, Zabel RW, Sandford BP (2009) Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhynchus* spp.) J Appl Ecol 46, 983–990.

Schmidt-Nielsen K (1997) Animal Physiology: Adaption and Environment, 4th edition. Cambridge University Press, New York.

Sklan D, Prag T, Lupatsch I (2004) Apparent digestibility coefficients of feed ingredients and their prediction in diets for tilapia *Oreochromis niloticus* × *Oreochromis aureus* (Teleostei, Cichlidae) Aquacult Res 35, 358–364.

Stewart DJ, Ibarra M (1991) Predation and production by salmonine fishes in Lake Michigan, 1978–88. Can J Fish Aquat Sci 48, 909–922.

Steele JH (1991) Can ecological theory cross the land-sea boundary? J Theor Biol 153, 425–436.

Teel DJ, Bottom DL, Hinton SA, Kuligowski DR, McCabe GT, McNatt R, Roegner GC, Stamatiou LA, Simenstad CA (2014) Genetic identification of Chinook salmon in the Columbia River estuary: Stock-specific distributions of juveniles in shallow tidal and freshwater habitats. N Am J Fish Man 34, 621–641.

Teel DJ, Burke BJ, Kuligowski DR, Morgan CA, Van Doornik DM (2015) Genetic identification of Chinook Salmon: stock-specific distributions of juveniles along the Washington and Oregon coasts. Mar Coast Fish 7, 274–300.

Thayer JA, Field JC, Sydeman WJ (2014) Changes in California Chinook salmon diet over the past 50 years: relevance to the recent population crash. Mar Ecol Prog Ser 498, 249–261.

Thornton KW, Lessem AS (1978) A temperature algorithm for modifying biological rates. Trans Am Fish Soc 107, 284–287.

Tomaro LM, Teel DJ, Peterson WT, Miller JA (2012) When is bigger better? Early marine residence of middle and upper Columbia River spring Chinook salmon. Mar Ecol Prog Ser 452, 237−252.

Trudel M, Tucker S, Zamon JE, Morris JFT, Higgs DA, Welch DW (2002) Bioenergetic response of coho salmon to climate change. N Pac Anadr Fish Comm Tech Rep 4, 59–61.

Trudel, M, Welch DW (2005) Modeling the oxygen consumption rates in Pacific salmon and steelhead: model development. Trans Am Fish Soc 134, 1542–1561.

Trudel M, Tucker S, Morris JFT, Higgs DA, Welch DW (2005) Indicators of energetic status in juvenile coho salmon and Chinook salmon N Am J Fish Manage 25, 374–390.

Wainwright TC, Weitkamp LA (2013) Effects of climate change on Oregon Coast coho salmon: Habitat and life-cycle interactions. Northwest Sci, 87, 219–242.

Weitkamp LA (2004) Ocean conditions, marine survival, and performance of juvenile Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in SE Alaska. PhD Dissertation, University of Washington, Seattle.

Weitkamp LA, Sturdevant MV (2008) Food habits and marine survival of juvenile Chinook and coho salmon from marine waters of Southeast Alaska. Fish Oceanogr 17, 380–395.

Weitkamp LA, Teel DJ, Liermann M, Hinton SA, Van Doornik DM, Bentley PJ (2015) Stock-specific size and timing at ocean entry of Columbia River juvenile Chinook Salmon and steelhead: implications for early ocean growth. Mar Coast Fish 7, 370–392.

Wells BK, Santora JA, Field JC, MacFarlane RB, Marinovic BB, Sydeman WJ (2012) Population dynamics of Chinook salmon *Oncorhynchus tshawytscha* relative to prey availability in the central California coastal region. Mar Ecol Prog Ser 457, 125–137.

Wells BK, Santora JA, Schroeder ID, Mantua N, Sydeman WJ, Huff DD, Field JC (2016) Marine ecosystem perspectives on Chinook salmon recruitment: a synthesis of empirical and modeling studies from a California upwelling system. Mar Ecol Prog Ser 552, 271–284.

Woodson LE, Wells BK, Weber PK, MacFarlane RB, Whitman GE, Johnson RC (2013) Size, growth, and origin-dependent mortality of juvenile Chinook salmon *Oncorhynchus tshawytscha* during early ocean residence. Mar Ecol Prog Ser 487, 163–175.

Yang LH, Rudolf VHW (2009) Phenology, ontogeny, and the effects of climate change on the timing of species interactions. Ecol Lett 13, 1–10.

**Figure 4.1** Map of study area where subyearling Chinook salmon (*Oncorhynchus tshawytscha*) and their potential prey were sampled in 2011 and 2012 (estuary = triangles, ocean = circles). Prey samples were collected in the stations indicated by filled circles; temperature data collected at buoys indicated by stars.

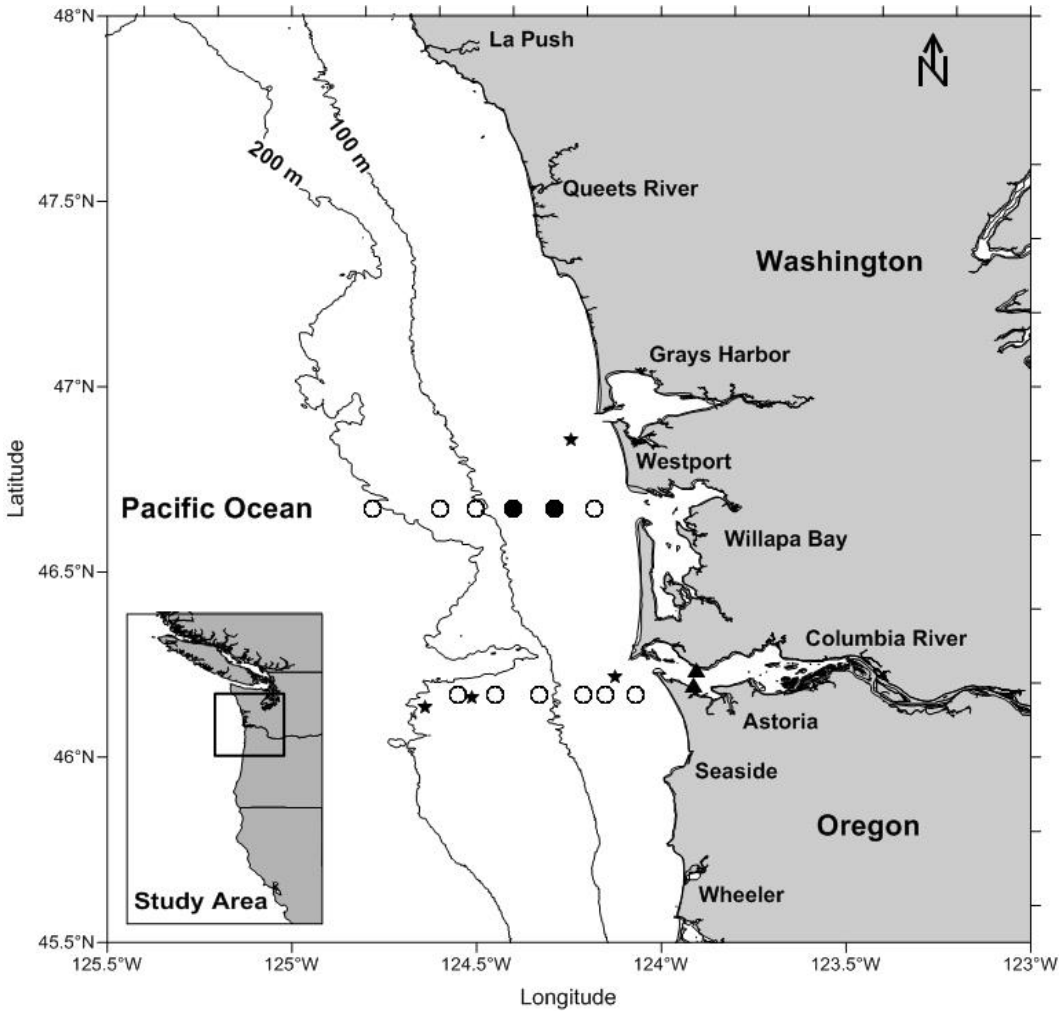


**Figure 4.2** Average diet composition of subyearling Chinook salmon (*Oncorhynchus tshawytscha*) as a proportion of wet mass, with an emphasis on northern anchovy (*Engraulis mordax*). Invertebrates are shown in grayscale; fish categories are in color.

**Figure 4.3** Mass (g) of salmon a) reared in the laboratory from June through September 2013, or captured in the estuary and ocean from June through September in b) 2011 and c) 2012. Colored symbols indicate laboratory fish marked with a passive integrated transponder (PIT) tag. Averages used to calculate growth denoted by solid lines.

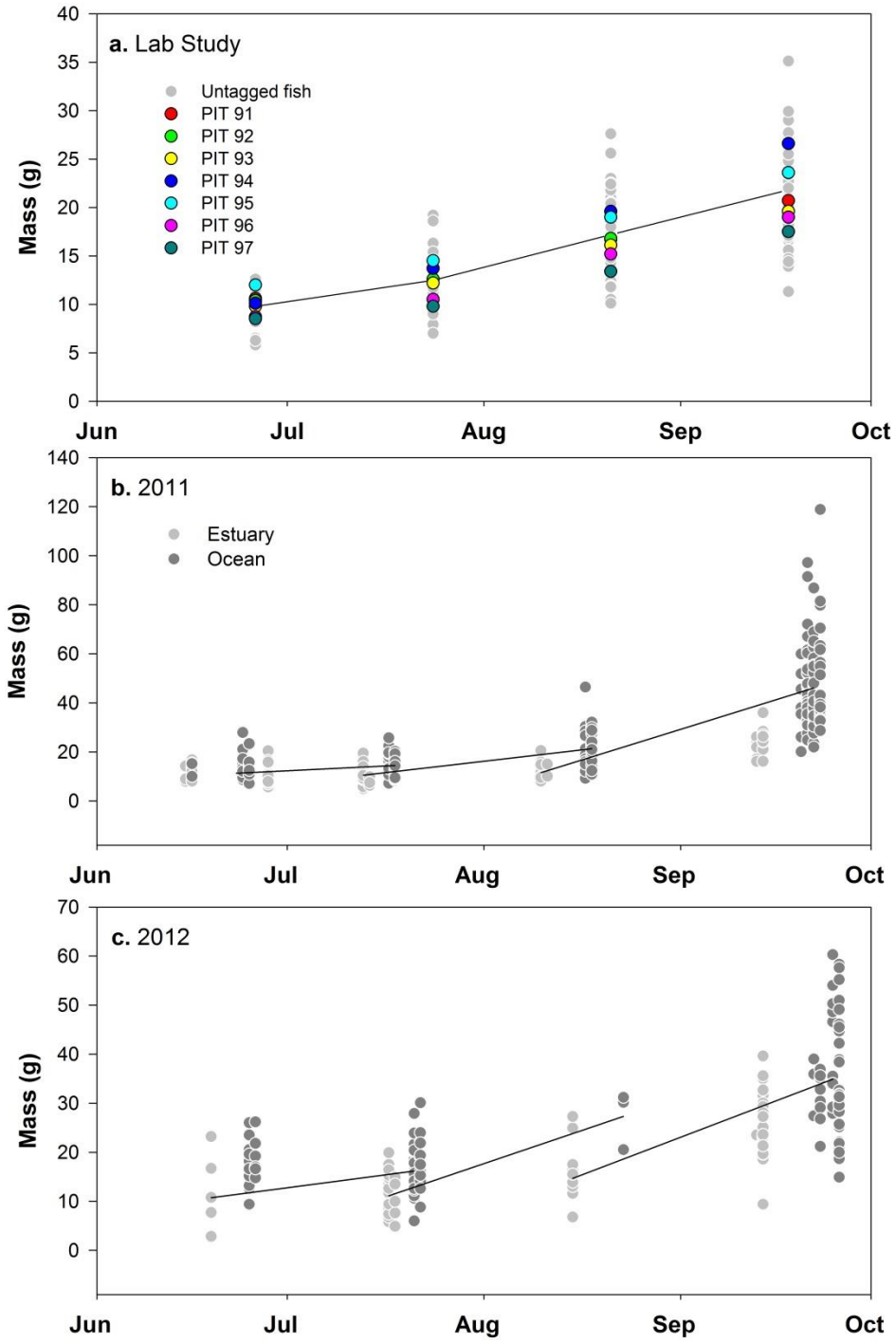


**Figure 4.4** Average a) salmon growth rate, b) prey biomass, c) diet energy density, d–f) consumption, and g) feeding rate of salmon measured for each sampling period of the study.

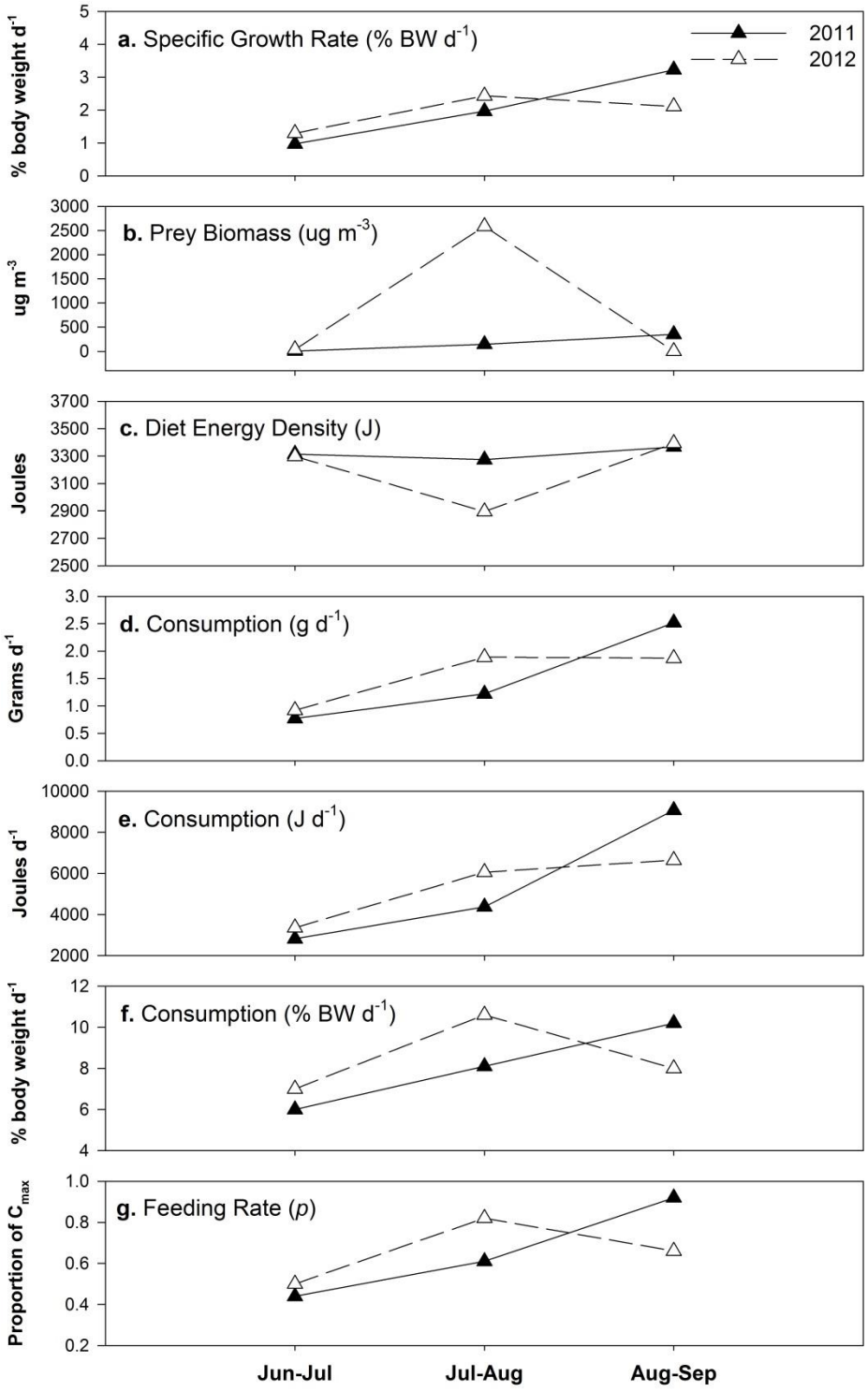


**Figure 4.5** Average (± SD) specific growth rates (SGR; g, % body weight $d^{-1}$) of subyearling Chinook salmon (*Oncorhynchus tshawytscha*) ranging from 5 – 25 g (a – c) feeding at the minimum, average, and maximum observed feeding rates (% of maximum consumption $C_{max}$), diet energy densities (J $g^{-1}$), and temperatures (°C) measured during the field study. Also shown (d – f) is the average percent change in growth relative to average conditions.

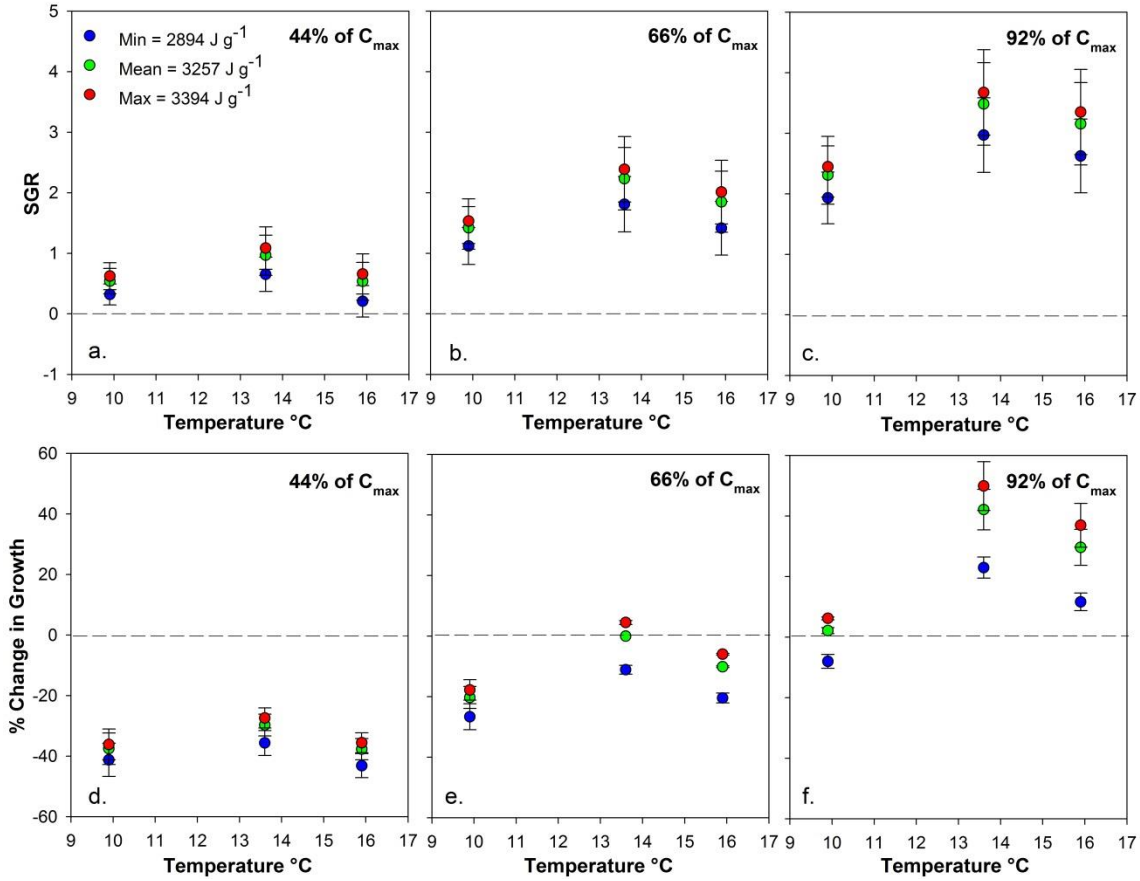


**Table 4.1** Average mass (g) and size range of subyearling Chinook salmon (*Oncorhynchus tshawytscha*) from the upper Columbia summer-fall genetic stock group collected in the lower estuary and ocean. Sample sizes, days before capture in the ocean after ocean entry, and specific growth rate (g, % body weight $d^{-1}$) are also presented.

| | Mass in estuary (g) | n | Mass in ocean (g) | n | Days in ocean | Specific Growth Rate |
|---|---|---|---|---|---|---|
| **2011** | | | | | | |
| Jun-Jul | 11.3 (5.6 – 20.4) | 31 | 14.4 (7.2 – 25.7) | 38 | 25 | 0.97 |
| Jul-Aug | 10.5 (5.0 – 19.5) | 26 | 21.3 (9.1 – 32.1) | 33 | 36 | 1.96 |
| Aug-Sep | 11.5 (7.6 – 20.5) | 30 | 46.0 (20.1 – 118.8) | 98 | 43 | 3.22 |
| **2012** | | | | | | |
| Jun-Jul | 10.7 (2.8 – 23.2) | 6 | 16.2 (6.0 – 30.1) | 48 | 32 | 1.30 |
| Jul-Aug | 11.1 (4.9 – 19.9) | 33 | 27.3 (20.5 – 31.2) | 3 | 37 | 2.43 |
| Aug-Sep | 14.7 (6.8 – 27.3) | 27 | 34.9 (14.9 – 60.3) | 53 | 41 | 2.11 |

**Table 4.2** Diet proportions, sample size, (average ± SD) mass, and amount of northern anchovy (*Engraulis mordax*) and crab larvae (*Metacarcinus magister* and *Cancer* spp.) consumed by subyearling Chinook salmon (*Oncorhynchus tshawytscha*) for each sampling period.

| **Prey Type** | **2011** | | | **2012** | | |
|---|---|---|---|---|---|---|
| | Jun-Jul | Jul-Aug | Aug-Sep | Jun-Jul | Jul-Aug | Aug-Sep |
| *Northern anchovy* | | | | | | |
| Diet proportion | 0 | 0.025 | 0.394 | 0 | 0.254 | 0.034 |
| n = | 0 | 120 | 239 | 97 | 90 | 11 |
| Average mass (g) | 0 | 0.25 ± 0.05 | 0.64 ± 0.45 | 0.15 ± 0.03 | 0.35 ± 0.14 | 0.27 ± 0.21 |
| Consumption (g $d^{-1}$) | 0 | 0.03 ± 0.005 | 0.99 ± 0.29 | 0 | 0.48 ± 0.09 | 0.06 ± 0.01 |
| Consumption (no. $d^{-1}$) | 0 | 0.1 | 1.6 | 0 | 1.4 | 0.2 |
| *Crab larvae* | | | | | | |
| Diet proportion | 0.176 | 0.003 | 0.109 | 0.124 | 0 | 0.329 |
| n = | 47 | 3 | 1 | 14 | 0 | 1 |
| Average mass (g) | 0.04 ± 0.02 | 0.04 ± 0.01 | 0.04 | 0.03 ± 0.05 | 0 | 0.02 |
| Consumption (g $d^{-1}$) | 0.14 ± 0.02 | 0.004 ± 0.001 | 0.27 ± 0.08 | 0.11 ± 0.01 | 0 | 0.61 ± 0.11 |
| Consumption (no. $d^{-1}$) | 3.1 | 0.1 | 3.9 | 3.6 | 0 | 25.6 |

**Table 4.3** Simulated percent change in salmon specific growth rates relative to average conditions when feeding rate, diet energy density, and temperature were increased and decreased to the maximum and minimum observed values throughout two years of field observations in 2011 and 2012. Data represent mean ± SE for fish with starting masses of 5 – 25 g.

| **Model Attribute** | **% Change in Growth Relative to Average at Maximum Value** | **% Change in Growth Relative to Average at Minimum Value** |
|---|---|---|
| Feeding Rate (*p* of $C_{max}$) | 42.1 ± 3.0 | -29.7 ± 1.6 |
| Diet Energy Density (J $g^{-1}$) | 4.5 ± 0.3 | -11.1 ± 0.7 |
| Temperature (° C) | -10.1 ± 0.1 | -20.3 ± 1.6 |

# CHAPTER 5

# GENERAL CONCLUSION

The overall goal of this work was to address a gap in the understanding of predator-prey interactions that impact juvenile Pacific salmon (*Oncorhynchus* spp.) during early marine residence. Specific objectives were to measure prey quantity, prey quality, and environmental conditions throughout the early marine residence period and determine the relative influence of these factors on salmon growth, with implications for future survival. Three studies were conducted to address these objectives – a laboratory rearing experiment to evaluate the effects of dietary fatty acids and fasting on salmon growth, biochemical composition, and swimming speed; a longitudinal field study to measure prey community composition and abundance over two years relative to salmon growth, condition, lipids, and stable isotopes; and a bioenergetics modeling study to evaluate the relative importance of prey quantity, quality, and temperature on salmon growth. A population of subyearling Chinook salmon (*O. tshawytscha*) from the upper Columbia River summer-fall (UCSF) was used as a model species in each study.

The working hypothesis at the onset of the dissertation was that marine fish prey are superior to invertebrate prey for juvenile salmon growth and that differences in prey quality might be related to prey fatty acids. There was also the expectation that the overall abundance of prey might be directly related to salmon growth, although knowledge of seasonal and interannual variability in the prey field was limited. Lastly, there was the expectation that sea surface temperature (SST) has a role in determining

growth rates, both directly by influencing metabolic rates, and indirectly as a proxy for ocean conditions.

Results from this work found that marine prey are superior to invertebrate prey when their biomass is high (>350 µg $m^{-3}$), enabling subyearlings to feed at >80% of their daily theoretical maximum consumption rate and grow quickly (2.43 to 3.22 % body weight $d^{-1}$). However, there was no evidence to suggest that differences in growth rates over time were related to prey energy density or prey fatty acids, specifically ratios of docosahexaenoic and eicosapentaenoic acids (DHA:EPA). Instead, it appears that marine fish prey are bioenergetically favorable for juvenile salmon growth because of the reduced metabolic costs of pursuing, capturing, and digesting larger fish prey as opposed to smaller invertebrates with hard exoskeletons. Prey distributions are often patchy and aggregate in space with varying densities (Holt 1987; Benoit-Bird et al. 2013). It may be that marine fish prey patches are bioenergetically favorable for foraging salmon because they occur at higher densities than invertebrate patches, allowing salmon to feed at high rates and grow quickly.

Salmon metabolic rates are affected by ocean temperatures, with slower growth expected at lower (< 10 °C) and upper (>20 °C) thermal limits (Beauchamp 2009). At the range of temperatures experienced by salmon during the two years of this study (9.9 – 15.9 °C) it was determined that variations in temperature contributed less to growth rate differences than variations in feeding rate. However, warming ocean temperatures as a result of climate change in excess of 16 °C could have negative effects on salmon growth. During warm ocean conditions, the abundance of lipid-rich zooplankton in the northern California Current declines (Peterson et al. 2014), affecting productivity of salmon prey

species like northern anchovy (*Engraulis mordax*; Litz et al. 2008). When ocean temperatures are warm, the effects on salmon growth are twofold – metabolic rates increase and prey abundance decreases. Moreover, abundances of salmon predators are also higher during warm ocean conditions (Emmett et al. 2006; Burke et al. 2013), meaning that predation pressure also increases in a warm ocean, which is unfavorable for salmon production.

This study showed that salmon growth during early marine residence was not affected by dietary levels of the essential fatty acids DHA and EPA. Previous research on rainbow trout (*O. mykiss*) determined that dietary linoleic acid (LA) and α-linolenic acid (ALA) may be the limiting essential fatty acids through early development phases (NRC 2011). Rainbow trout can use ALA to synthesize EPA and DHA (Tocher 2010) and juvenile Chinook salmon may also have this capability. Future research might consider altering dietary ALA concentrations to establish whether this fatty acid has an effect on juvenile salmon growth. The formulated diets used in this study also contained equal amounts (9.4% wet weight) of hatchery food (Otohime Fish Diet®). Removing Otohime Fish Diet® from future diet treatments may improve the ability to detect growth rate differences attributable solely to dietary fish or invertebrate fatty acids.

Fatty acid biomarkers and bulk stable isotopes of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) are being increasingly used to estimate diet sources of fish in the field (Stowasser et al. 2009; Copeman et al. 2016; Giraldo et al. 2016). Despite this, laboratory-derived measurements for the time it takes for fish to reflect dietary fatty acids or isotopes (turnover) are limited, although modeled estimates may perform quite well for stable isotopes (Vander Zanden et al. 2015). Laboratory measurements that compare dietary

values with consumer fatty acid or isotope values (fractionation) are also generally lacking, especially for fatty acids. This work provides important information on the expression of dietary fatty acids and stable isotopes in juvenile Chinook salmon muscle tissue that can be used in the interpretation of field-derived data (Daly et al. 2010; Hertz et al. 2015) and in fatty acid and stable isotope mixing models (Phillips et al. 2014; Galloway et al. 2015). Further efforts to characterize diet from fatty acids or isotopes in other tissue types (fin, blood, liver) may also be useful for addressing research questions where dietary sources over days to weeks may be important (Heady and Moore 2013).

Nitrogen stable isotope ratios ($\delta^{15}N$) are commonly used to estimate the trophic position of a consumer (Post 2002). This is a result of the preferential excretion of the lighter isotope during protein synthesis which enriches the $^{15}N$ of the consumer relative to its diet. A contribution from this work was establishing the ratio of DHA:EPA as complementary biomarker of trophic position in juvenile Chinook salmon, especially for determining the contribution of marine fish prey in salmon diet following an ontogenetic shift in diet to fish prey. Values of $\delta^{15}N$ and DHA:EPA reflected the relative contribution of dietary marine fish fatty acids in the laboratory study (Chapter 2) and $\delta^{15}N$ and DHA:EPA were highly correlated in salmon collected from the field throughout the early marine period when diets shifted gradually from mostly invertebrates to mostly fish (Chapter 3). It would be interesting to validate DHA:EPA as a trophic biomarker of piscivory across a variety of marine piscivores.

Integrating fatty acid and stable isotope data from UCSF subyearlings presented in this work also established other potentially useful dietary biomarkers. The ratio of 16:18 PUFA (polyunsaturated fatty acids containing 16 and 18 carbons) is a biomarker of

marine phytoplankton, and 18:3n-3 + 18:2n-6 (the sum of ALA and LA) is a biomarker of freshwater (nearshore) dietary sources. Because both varied significantly with $\delta^{13}C$ (positively for 16:18 PUFA and negatively for 18:3n-3 + 18:2n-6), these fatty acid biomarkers may be useful as a way to understand ontogenetic shifts in diet that occur with shifts in habitat from freshwater to saltwater in other fish, including catadromous species like eels whose life history migration patterns are opposite to those of salmon. The biochemical signatures of catadromous species transitioning from marine to freshwater would probably display the opposite trends observed in juvenile salmon transitioning from freshwater to the ocean.

Prior to this study, a gap existed in the understanding of seasonal composition and abundance of pelagic micronekton including amphipods, krill, decapod larvae, and age-0 marine fishes that make up the majority of juvenile Chinook and coho (*O. kisutch*) salmon diets (Brodeur et al. 2011). Lack of information on the available prey field resulted in limited appreciation for the interacting effects of prey quantity, prey quality, and environmental variability on salmon growth and survival. Previous observations supported both top-down (predation) and bottom-up (resource) regulation of salmon populations (Beamish and Mahnken 2001; Miller et al. 2013; Hertz et al. 2016), indicating both predation and prey are important for salmon survival. Novel contributions of this work include better awareness of seasonality in the prey field, appreciation for temporal variation in diet, and better mechanistic understanding of the role of prey availability in determining short-term growth rates.

Ocean conditions are considered favorable for salmon growth in the Pacific Northwest when SSTs are cooler than average during the upwelling season in summer, a

condition that is usually accompanied by greater southward alongshore transport, higher primary and secondary productivity rates on the continental shelf, more forage fish species to serve as alternative prey, and fewer piscivorous predators compared to warmer years (Mantua et al. 1997; Emmett et al. 2006; Peterson et al. 2014). This work was conducted during two years of relatively high survival. Future sampling of the prey field would benefit from sampling during a year of poor salmon ocean survival. In a warm year, juvenile salmonids arriving in an unproductive ocean may find low overall abundances and poor lipid quality of marine prey. Because warm ocean conditions may also lead to earlier reproductive timing in some marine species (Asch 2015), the potential for a temporal mismatch between salmon and their prey may also be greater during a poor survival year.

Despite high growth rates (>2.4 % body weight $d^{-1}$) obtained by juvenile salmon during the two years of this study, there were seasonal differences in the timing of peak growth. Peak growth occurred when northern anchovy biomass was highest. It might be expected that during a poor ocean year overall anchovy biomass is reduced. Associations between the Columbia River plume, spawning anchovy, and salmon survival have previously been identified (Richardson 1973; Miller et al. 2013), but more work could be done to better understand positive correlations between anchovy, SST, and fluorescence, and the negative correlation between anchovy and Columbia River plume volume. Because anchovy are clearly an important prey item for subyearlings, better mechanistic understanding of relationships between plume habitat and anchovy spawning timing and recruitment success could lead to better predictions of about seasonal timing of peak anchovy biomass and therefore prey availability for subyearlings.

Bioenergetics modeling of UCSF subyearling growth throughout the early marine period revealed three major insights about salmon energy dynamics and foraging ecology (Chapter 4). The first was that the Wisconsin bioenergetics model tends to overestimate consumption and underestimate growth if predator energy density is not adjusted to reflect juvenile values, because the default model, parameterized for Chinook salmon, is based on adult measurements (Stewart and Ibarra 1991). The second insight was that short-term growth varied most with feeding rate than with prey energy density or temperature within the range of values measured over two years. What this revealed was that the relative importance of variation in prey quantity was greater than variation in prey quality or temperature. The final unexpected insight was that consuming crab larvae could result in growth rates that were comparable to consuming anchovy, suggesting that the ontogenetic shift to piscivory is not a requirement for faster growth.

High prey availability and feeding rates on multiple prey types, including both invertebrates and marine fish, may be ultimately what are determining ocean growth rates of juvenile salmonids. Quantifying the composition and abundance of prey throughout the early marine period (April through October) could be used to estimate how large a population could be supported by the available prey. Longer time series measurements of the prey field could also be useful in documenting impacts of climate change on the composition and phenology of prey resources. Also, measurements of prey on a broader scale (i.e. coastwide throughout the California Current Ecosystem) could be used to determine how spatially homogenous prey are throughout salmon's range. These data could be useful for evaluating potential density-dependent effects where multiple salmonids overlap spatially and temporally, such as in the Columbia River plume.

Understanding the mechanistic linkages between the environment and the prey community is consistent with the objectives of ecosystem-based fisheries management, especially knowledge of forage fish and important trophic interactions (Pikitch et al. 2004).

Mortality during the early life history of fishes may occur disproportionately in smaller or slower growing individuals, a phenomenon known as negative size-selective mortality (Sogard 1997). Evidence for negative size-selection has been demonstrated in some populations of Pacific salmon (Moss et al. 2005; Claiborne et al. 2011; Duffy and Beauchamp 2011) although for subyearling Chinook salmon identifying when and if size-selective mortality occurs has been a challenge (Claiborne et al. 2014; Gamble 2016). For subyearlings, evidence for size-selective mortality during summer is usually only documented in poor survival years (Woodson et al. 2013).

Body condition of UCSF subyearlings in September is an indicator of adult returns (Miller et al. 2013). During high survival years subyearlings in September are in poorer condition and also tend to consume higher proportions of invertebrates (Dale et al. 2017) compared to poor survival years. These results suggest that competition may be greater during high survival years. The relationship between body condition in September and adult returns also suggests that there may be a size (mass) threshold subyearlings must attain prior to the first ocean winter, and growth during early marine residence sets the population up for winter consistent with the "critical size, critical period" hypothesis (Beamish and Mahnken 2001). If growth during the early marine residence period is important for overwinter survival, this work highlights the benefit of following a cohort

throughout the critical period during the first ocean summer to better understand seasonal variation which may be driving larger patterns in growth or survival.

Predation is considered the major source of mortality for juvenile salmon during early marine residence. Better quantitative estimates of salmon predators alongside the prey could help to disentangle the relative effects of competition and predation as drivers of UCSF ocean growth during early ocean residence. This information could be incorporated into salmon management, such as determining optimal hatchery release timing to maximize survival. For example, coordinating hatchery release timing with anchovy spawning might ensure temporal matches between salmon and prey. Releases when major piscivorous predator (fish, birds, marine mammals) abundances are low may also help facilitate early marine survival.

Observations of the prey field and environmental conditions used in this study were collected in years when ecosystem indicators of ocean conditions were considered favorable for juvenile salmon survival (Peterson et al. 2014). Adult returns of subyearlings that entered the ocean from 2011 – 2012 were relatively high (see "Salmon Forecasts" link available from https://www.nwfsc.noaa.gov). Projections for adult survival of salmonids, including yearling Chinook and coho salmon, that entered the ocean in 2014 or later, are not as favorable, in part due to anomalously warm SSTs, intensified upwelling patterns, and greater richness of warm water, lipid-poor copepod species that reflect oceanographic changes that occurred on a basin-scale.

Beginning in late 2013, a resilient ridge of high pressure over the North Pacific altered atmospheric circulation patterns and resulted in SST anomalies that were >3 SD and up to 3 °C higher than average conditions (Bond et al. 2015; DiLorenzo and Mantua

2016). This unprecedented warming of the Northeast Pacific, referred to as a marine heatwave, was followed by one of the largest El Niño's on record. Abundance of winter-spawning (January through March) ichthyoplankton was low in 2014, but high in 2015 and 2016, and related in part to earlier spawning timing of northern anchovy and Pacific sardine (*Sardinops sagax*; Auth, unpublished data). Although salmon production has historically declined in the Pacific Northwest during periods of persistent warming, only to rebound in cooler years (Beamish and Bouillon 1993; Mantua et al. 1997; Meuter et al. 2002), it is unclear how long it will take populations to rebound after these unprecedented conditions.

One of the challenges in fisheries oceanography will be to account for ecosystem changes in a changing climate. It is possible that the SST anomalies and variable upwelling patterns of recent years may not reflect former decadal-scale fluctuations in climate, but may be more representative of future conditions. Recent analyses of an ensemble of coupled ocean-atmosphere models (Rykaczewski et al. 2015) found that upwelling favorable winds will likely intensify during summer as a result of anthropogenic climate change. In addition to an overall warming trend in ocean temperature, increased upwelling is expected to have an effect on coastal ecosystems, such as increased coastal hypoxia, ocean acidification, and eutrophication (Bakun et al. 2015). The research presented in this dissertation illustrates how sampling the abundance, size, and distribution of prey fields for juvenile salmon during ocean residence may help to understand the bottom-up mechanisms affecting the composition, phenology, or distribution of prey resources. Knowledge of seasonality in the prey field and in salmon

early marine growth can lead to better estimates of ecosystem carrying capacity and marine survival, important for sustainable management of this valuable resource.

## LITERATURE CITED

Asch RG (2015) Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. Proc Nat Acad Sci USA112, E4065–E4074.

Bakun A, Black BA, Bograd SJ, García-Reyes, Miller AJ, Rykaczewski RR, Sydeman WJ (2015) Anticipated effects of climate change on coastal upwelling ecosystems. Curr Clim Change Rep 1, 85–93.

Beamish RJ, Bouillon DR (1993) Pacific salmon production trends in relation to climate. Can J Fish Aquat Sci 50, 1002–1016.

Beamish RJ, Mahnken C (2001) A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog Oceanogr 49, 423–437.

Beauchamp DA (2009) Bioenergetic ontogeny: linking climate and mass-specific feeding to life-cycle growth and survival of salmon Am Fish Soc Symp 70, 1–19.

Benoit Bird KJ, Battaile BC, Heppell SA, Hoover B, Irons D, Jones N, Kuletz KJ, Nordstrom CA, Paredes R, Suryan RM, Waluk CM, Trites AW (2013) Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. PLoS ONE 8(1), e53348.

Bond NA, Cronin MF, Freeland, H, Mantua N (2015) Causes and Impacts of the 2014 warm anomaly in the NE Pacific. Geophys Res Lett 42, 3414–3420.

Brodeur RD, Daly EA, Benkwitt CE, Morgan CA, Emmett RL (2011) Catching the prey: sampling juvenile fish and invertebrate prey fields of juvenile coho and Chinook salmon during their early marine residence. Fish Res 108, 65–73.

Burke BJ, Peterson WT, Beckman BR, Morgan CA, Daly EA, Litz MNC (2013) Multivariate models of adult Pacific salmon returns. PLoS ONE 8(1), e54134.

Claiborne AM, Fisher JP, Hayes SA, Emmett RL (2011) Size at release, size-selective mortality, and age of maturity of Willamette River hatchery yearling Chinook Salmon. Trans Am Fish Soc 140, 1135–1144.

Claiborne AM, Miller JA, Weitkamp LA, Teel DJ (2014) Evidence for selective mortality in marine environments: the role of fish migration size, timing, and production type Mar Ecol Prog Ser 515, 187–202.

Copeman LA, Laurel BJ, Boswell KM, Sremba AL, Klinck K, Heintz RA, Vollenweider JJ, Helser TE, Spencer ML (2016) Ontogenetic and spatial variability in trophic biomarkers of juvenile saffron cod (*Eleginus gracilis*) from the Beaufort, Chukchi, and Bering Seas. Polar Biol 39, 1109–1126.

Dale KE, Daly EA, Brodeur RD (2017) Interannual variability in the feeding and condition of subyearling Chinook salmon off Oregon and Washington in relation to fluctuating ocean conditions. Fish Oceanogr 26, 1–16.

Daly EA, Benkwitt CE, Brodeur RD, Litz MNC, Copeman LA (2010) Fatty acid profiles of juvenile salmon indicate prey selection strategies in coastal marine waters. Mar Biol 157, 1975–1987.

Di Lorenzo E, Mantua M (2016) Multi-year persistence of the 2014/2015 North Pacific marine heatwave. Nat Clim Change 6, 1042–1047.

Duffy EJ, Beauchamp DA (2011) Rapid growth in the early marine period improves marine survival of Puget Sound Chinook Salmon. Can J Fish Aquat Sci 68, 232–240.

Emmett RL, Krutzikowsky GK, Bentley P (2006) Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998–2003: Relationship to oceanographic conditions, forage fishes, and juvenile salmonids. Prog Oceanogr 68, 1–26.

Galloway AWE, Brett MT, Holtgrieve GW, Ward EJ, Ballantyne AP, Burns CW, Kainz MJ, Müller-Navarra DC, Persson J, Ravet JL, Strandberg U, Taipale SJ, Alhgren G (2015) A fatty acid based Bayesian approach for inferring diet in aquatic consumers. PLoS ONE 10(6), e0129723.

Gamble MM (2016) Size-selective mortality and environmental factors affecting early marine growth during marine life stages of sub-yearling Chinook salmon in Puget Sound, Washington. MS Thesis, University of Washington, Seattle.

Giraldo C, Stasko A, Choy ES, Rosenberg B, Majewski A, Power M, Swanson H, Loseto L, Reist JD (2016) Trophic variability of Arctic fishes in the Canadian Beaufort Sea: a fatty acids and stable isotopes approach. Polar Biol 39, 1267–1282.

Heady WN, Moore JW (2013) Tissue turnover and stable isotope clocks to quantify resource shifts in anadromous rainbow trout. Oecologia 172, 21–34.

Hertz E, Trudel M, Brodeur RD, Daly EA, Eisner L, Farley Jr EV, Harding JA, MacFarlane RB, Mazumder S, Moss JH, Murphy JM, Mazumder A (2015) Continental-scale variability in the feeding ecology of juvenile Chinook Salmon along the coastal Northeast Pacific Ocean. Mar Ecol Prog Ser 537, 247–263.

Hertz E, Trudel M, Tucker S, Beacham TD, Parken C, Mackas D, Mazumder A (2016) Influences of ocean conditions and feeding ecology on the survival of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Fish Oceanogr 25, 407–419.

Holt RD (1987) Prey communities in patchy environments. Oikos 50, 276–290.

Litz MNC, Emmett RL, Heppell SS, Brodeur RD (2008) Ecology and distribution of the northern subpopulation of northern anchovy (*Engraulis mordax*) off the U.S. west coast. Calif Coop Ocean Fish Invest Rep 49, 167–182.

Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. Bull Am Meteorol Soc 78, 1069–1079.

Meuter FJ, Peterman RM, Pyper BJ (2002) Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. Can J Fish Aquat Sci 59, 456–463.

Miller JA, Teel DJ, Baptista A, Morgan CA (2013) Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook salmon (*Oncorhynchus tshawytscha*). Can J Fish Aquat Sci 70, 617–629.

Moss JH, Beauchamp DA, Cross AD, Myers KW, Farley EV Jr, Murphy JM, Helle JH (2005) Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. Trans Am Fish Soc 134, 1313–1322.

National Research Council (NRC) (2011) Nutrient Requirements of Fish and Shrimp. The National Academies Press, Washington DC.

Peterson WT, Fisher JL, Peterson JO, Morgan CA, Burke BJ, Fresh KL (2014) Applied fisheries oceanography: Ecosystem indicators of ocean conditions inform fisheries management in the California Current. Oceanography 27, 80–89.

Phillips DL, Inger R, Bearhop S, Jackson AL, Moore JW, Parnell AC, Semmens BX, Ward EJ (2014) Best practices for use of stable isotope mixing models in food-web studies. Can J Fish Aquat Sci 92, 823–835.

Pikitch EK, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO, Dayton P, Doukakis P, Fluharty D, Heneman B, Houde ED, Link J, Livingston PA, Mangel M,

McAllister MK, Pope J Sainsbury KJ (2004) Ecosystem-based fishery management. Science 305, 346–347.

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703–718.

Richardson S (1973) Abundance and distribution of larval fishes in waters off Oregon, May-October 1969, with special emphasis on the northern anchovy, *Engraulis mordax*. Fish Bull 71, 697–711.

Rykaczewski RR, Dunne JP, Sydeman WJ, García-Reyes M, black BA, Bograd SJ (2015) Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern boundary currents through the 21st century. Geophys Res Lett 42, 6424–6431.

Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull Mar Sci 60, 1129–1157.

Stewart DJ, Ibarra M (1991) Predation and production by salmonine fishes in Lake Michigan, 1978–88. Can J Fish Aquat Sci 48, 909–922.

Stowasser G, McAllen R, Pierce GJ, Collins MA, Moffat CF, Priede IG, Pond DW (2009) Trophic position of deep-sea fish – Assessment through fatty acid and stable isotope analyses. Deep-Sea Res Pt I 56, 812–826.

Tocher DR (2010) Fatty acid requirements in ontogeny of marine and freshwater fish. Aquacult Res 41, 717–732.

Vander Zanden MJ, Clayton MK, Moody EK, Solomon CT, Weidel BC (2015) Stable isotope turnover and half-life in animal tissues: a literature synthesis. PLoS ONE 10(1), e0116182.

Woodson LE, Wells BK, Weber PK, MacFarlane RB, Whitman GE, Johnson RC (2013) Size, growth, and origin-dependent mortality of juvenile Chinook salmon *Oncorhynchus tshawytscha* during early ocean residence. Mar Ecol Prog Ser 487, 163–175.

# BIBLIOGRAPHY

Ackman RG, Tocher CS, McLachlan J (1968) Marine phytoplankter fatty acids. J Fish Res Board Can 25, 1603–1620.

Ainley DG, Dugger KD, Ford RG, Pierce SD, Reese DC, Brodeur RD, Tynan CT, Barth JA (2009) Association of predators and prey at frontal features in the California Current: competition, facilitation, and co-occurrence. Mar Ecol Prog Ser 389, 271–294.

Allen D, Rosenfeld J, Richards J (2016) Physiological basis of metabolic trade-offs between growth and performance among different strains of rainbow trout. Can J Fish Aquat Sci 73, 1493–1506.

Alverson DL (1992) A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): The conflict arena. Rev Aquat Sci 6, 203–256.

Anderson JT (1988) A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J Northw Atl Fish Sci 8, 55–66.

Anderson, JJ, Gurarie, E, Bracis, C, Burke, BJ, Laidre, KL (2013) Modeling climate change impacts on phenology and population dynamics of migratory marine species. Ecol Model 264, 83–97.

Anthony JA, Roby DD, Turco KR (2000) Lipid content and energy density of forage fishes from the northern Gulf of Alaska. J Exp Mar Biol Ecol 248, 53–78.

Armstrong JB and Schindler DE (2011) Excess digestive capacity in predators reflects a life of feast and famine. Nature 476, 84–87.

Arts MT, Brett MT, Kainz MJ (2009) Lipids in aquatic ecosystems. Springer, New York.

Asch RG (2015) Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. Proc Nat Acad Sci USA112, E4065–E4074.

Auth TD (2011) Analysis of the spring-fall epipelagic ichthyoplankton community in the northern California Current in 2004-2009 and its relation to environmental factors. Calif Coop Oceanic Fish Invest Rep 52, 148–167.

Auth TD, Brodeur RD, Peterson JO (2015) Anomalous ichthyoplankton distributions and concentrations in the northern California Current during the 2010 El Niño and La Niña events. Prog Oceanogr 137, 103–120.

Bakun A, Black BA, Bograd SJ, García-Reyes, Miller AJ, Rykaczewski RR, Sydeman WJ (2015) Anticipated effects of climate change on coastal upwelling ecosystems. Curr Clim Change Rep 1, 85–93.

Beamish RJ, Bouillon DR (1993) Pacific salmon production trends in relation to climate. Can J Fish Aquat Sci 50, 1002–1016.

Beamish RJ, Mahnken C (2001) A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog Oceanogr 49, 423–437.

Beamish RJ, Poier KL, Mahnken C (2001) Evidence of the validity of the critical size and critical period hypothesis. N Pac Anadr Fish Comm 564, 1–16.

Beamish RJ, Sweeting RM, Neville CM (2004) Improvement of juvenile Pacific salmon production in a regional ecosystem after the 1998 climatic regime shift. Trans Am Fish Soc 133, 1163–1175.

Beauchamp DA, Cross AD, Armstrong JL, Myers KW, Moss JH, Boldt JL, Haldorson LJ (2007) Bioenergetic responses by Pacific salmon to climate change and ecosystem variation. N Pac Anadr Fish Comm Bull 4, 247–269.

Beauchamp DA (2009) Bioenergetic ontogeny: linking climate and mass-specific feeding to life-cycle growth and survival of salmon. Am Fish Soc Symp 70, 1–19.

Bell WH, Terhune DB (1970) Water tunnel design for fisheries research. Fish Res Bd Can Tech Rep 195. Fisheries Research Board of Canada, Nanaimo.

Bell MV, Batty RS, Dick JR, Fretwell K, Navarro JC, Sargent JR (1995) Dietary deficiency of docosahexaenoic acid impairs vision at low light intensities in juvenile herring (*Clupea harengus* L.). Lipids 30, 443–449.

Benoit Bird KJ, Battaile BC, Heppell SA, Hoover B, Irons D, Jones N, Kuletz KJ, Nordstrom CA, Paredes R, Suryan RM, Waluk CM, Trites AW (2013) Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. PLoS ONE 8(1), e53348.

Berryman AA (1992) The origins and evolution of predator-prey theory. Ecology 73, 1530–1535.

Boldt JL, Haldorson LJ (2002) A bioenergetics approach to estimating consumption of zooplankton by juvenile pink salmon in Prince William Sound, Alaska. Alaska Fish Res Bull 9, 111–127.

Bond NA, Cronin MF, Freeland, H, Mantua N (2015) Causes and Impacts of the 2014 Warm Anomaly in the NE Pacific. Geophys Res Lett 42, 3414–3420.

Both C, van Asch M, Bijlsma RG, Burg Van Den AB, Visser ME (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptions? J

Anim Ecol 78, 73–83.

Brett JR (1964) The respiratory metabolism and swimming performance of young sockeye salmon. J Fish Res Bd Can 21, 1183–1226.

Brodeur RD (1991) Ontogenetic variations in the type and size of prey consumed by juvenile coho, *Oncorhynchus kisutch*, and chinook, *O. tshawytscha*, salmon. Environ Biol Fish 30, 303–315.

Brodeur RD, Francis RC, Pearcy WG (1992) Food consumption of juvenile coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) on the continental shelf off Washington and Oregon. Can J Fish Aquat Sci 49, 1670–1685.

Brodeur RD, Fisher JP, Teel DJ, Emmett RL, Casillas E, Miller TW (2004) Juvenile salmonid distribution, growth, condition, origin, environmental and species associations in the northern California Current. Fish Bull 102, 25–46.

Brodeur RD, Fisher JP, Emmett RL, Morgan CA, Casillas E (2005) Species composition and community structure of pelagic nekton off Oregon and Washington under variable conditions. Mar Ecol Prog Ser 298, 41–57.

Brodeur RD, Daly EA, Sturdevant MV, Miller TW, Moss JH, Thiess ME, Trudel M, Weitkamp LA, Armstrong J, Norton EC (2007) Regional comparisons of juvenile salmon feeding in coastal marine waters off the west coast of North America. In Grimes CB, Brodeur RD, Haldorson LJ, McKinnell SM (eds) The Ecology of Juvenile Salmon in the Northeast Pacific Ocean: Regional Comparisons. American Fisheries Society, Bethesda, pp 183–203.

Brodeur RD, Daly EA, Benkwitt CE, Morgan CA, Emmett RL (2011) Catching the prey: sampling juvenile fish and invertebrate prey fields of juvenile coho and Chinook Salmon during their early marine residence. Fish Res 108, 65–73.

Brodeur RD, Morgan CA (2016) Influence of a coastal riverine plume on the cross-shelf variability in hydrography, zooplankton, and juvenile salmon diets. Estuar Coasts 39, 1183–1198.

Budge SM, Parrish CC (1998) Lipid biogeochemistry of plankton, settling matter, and sediments in Trinity Bay, Newfoundland. II. Fatty acids. Org Geochem 29, 1547–1559.

Budge SM, Iverson SJ, Bowen WD, Ackman RG (2002) Among and within species variability in fatty acid signatures of marine fish and invertebrates on the Scotian Shelf, Georges Bank and southern Gulf of St. Lawrence. Can J Fish Aquat Sci 59, 886–898.

Budge SM, Iverson SJ, Koopman HN (2006) Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. Mar Mam Sci 22, 759–801.

Budge SM, Wooller MJ, Springer AM, Iverson SJ, McRoy CP, Divorky J (2008) Tracing carbon flow in an Arctic marine food web using fatty acid-stable isotope analysis. Oecologia 157, 117–129.

Budge SM, Penney SN, Lall SP (2011) Response of tissue lipids to diet variation in Atlantic salmon (*Salmo salar*): Implications for estimating diets with fatty acid analysis. J Exp Mar Bio Ecol 409, 267–274.

Burke BJ, Peterson WT, Beckman BR, Morgan CA, Daly EA, Litz MNC (2013) Multivariate models of adult Pacific salmon returns. PLoS ONE 8(1), e54134.

Burke BJ, Anderson JJ, Miller JA, Tomaro L, Teel DJ, Banas NS, Baptista AM (2016) Estimating behavior in a black box: how coastal oceanographic dynamics influence yearling Chinook salmon marine growth and migration behaviors. Environ Biol Fish, 99, 671–686.

Burkhardt S, Riebesell U, Zondervan I (1999). Effects of growth rate, $CO_2$ concentration, and cell size on the stable carbon isotope fractionation in marine phytoplankton. Geochim Cosmochim Acta 63, 3729–3741.

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.

Canale RP, Breck JE (2013) Comments on proper (and improper) solutions of bioenergetics equations for modeling fish growth. Aquaculture 404-405, 41–46.

Carlton JT (ed) (2007) The Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon. Fourth Edition. University of California Press, Berkeley.

Charnov EL (1976) Optimal foraging: The marginal value theorem. Theor Popul Biol 9, 129–136.

Chipps SR, Wahl DH (2008) Bioenergetics modeling in the 21st century: reviewing new insights and revisiting old constraints. Trans Am Fish Soc 137, 298–313.

Chittenden CM, Jensen JLA, Ewart D, Anderson S, Balfry S, Downey E, Eaves A, Saksia S, Smith B, Vincent S, Welch D, McKinley RS (2010) Recent salmon declines: A result of lost feeding opportunities due to bad timing? PLoS ONE 5(8), e12423.

Claiborne AM, Fisher JP, Hayes SA, Emmett RL (2011) Size at release, size-selective mortality, and age of maturity of Willamette River hatchery yearling Chinook Salmon. Trans Am Fish Soc 140, 1135–1144.

Claiborne AM, Miller JA, Weitkamp LA, Teel DJ (2014) Evidence for selective mortality in marine environments: the role of fish migration size, timing, and production type. Mar Ecol Prog Ser 515, 187–202.

Clarke A, Holmes LJ, Gore DJ (1992) Proximate and elemental composition of gelatinous zooplankton from the southern-Ocean. J Exp Mar Biol Ecol 155, 55–68.

Cober ER, Fregeau-Reid JA, Butler G, Voldeng HD (2006) Genotype-environment analysis of parameters describing water uptake in Natto Soybean. Crop Sci 46, 2415–2419.

Collie JS, Botsford LW, Hastings A, Kaplan IC, Largier JL, Livingston PA, Plagányi É, Rose KA, Wells BK, Werner FE (2016) Ecosystem models for fisheries management: finding the sweet spot. Fish Fish 17, 101–125.

Copeman LA, Parrish CC, Brown JA, Harel M (2002) Effects of docsahexaenoic, eicosapentaenoic, and arachidonic acids on the early growth, survival, lipid composition and pigmentation of yellowtail flounder (*Limanda ferruginea*): a live food enrichment experiment. Aquaculture 210, 285–304.

Copeman LA, Parrish CC Gregory RS, Jamieson RE, Wells J, Whiticar MJ (2009) Fatty acid biomarkers in coldwater eelgrass meadows: elevated terrestrial input to the food web of age-0 Atlantic cod *Gadus morhua*. Mar Ecol Prog Ser 386, 237–251.

Copeman LA, Laurel BJ (2010) Experimental evidence of fatty acid limited growth and survival in Pacific cod larvae. Mar Ecol Prog Ser 412, 259–272.

Copeman LA, Laurel BJ, Parrish CC (2013) Effect of temperature and tissue type on fatty acid signatures of two species of North pacific juvenile gadids: A laboratory feeding study. J Exp Mar Biol Ecol 448, 188–196.

Copeman LA, Laurel BJ, Boswell KM, Sremba AL, Klinck K, Heintz RA, Vollenweider JJ, Helser TE, Spencer ML (2016) Ontogenetic and spatial variability in trophic biomarkers of juvenile saffron cod (*Eleginus gracilis*) from the Beaufort, Chukchi and Bering Seas. Polar Biol 39, 1109–1126.

Cowen RK, Guigand CM (2008) *In situ* ichthyoplankton imaging system (*IS*IIS): system design and preliminary results. Limnol Oceanogr-Meth 6, 126–132.

Cushing DH (1972) The production cycle and the numbers of marine fish. Symp Zool Soc Lond 29, 213–232.

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26, 249–293.

Dale KE, Daly EA, Brodeur RD (2017) Interannual variability in the feeding and condition of subyearling Chinook salmon off Oregon and Washington in relation to fluctuating ocean conditions. Fish Oceanogr 26, 1–16.

Dalsgaard J, St. John M, Kattner G, Müeller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46, 224–340.

Daly EA, Brodeur RD, Weitkamp LA (2009) Ontogenetic shifts in diets of juvenile and subadult coho and Chinook Salmon in coastal marine waters: Important for marine survival? Trans Am Fish Soc 138, 1420–1438.

Daly EA, Benkwitt CE, Brodeur RD, Litz MNC, Copeman LA (2010) Fatty acid profiles of juvenile salmon indicate prey selection strategies in coastal marine waters. Mar Biol 157, 1975–1987.

Daly EA, Auth TA, Brodeur RD, Peterson WT (2013) Winter ichthyoplankton biomass as a predictor of early summer prey fields and survival of juvenile salmon in the northern California Current. Mar Ecol Prog Ser 484, 203–217.

Daly EA, Scheurer JA, Brodeur RD, Weitkamp LA, Beckman BR, Miller JA (2014) Juvenile steelhead distribution, migration, feeding, and growth in the Columbia River estuary, plume, and coastal waters. Mar Coast Fish 6, 62–80.

Daly EA, Brodeur RD (2015) Warming ocean conditions relate to increased trophic requirements of threatened and endangered salmon. PLoS ONE 10(12), e0144066.

Di Lorenzo E, Mantua M (2016) Multi-year persistence of the 2014/2015 North Pacific marine heatwave. Nat Clim Change 6, 1042–1047.

Doyle TK, Houghton JDR, McDevitt R, Davenport J, Hays G (2007) The energy density of jellyfish: estimates from bomb-calorimetry and proximate-composition. J Exp Mar Biol Ecol 343, 239–252.

Duffy EJ, Beauchamp DA, Sweeting RM, Beamish RJ, Brennan JS (2010) Ontogenetic diet shifts of juvenile Chinook Salmon in nearshore and offshore habitats of Puget Sound. Trans Am Fish Soc 139, 803–823.

Duffy EJ, Beauchamp DA (2011) Rapid growth in the early marine period improves marine survival of Puget Sound Chinook Salmon. Can J Fish Aquat Sci 68, 232–240.

El-Sabaawi R, Dower JF, Kainz M, Mazumder A (2009) Characterizing dietary variability and trophic positions of coastal calanoid copepods: insight from stable isotopes and fatty acids. Mar Biol 156, 225–237.

Emmett RL, Miller DR, Blahn TH (1986) Food of juvenile Chinook, *Oncorhynchus tshawytscha*, and coho, *O. kisutch*, salmon off the northern Oregon and southern Washington coasts, May–September 1980. Calif Fish Game 72, 38–46.

Emmett RL, Brodeur RD, Orton PM (2004) The vertical distribution of juvenile salmon (*Oncorhynchus* spp.) and associated fishes in the Columbia River plume Fish Oceanogr 13, 392–402.

Emmett RL, Brodeur RD, Miller TW, Pool SS, Krutzikowsky GK, Bentley PJ, McCrae J (2005) Pacific sardine (*Sardinops sagax*) abundance, distribution, and ecological relationships in the Pacific Northwest. Calif Coop Ocean Fish Invest Rep 46, 122–143.

Emmett RL, Krutzikowsky GK, Bentley P (2006) Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998–2003: Relationship to oceanographic conditions, forage fishes, and juvenile salmonids. Prog Oceanogr 68, 1–26.

Emmett RL, Krutzikowsky GK (2008) Nocturnal feeding of Pacific hake and jack mackerel off the mouth of the Columbia River, 1998–2004: Implications for juvenile salmon predation. Trans Am Fish Soc 137, 657–676.

Evans AF, Hostetter NJ, Collis K, Lyons DE, Sandford BP, Ledgerwood RD, Sebring S (2012) Systemwide evaluation of avian predation on juvenile salmonids from the Columbia River based on recoveries of passive integrated transponder tags. Trans Am Fish Soc 141, 975–989.

Farley EV Jr, Moss JH, Beamish RJ (2007) A review of the critical size, critical period hypothesis for juvenile Pacific salmon. N Pac Anadr Fish Comm Bull 4, 311–317.

Fisher JP, Pearcy WG (1988) Growth of juvenile coho salmon (*Oncorhynchus kisutch*) off Oregon and Washington, USA, in years of differing coastal upwelling. Can J Fish Aquat Sci 45, 1036–1044.

Fisher JP, Weitkamp LA, Teel DJ, Hinton SA, Trudel M, Morris JFT, Theiss ME, Sweeting RM, Orsi JA, Farley Jr EV (2014) Early ocean dispersal patterns of Columbia River Chinook and Coho Salmon. Trans Am Fish Soc 143, 252–272.

Folch J, Lees M, Stanley GHS (1957) A simple method for the isolation and purification of total lipid from animal tissues. J Biol Chem 226, 497–509.

Fry B (2006) Stable Isotope Ecology. Springer, New York.

Furey NB, Hinch SG, Mesa MG Beauchamp DA (2016) Piscivorous fish exhibit temperature-influenced binge feeding during an annual prey pulse. J Anim Ecol 85, 1307–1317.

Galloway AWE, Brett MT, Holtgrieve GW, Ward EJ, Ballantyne AP, Burns CW, Kainz MJ, Müller-Navarra DC, Persson J, Ravet JL, Strandberg U, Taipale SJ, Alhgren G (2015) A fatty acid based Bayesian approach for inferring diet in aquatic consumers. PLoS ONE 10(6), e0129723.

Gamble MM (2016) Size-selective mortality and environmental factors affecting early marine growth during marine life stages of sub-yearling Chinook salmon in Puget Sound, Washington. MS Thesis, University of Washington, Seattle.

Giraldo C, Stasko A, Choy ES, Rosenberg B, Majewski A, Power M, Swanson H, Loseto L, Reist JD (2016) Trophic variability of Arctic fishes in the Canadian Beaufort Sea: a fatty acids and stable isotopes approach. Polar Biol 39, 1267–1282.

Gnaiger E, Bitterlich G (1984) Proximate biochemical composition and caloric content calculated from elemental CHN analysis – a stoichiometric concept. Oecologia 62, 289–298.

Gregory RS, Northcote TG (1993) Surface, planktonic, and benthic foraging by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. Can J Fish Aquat Sci 50, 233–240.

Haeseker SL, Peterman RM, Su Z, Wood CC (2008) Retrospective evaluation of preseason forecasting models for sockeye and chum salmon. N Am J Fish Manage 28, 12–29.

Hansen MJ, Boisclair D, Brandt SB, Hewett SW (1993) Applications of bioenergetics models to fish ecology and management – where do we go from here? Trans Am Fish Soc 122, 1019–1030.

Hanson PC, Johnson TB, Schindler DE, Kitchell JF (1997) Fish Bioenergetics 3.0 for Windows. Center for Limnology, University of Wisconsin-Madison and the University of Wisconsin Sea Grant Institute. WISCU-T-97–001.

Hartt AC (1980) Juvenile salmonids in the oceanic ecosystem—the first critical summer. In McNeil WJ, Himsworth DC (eds) Salmonid Ecosystems of the North Pacific. Oregon State University Press, Corvallis, pp 25–57.

Heady WN, Moore JW (2013) Tissue turnover and stable isotope clocks to quantify resource shifts in anadromous rainbow trout. Oecologia 172, 21–34.

Healey MC (1991) Life history of Chinook salmon (*Oncorhynchus tshawytscha*). In Groot C, Margolis L (eds) Pacific Salmon Life Histories, UBC Press, Vancouver, pp 313–393.

Hertz E, Robinson JPW, Trudel M, Mazumder A, Baum JK (2014) Estimation of predator-prey mass ratios using stable isotopes: sources of errors. Mar Ecol Prog Ser 516, 1–6.

Hertz E, Trudel M, Brodeur RD, Daly EA, Eisner L, Farley Jr EV, Harding JA, MacFarlane RB, Mazumder S, Moss JH, Murphy JM, Mazumder A (2015) Continental-scale variability in the feeding ecology of juvenile Chinook Salmon along the coastal Northeast Pacific Ocean. Mar Ecol Prog Ser 537, 247–263.

Hertz E, Trudel M, Cox MK, Mazumder A (2015) Effects of fasting and nutritional restriction on the isotopic ratios of nitrogen and carbon: a meta-analysis. Ecol Evol 8, 4829–4839.

Hertz E, Trudel M, Tucker S, Beacham TD, Parken C, Mackas D, Mazumder A (2016) Influences of ocean conditions and feeding ecology on the survival of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Fish Oceanogr 25, 407–419.

Hertz E, Trudel M, El-Sabaawi R, Tucker S, Dower JF, Beachum TD, Edwards AM, Mazumder A (2016) Hitting the moving target: modelling ontogenetic shifts with stable isotopes reveals the importance of isotopic turnover. J An Ecol 85, 681–691.

Hertz E, Trudel M, Tucker S Beacham TD, Mazumder A (in press) Overwinter shifts in the feeding ecology of juvenile Chinook salmon. ICES J Mar Sci doi:10.1093/icesjms/fsw140.

Hickey, B.M., Banas, N. 2003. Oceanography of the Pacific Northwest coastal ocean and estuaries with application to coastal ecosystems. Estuaries, 26, 1010–1031.

Hjort J (1914) Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Reun. Cons. Int. Explo. Mer 20, 1–228.

Holling CS (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can Entomol 91, 293–320.

Holt RD (1987) Prey communities in patchy environments. Oikos 50, 276–290.

Hooff R, Peterson WT (2006) Copepod biodiversity as an indicator of changes in ocean and climate conditions of the northern California current ecosystem. Limnol Oceanogr 51, 2607–2620.

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50, 346–363.

Houde ED (2008) Emerging from Hjort's shadow. J Northw Atl Fish Sci 41, 53–70.

Hunsicker ME, Ciannelli L, Bailey KM, Buckel JA, White JW, Link JS, Essington TE, Gaichas S, Anderson TW, Brodeur RD, Chan KS, Chen K, Englund G, Frank KT, Fritas V, Hixon MA, Hurst T, Johnson DW, Kitchell JF Reese D, Rose GA, Sjodin H, Sydeman WJ, van der Veer HW, Vollset K, Zador S (2011) Functional responses and scaling in predator-prey interactions of marine fishes: contemporary issues and emerging concepts. Ecol Lett 14, 1288–1299.

Hurst TP (2007) Causes and consequences of winter mortality in fishes. J Fish Biol 71, 315–345.

Hurst TP (2007) Thermal effects on behavior of juvenile walleye Pollock (*Theragra chalcogramma*): implications for energetics and food web models. Can J Fish Aquat Sci 64, 449–457.

Hussey NE, MacNeil MA, McMeans BC, Olin JA, Dudley SFJ, Cliff G, Wintner SP, Fennessy ST, Fisk AT (2014) Rescaling the trophic structure of marine food webs. Ecol Lett 17, 239–250.

Hutchinson P, Welch D, Boehlert G, Whelan K (2002) A synthesis of the joint meeting: causes of marine mortality of salmon in the North Pacific and North Atlantic Oceans and in the Baltic Sea. N Pac Anadr Fish Comm Tech Rep 4, 93–96.

Iverson SJ, Frost KJ, Lang SLC (2002) Fat content and fatty acid composition of forage fish and invertebrates in Prince William Sound, Alaska: factors contributing to among and within species variability. Mar Ecol Prog Ser 241, 161–181.

Iwama GK, Tautz AF (1981) A simple growth model for salmonids in hatcheries. Can J Fish Aquat Sci 38, 649–656.

Izquierdo MS (1996) Essential fatty acid requirements of cultured marine fish larvae. Aquacult Nutr 2, 183–191.

Jakob EM, Marshall SD, Uetz GW (1996) Estimating fitness: a comparison of body condition indices. Oikos 77, 61–67.

Juanes F (1994) What determines prey size selectivity in piscivorous fishes? In Stouder DJ, Fresh KL, Feller RJ (eds) Theory and Application in Fish Feeding Ecology. University of South Carolina Press, Columbia, pp 79–100.

Juanes F, Buckel JA, Scharf FS (2002) Feeding ecology of piscivorous fishes. In Hart PJB, Reynolds JB (eds) Handbook of Fish Biology and Fisheries, Volume 1: Fish Biology. Blackwell Scientific Publications, Oxford, pp 267–283.

Kalinowski ST, Manlove KR, Taper ML (2007) ONCOR: a computer program for genetic stock identification. Montana State University, Bozeman.

Kaltenberg AM, Emmett RL, Benoit-Bird KJ (2010) Timing of forage fish seasonal appearance in the Columbia River plume and link to ocean conditions. Mar Ecol Prog Ser 419, 171–184.

Kleiber M (1975) The Fire of Life: An Introduction to Animal Energetics. RE Krieger Publ, Huntington, New York.

Kruskal JB (1964) Nonmetric multidimensional scaling: a numerical method. Psychometrika 29, 115–129.

Lamb J (2011) Comparing the hydrography and copepod community structure of the continental shelf ecosystems of Washington and Oregon, USA from 1998 to 2009: Can a single transect serve as an index of ocean conditions over a broader area? MS thesis, Oregon State University, Corvallis.

Lasker R (1978) The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp P-V Reun Cons Int Explo Mer 173, 212–230.

Laws EA, Popp BN, Bidigare RR, Kennicutt MC, Macko SA (1995) Dependence of phytoplankton carbon isotopic composition on growth rate and $[CO_2]_{aq}$: theoretical considerations and experimental results. Geochim Cosmochim Acta 59, 1131–1138.

Lawson JW, Magalhães AM, Miller EH (1998) Important prey species of marine vertebrate predators in the northwest Atlantic: proximate composition and energy density. Mar Ecol Prog. Ser 164, 13–20.

Lee RF, Nevenzel JC, Paffenhöffer G-A (1971) Importance of wax esters and other lipids in the marine food chain: phytoplankton and copepods. Mar Biol 9, 99–108.

Lima S (1998) Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv Study Behav 27, 215–290.

Lima SL (1998) Nonlethal effects in the ecology of predator-prey interactions. BioScience 48, 25–34.

Litz MNC, Emmett RL, Heppell SS, Brodeur RD (2008) Ecology and distribution of the northern subpopulation of northern anchovy (*Engraulis mordax*) off the U.S. west coast. Calif Coop Ocean Fish Invest Rep 49, 167–182.

Litz MNC, Brodeur RD, Emmett RL, Heppell SS, Rasmussen RS, O'Higgins L, Morris MS (2010) Effects of variable oceanographic conditions on forage fish lipid content and fatty acid composition in the northern California Current. Mar Ecol Prog Ser 405, 71–85.

Litz MNC, Miller JA, Copeman LA, Teel DJ, Weitkamp LA, Daly EA, Claiborne AM (in press) Ontogenetic shifts in diets of juvenile salmon: new insight from stable isotopes and fatty acids. Environ Biol Fish doi:10.1007/s10641-016-0542-5.

Litzow MA, Bailey KM, Prahl FG, Heinz R (2006) Climate regime shifts and reorganization of fish communities: the essential fatty acid limitation hypothesis. Mar Ecol Prog Ser 315, 1–11.

Logerwell EA, Mantua NJ, Lawson PW, Francis RC, Agostini VN (2003) Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (*Oncorhynchus kisutch*) marine survival. Fish Oceanogr 12, 554–568.

Losee J, Miller JA, Peterson WT, Teel DJ, Jacobson KC (2014) Influence of ocean ecosystem variation on trophic interactions and survival of juvenile coho and Chinook Salmon. Can J Fish Aquat Sci 71, 1747–1757.

Lotka AJ (1925) Elements of Physical Biology. Williams and Wilkins, Baltimore, MD.

Lu Y, Ludsin SA, Fanslow DL, Pothoven SA (2008) Comparison of three microquantity techniques for measuring total lipids in fish. Can J Fish Aquat Sci 65, 2233–2241.

MacFarlane RB, Norton EC (2002) Physiological ecology of juvenile chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California. Fish Bull 100, 244–257.

MacFarlane RB (2010) Energy dynamics and growth of Chinook Salmon (*Oncorhynchus tshawytscha*) from the Central Valley of California during the estuarine phase and first ocean year. Can J Fish Aquat Sci 67, 1549–1565.

Madenjian CP, O'Connor DV, Cheryak SM, Rediske RR, O'Keefe JP (2004) Evaluation of a Chinook salmon (*Oncorhynchus tshawytscha*) bioenergetics model. Can J Fish Aquat Sci 61, 627–635.

Madenjian CP, David SR, Pothaven SA (2012) Effects of activity and energy budget balancing algorithm on laboratory performance of a fish bioenergetics model. Trans Am Fish Soc 141, 1328–1337.

Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. Bull Am Meteorol Soc 78, 1069–1079.

Marin Jarrin J (2012) Sandy Beach Surf Zones: What is their Role in the Early Life History of Juvenile Chinook Salmon (*Oncorhynchus tshawytscha*)? PhD Dissertation, Oregon State University, Corvallis.

Matarese AC, Kendall Jr AW, Blood DM, Vinter BM (1989) Laboratory guide to early life history stages of Northeast Pacific fishes. NOAA Technical Report NMFS 80.

Mather PM (1976) Computational Methods of Multivariate Analysis in Physical Geography. J.Wiley and Sons, London.

Maynz D, Toft S, Vollrath F (2003) Effects of prey quality and availability on the life history of a trap-building predator. Oikos 101, 631–638.

Mazur MM, Wilson MT, Dougherty AB, Buchheister A, Beauchamp DA (2007) Temperature and prey quality effects on growth of juvenile walleye Pollock *Theragra chalcogramma* (Pallas): a spatially explicit bioenergetics approach. J Fish Biol 70, 816–836.

McConnaughey T, McRoy CP (1979) $^{13}C$ label identifies eelgrass (*Zostera marina*) carbon in an Alaskan estuarine food web. Mar Biol 53, 263–269.

McCune B, Grace JB (2002) Analysis of Ecological Communities. MjM Software Design, Gleneden Beach.

Meuter FJ, Peterman RM, Pyper BJ (2002) Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. Can J Fish Aquat Sci 59, 456–463.

Mielke Jr PW, Berry KJ (2001) Permutation Methods: a distance function approach. Springer, New York.

Miller CB, Morgan CA, Prahl FG, Sparrow MA (1998) Storage lipids of the copepod *Calanus finmarchicus* from Georges Bank and the Gulf of Maine. Limnol Oceanogr 43, 488–497.

Miller TW, Brodeur RD, Rau G (2008) Carbon stable isotopes reveal relative contribution of shelf-slope production to the northern California Current pelagic community. Limnol Oceanogr 53, 1493–1503.

Miller TW, Brodeur RD, Rau G, Omori K (2010) Prey dominance shapes trophic structure of the northern California Current pelagic food web: evidence from stable isotopes and diet analysis. Mar Ecol Prog Ser 420, 15–26.

Miller JA, Teel DJ, Baptista A, Morgan CA (2013) Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook Salmon (*Oncorhynchus tshawytscha*). Can J Fish Aquat Sci 70, 617–629.

Miller JA, Teel DJ, Peterson WT, Baptista AM (2014) Assessing the relative importance of local and regional processes on the survival of a threatened salmon population PLoS ONE 9(6), e99814.

Mittelbach GG, Persson L (1998) The ontogeny of piscivory and its ecological consequences. Can J Fish Aquat Sci 55, 1454–1465.

Mjaavatten O, Levings CD, Poon P (1998) Variation in the fatty acid composition of juvenile Chinook and coho salmon from Fraser River estuary determined by multivariate analysis; role of environment and genetic origin. Comp Biochem Physiol B 120, 291–309.

Mohan SD, Mohan JA, Connelly TL, Walther BD, McClelland JW (2016) Fatty acid biomarkers and tissue-specific turnover: validation from a controlled feeding study in juvenile Atlantic croaker *Micropogonias undulatus* J Fish Biol 89, 2004–2023.

Moss JH, Beauchamp DA, Cross AD, Myers KW, Farley EV Jr, Murphy JM, Helle JH (2005) Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. Trans Am Fish Soc 134, 1313–1322.

National Research Council (NRC) (2011) Nutrient Requirements of Fish and Shrimp. The National Academies Press, Washington DC.

Neilson JD, Geen GH (1986) First-year growth rate of Sixes River Chinook salmon as inferred from otoliths: effects on mortality and age at maturity. Trans Am Fish Soc 115, 28–33.

Ney JJ (1993) Bioenergetics modeling today – growing pains on the cutting edge. Trans Am Fish Soc 122, 736–748.

Österblom H, Olsson O, Blenckner T, Furness RW (2008) Junk-food in marine ecosystems. Oikos 117, 967–977.

Paine RT (1969) The *Pisaster-Tegula* interaction: prey patches, predator food preference, and intertidal community structure. Ecology 50, 950–961.

Parnel MM, Emmett RL, Brodeur RD (2008) Ichthyoplankton community in the Columbia River plume off Oregon: effects of fluctuating oceanographic conditions. Fish Bull 106, 161–173.

Parrish CC (1999) Determination of total lipids, lipid classes and fatty acids in aquatic samples. In Arts MT, Wainmann BC (eds) Lipids in Freshwater Ecosystems. Springer, New York, pp 4–20.

Parrish CC (2013) Lipids in marine ecosystems. ISRN Oceanography 2013 Article ID 604045, 16 pp.

Pearcy WG (1992) Ocean Ecology of North Pacific Salmonids. Washington Sea Grant Program University of Washington Press, Seattle.

Pearcy WG, McKinnell SM (2007) The ocean ecology of salmon in the northeast Pacific Ocean – an abridged history. In Grimes CB, Brodeur RD, Halderson LJ, McKinnell SM (eds) The Ecology of Juvenile Salmon in the Northeast Pacific Ocean: Regional Comparisons. American Fisheries Society, Bethesda, pp 7–30.

Peterman RM (1982) Model of salmon age structure and its use in preseason forecasting and studies of marine survival. Can J Fish Aquat Sci 39, 1444–1452.

Peterson WT, Brodeur RD, Pearcy WG (1982) Food habits of juvenile salmon in the Oregon coastal zone, June 1979. Fish Bull 80, 841–851.

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18, 293–320.

Peterson JO, Peterson WT (2008) Influence of the Columbia River plume (USA) on the vertical and horizontal distribution of mesozooplankton over the Washington and Oregon shelf. ICES J Mar Sci 65, 477–483.

Peterson WT, Fisher JL, Peterson JO, Morgan CA, Burke BJ, Fresh KL (2014) Applied fisheries oceanography: Ecosystem indicators of ocean conditions inform fisheries management in the California Current. Oceanography 27, 80–89.

Phillips AJ, Brodeur RD, Suntsov AV (2009) Micronekton community structure in the epipelagic zone of the northern California Current upwelling system. Prog Oceanogr 80, 74–92.

Phillips DL, Inger R, Bearhop S, Jackson AL, Moore JW, Parnell AC, Semmens BX, Ward EJ (2014) Best practices for use of stable isotope mixing models in food-web studies. Can J Fish Aquat Sci 92, 823–835.

Pierce BJ, McWilliams SR (2014) The fat of the matter: How dietary fatty acids can affect exercise performance. Int Comp Biol 54, 903–912.

Pikitch EK, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO, Dayton P, Doukakis P, Fluharty D, Heneman B, Houde ED, Link J, Livingston PA, Mangel M, McAllister MK, Pope J Sainsbury KJ (2004) Ecosystem-based fishery management. Science 305, 346–347.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2016) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-128. http://CRAN.R-project.org/package=nlme.

Plaut I (2001) Critical swimming speed: its ecological relevance. Comp Biochem Phys A 131, 41–50.

Plumb JM, Moffitt CM (2015) Re-estimating temperature-dependent consumption parameters in bioenergetics models for juvenile Chinook salmon. Trans Am Fish Soc 144, 323–330.

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703–718.

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods, and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152, 179–189.

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703–718.

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods, and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152, 179–189.

Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86, 501–509.

Quinn TP Myers KW (2004) Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited. Rev Fish Biol Fisher 14, 421–442.

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org/.

Rannala B, Mountain JL (1997) Detecting immigration by using multilocus genotypes. P Natl Acad Sci USA 94, 9197–9201.

Renkawitz MD, Sheehan TF, Dixon HJ, Nygaard R (2015) Changing trophic structure and energy dynamics in the Northwest Atlantic: implications for Atlantic salmon feeding at West Greenland. Mar Ecol Prog Ser 538, 197–211.

Richardson S (1973) Abundance and distribution of larval fishes in waters off Oregon, May-October 1969, with special emphasis on the northern anchovy, *Engraulis mordax*. Fish Bull 71, 697–711.

Rindorf A, Lewy P (2011) Bias in estimating food consumption of fish by stomach-content analysis. Can J Fish Aquat Sci 61, 2487–2498.

Rodrìguez C, Pèrez JA, Dìaz M, Izquierdo MS, Fernandez-Palacios H, Lorenzo A (1997) Influence of the EPA/DHA ratio in rotifers on gilthead seabream (*Sparus aurata*) larval development. Aquaculture 150, 77–89.

Roughgarden J (1983) Competition and theory in community ecology. Am Nat 122, 583–601.

Rounsefell GA (1958) Anadromy in North American Salmonidae. Fish Bull 131, 171–185.

Ruggerone GT, Nielsen JL (2004) Evidence for competitive dominance of Pink salmon (*Oncorhynchus gorbuscha*) over other Salmonids in the North Pacific Ocean. Rev Fish Biol Fish 14, 371–390.

Rykaczewski RR, Dunne JP, Sydeman WJ, García-Reyes M, black BA, Bograd SJ (2015) Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern boundary currents through the 21$^{st}$ century. Geophys Res Lett 42, 6424–6431.

Saito H, Ishihara K, Murase T (1996) Effect of prey fish lipids on the docosahexaenoic acid content of total fatty acids in the lipid of *Thunnus albacares* yellowfin tuna. Biosci Biotech Bioch 60, 962–965.

Sandell TA, Teel DJ, Fisher J, Beckman B, Jacobson KC (2015) Infections by *Renibacterium salmoninarum* and *Nanophyetus salmincola* Chapin are associated with reduced growth of juvenile Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Northeast Pacific Ocean. J Fish Disease 38, 365–378.

Sargent JR, Bell JG, Bell MV, Henderson RJ, Tocher DR (1995) Requirement criteria for essential fatty acids. J Applied Ich 11, 183–198.

Sargent J, Bell G, McEvoy L, Tocher D, Estevez A (1999) Recent developments in the essential fatty acid nutrition of fish. Aquaculture 177, 191–199.

Schabetsberger R, Morgan CA, Brodeur RD, Potts CL, Peterson WT, Emmett RL (2003) Prey selectivity and diel feeding chronology of juvenile Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Columbia River plume. Fish Oceanogr 12, 523–540.

Scheuerell MD, Zabel RW, Sandford BP (2009) Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhynchus* spp.). J Appl Ecol 46, 983–990.

Schmidt-Nielsen K (1997) Animal Physiology: Adaption and Environment, 4th edition. Cambridge University Press, New York.

Schultz ET, Conover DO (1999) The allometry of energy reserve depletion: test of a mechanism for size-dependent winter mortality. Oecologia 119, 474–483.

Seeb LW, Antonovich A, Banks MA, Beachem TD, Bellinger, MR, Blankenshipp, SM, Campbell, MR, Decovich, NA, Garza, JC, Guthrie III, CM, Lundrigan, TA, Moran, P, Narum, SR, Stephanson, JJ, Supernault, KJ, Teel, DJ, Templin, WD, Wenburg, JK, Young, SF, Smith, CT (2007) Development of a standardized DNA database for Chinook Salmon. Fisheries 32, 540–549.

Sheridan MA (1994) Regulation of lipid metabolism in poikilothermic vertebrates. Comp Biochem Physiol B 107, 495–508.

Sklan D, Prag T, Lupatsch I (2004) Apparent digestibility coefficients of feed ingredients and their prediction in diets for tilapia *Oreochromis niloticus* × *Oreochromis aureus* (Teleostei, Cichlidae) Aquacult Res 35, 358–364.

Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull Mar Sci 60, 1129–1157.

Stachura MM, Mantua NJ, Scheuerell MD (2014) Oceanographic influences on patterns in North Pacific salmon abundance. Can J Fish Aquat Sci 71, 226–235.

Steele JH (1991) Can ecological theory cross the land-sea boundary? J Theor Biol 153, 425–436.

Stewart DJ, Ibarra M (1991) Predation and production by salmonine fishes in Lake Michigan, 1978–88. Can J Fish Aquat Sci 48, 909–922.

Stowasser G, McAllen R, Pierce GJ, Collins MA, Moffat CF, Priede IG, Pond DW (2009) Trophic position of deep-sea fish – Assessment through fatty acid and stable isotope analyses. Deep-Sea Res Pt I 56, 812–826.

Takeuchi T (2014) Progress on larval and juvenile nutrition to improve the quality and health of seawater fish: a review. Fish Sci 80, 389–403.

Teel, DJ, Bottom, DL, Hinton, SA, Kuligowski, DR, McCabe, GT, McNatt, R, Roegner, GC, Stamatiou, LA, Simenstad, CA (2014) Genetic identification of Chinook Salmon in the Columbia River estuary: Stock-specific distributions of juveniles in shallow tidal and freshwater habitats. N Am J Fish Man 34, 621–641.

Teel DJ, Burke BJ, Kuligowski DR, Morgan CA, Van Doornik DM (2015) Genetic identification of Chinook Salmon: stock-specific distributions of juveniles along the Washington and Oregon coasts. Mar Coast Fish 7, 274–300.

Thayer JA, Field JC, Sydeman WJ (2014) Changes in California Chinook salmon diet over the past 50 years: relevance to the recent population crash. Mar Ecol Prog Ser 498, 249–261.

Thornton KW, Lessem AS (1978) A temperature algorithm for modifying biological rates. Trans Am Fish Soc 107, 284–287.

Tocher DR (2003) Metabolism and functions of lipids and fatty acids in teleost fish. Rev Fish Sci 11, 107–184.

Tocher DR (2010) Fatty acid requirements in ontogeny of marine and freshwater fish. Aquacult Res 41, 717–732.

Tocher DR (2015) Omega-3 long-chain polyunsaturated fatty acids and aquaculture in perspective. Aquaculture 449, 94–107.

Tomaro LM, Teel DJ, Peterson WT, Miller JA (2012) When is bigger better? Early marine residence of middle and upper Columbia River spring Chinook salmon. Mar Ecol Prog Ser 452, 237−252.

Trudel M, Tucker S, Zamon JE, Morris JFT, Higgs DA, Welch DW (2002) Bioenergetic response of coho salmon to climate change. N Pac Anadr Fish Comm Tech Rep 4, 59–61.

Trudel, M, Welch DW (2005) Modeling the oxygen consumption rates in Pacific salmon and steelhead: model development. Trans Am Fish Soc 134, 1542–1561.

Trudel M, Tucker S, Morris JFT, Higgs DA, Welch DW (2005) Indicators of energetic status in juvenile coho salmon and Chinook salmon N Am J Fish Manage 25, 374–390.

Vander Zanden MJ, Rasmussen JB (1999) Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. Ecology 80, 1395–1404.

Vander Zanden MJ, Clayton MK, Moody EK, Solomon CT, Weidel BC (2015) Stable isotope turnover and half-life in animal tissues: a literature synthesis. PLoS ONE 10(1), e0116182.

Wainwright TC, Weitkamp LA (2013) Effects of climate change on Oregon Coast coho salmon: Habitat and life-cycle interactions. Northwest Sci, 87, 219–242.

Waples RS, Teel DJ, Myers J, Marshall A (2004) Life history divergence in Chinook Salmon: historic contingency and parallel evolution. Evolution 58, 386–403.

Watanabe T (1993) Importance of docosahexaenoic acid in marine larval fish. J World Aquacult Soc 24, 152–161.

Weitkamp LA (2004) Ocean conditions, marine survival, and performance of juvenile Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in SE Alaska. PhD Dissertation, University of Washington, Seattle.

Weitkamp LA, Sturdevant MV (2008) Food habits and marine survival of juvenile Chinook and coho salmon from marine waters of Southeast Alaska. Fish Oceanogr 17, 380–395.

Weitkamp LA, Bentley PJ, Litz MNC (2012) Seasonal and interannual variation in juvenile salmonids and associated fish assemblage in open waters of the lower Columbia River estuary. Fish Bull 110, 426–450.

Weitkamp LA, Teel DJ, Liermann M, Hinton SA, Van Doornik DM, Bentley PJ (2015) Stock-specific size and timing at ocean entry of Columbia River juvenile Chinook salmon and steelhead: implications for early ocean growth. Mar Coast Fish 7, 370–392.

Wells BK, Santora JA, Field JC, MacFarlane RB, Marinovic BB, Sydeman WJ (2012) Population dynamics of Chinook salmon *Oncorhynchus tshawytscha* relative to prey availability in the central California coastal region. Mar Ecol Prog Ser 457, 125–137.

Wells BK, Santora JA, Schroeder ID, Mantua N, Sydeman WJ, Huff DD, Field JC (2016) Marine ecosystem perspectives on Chinook salmon recruitment: a synthesis of empirical and modeling studies from a California upwelling system. Mar Ecol Prog Ser 552, 271–284.

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Syst 15, 393–425.

Winberg GG (1956) Rate of metabolism and food requirements of fishes. Fish Res Board Can Trans Ser 194.

Woodson LE, Wells BK, Weber PK, MacFarlane RB, Whitman GE, Johnson RC (2013)

Size, growth, and origin-dependent mortality of juvenile Chinook salmon *Oncorhynchus tshawytscha* during early ocean residence. Mar Ecol Prog Ser 487, 163–175.

Wu FC, Ting YY, Chen HY (2003) Dietary docosahexaenoic acid is more optimal than eicosapentaenoic acid affecting the level of cellular defense responses of the juvenile grouper *Epinephelus malabaricus*. Fish Shellfish Immunol 14, 223–238.

Yang LH, Rudolf VHW (2009) Phenology, ontogeny, and the effects of climate change on the timing of species interactions. Ecol Lett 13, 1–10.

Zabel RW, Williams JG (2002) Selective mortality in Chinook Salmon: what is the role of human disturbance? Ecol Appl 12, 173–183.

Zhang YL, Baptista AM (2008) SELFE: A semi-implicit Eulerian-Lagrangian finite-element model for cross-scale ocean circulation. Ocean Model 21, 71–96.

# APPENDICES

APPENDIX A

## Supplemental material for Chapter 3: Prey field biomass estimates

**Table A1** Average biomass of the juvenile salmon prey by cruise (month) estimated as wet weight (µg $m^{-3}$) from May through September 2011 and 2012.

| | | **2011** | | | | | **2012** | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Common Name** | **Scientific Name** | May | Jun | Jul | Aug | Sep | May | Jul | Aug | Sep |
| Pteropod | Limacinidae | 0.06 | | | | | | | | |
| Hyperiid amphipod | Hyperiidea | | | | | 0.07 | 0.01 | 0.004 | | |
| Gammarid amphipod | Gammaridea | | | | | | | 0.01 | | |
| Caprellid amphipod | Caprelloidea | | | | | | 0.01 | | | |
| Krill | *Thysanoessa spinifera* | 2.14 | 0.54 | | | 0.73 | 0.12 | | | |
| North Pacific krill | *Euphausia pacifica* | | 0.04 | | | | 0.18 | | | |
| Pandalid shrimp | Pandalidae | 0.01 | | | | | | | | |
| Crangon shrimp | Crangonidae | | 0.02 | | | | | | | |
| Red rock crab | *Cancer productus* | | 0.07 | | | | 0.001 | 0.09 | | |
| Dungeness crab | *Metacarcinus magister* | 2.10 | 2.40 | | 0.06 | 0.02 | 0.41 | 0.04 | | 0.01 |
| Pea crab | *Pinnotheres pisum* | | 0.003 | | | | | | | |
| Squid (unidentified) | Cephalopoda | | | | | | | | | 0.84 |
| California market squid | *Doryteuthis opalescens* | | 4.79 | 1.52 | 0.09 | 2.59 | 2.21 | | 6.28 | |
| Boreopacific armhook squid | *Gonatopsis borealis* | 1.51 | | | | | | | | |
| Magister armhook squid | *Berryteuthis magister* | | | | | | 0.14 | | | |
| Boreal clubhook squid | *Onychoteuthis borealijaponica* | | | | 0.29 | | | | | |
| East Pacific red octopus | *Octopus rubescens* | | | | | 0.11 | | | | |
| Northern anchovy | *Engraulis mordax* | | | | 142.29 | 341.79 | | 6.97 | 2577.22 | 0.72 |
| Smelt (unidentified) | Osmeridae | 8.47 | 84.31 | 1.23 | | | 64.74 | 27.62 | 1.73 | |
| Cod (unidentified) | Gadidae | | | | | | 0.02 | | | |
| Pacific tomcod | *Microgadus proximus* | | 0.12 | 0.48 | 1.26 | | 0.99 | | | |
| Rockfish (unidentified) | *Sebastes* spp. | 3.31 | 0.08 | 0.07 | 0.45 | 5.25 | 0.16 | 0.48 | | 0.05 |

**Table A1** (Continued)

| Common Name | Scientific Name | 2011 May | Jun | Jul | Aug | Sep | 2012 May | Jul | Aug | Sep |
|---|---|---|---|---|---|---|---|---|---|---|
| Yellowtail rockfish | *Sebastes flavidus* | | | 0.32 | | | | | | |
| Greenling (unidentified) | *Hexagrammidae* | 0.06 | | | | | | | | |
| Kelp greenling | *Hexagrammos decagrammus* | | | | | | 4.86 | | | |
| Lingcod | *Ophiodon elongatus* | 0.07 | | | | | | | | |
| Painted greenling | *Oxylebius pictus* | | | | | 0.54 | | | | |
| Calico sculpin | *Clinocottus embryum* | 0.03 | | | | | | | | |
| Brown Irish lord | *Hemilepidotus spinosus* | 0.51 | | | | | | | | |
| Pacific staghorn sculpin | *Leptocottus armatus* | | | | | | 0.05 | | | |
| Cabezon | *Scorpaenichthys marmoratus* | | | | | 0.06 | | | | |
| Poacher (unidentified) | Agonidae | 0.02 | | | | | | | | |
| Starsnout poacher (unidentified) | *Bathyagonus* spp. | | | | 1.34 | | | | | |
| Snailfish (unidentified) | Liparididae | 0.29 | 0.09 | | | 0.04 | | 0.03 | | |
| Northern ronquil | *Ronquilus jordani* | 0.05 | 1.68 | 3.93 | 0.18 | 0.07 | 0.13 | 1.57 | | |
| Bluebarred prickleback | *Plectobranchus evides* | 0.02 | | | | | | | | |
| Pacific sand lance | *Ammodytes hexapterus* | 0.22 | | | | | 0.07 | 0.02 | | |
| Pacific sanddab | *Citharichthys sordidus* | | | | | | 3.55 | | | |
| Speckled sanddab | *Citharichthys stigmaeus* | | | | | | 0.39 | | | |
| Flatfish (unidentified) | *Pleuronectidae* | 0.71 | | | | 0.01 | | | | |
| Arrowtooth flounder | *Atheresthes stomias* | 2.11 | | | | | | | | |
| Rex sole | *Glyptocephalus zachirus* | | | 0.24 | | | 0.24 | 0.78 | | |
| Butter sole | *Isopsetta isolepis* | 0.04 | 0.03 | | | | 0.05 | 0.02 | | |
| Rock sole | *Lepidopsetta bilineata* | 1.27 | 0.14 | | | | | | | |
| Slender sole | *Lyopsetta exilis* | | 0.04 | | | | 1.16 | | | 0.12 |
| English sole | *Parophrys vetulus* | 0.04 | | | | | | | | |
| Sand sole | *Psettichthys melanostictus* | 2.41 | 0.22 | | | 0.03 | 1.17 | 1.65 | | 0.02 |

APPENDIX B

**Supplemental material for Chapter 4:**
**Data for bioenergetics model simulations**

**Figure B1** Daily average sea surface temperatures (SSTs) measured at 30-minute intervals from station 46243 (Clatsop Spit, Oregon), station 46029 (Columbia River Bar 20 nautical miles west of Columbia River Mouth), station 46248 (Astoria Canyon, Oregon), and station 46211 (Grays Harbor, Washington) June through October 2011 (red) and 2012 (blue). Dotted lines represent minimum, mean, and maximum SST for the entire sampling period.

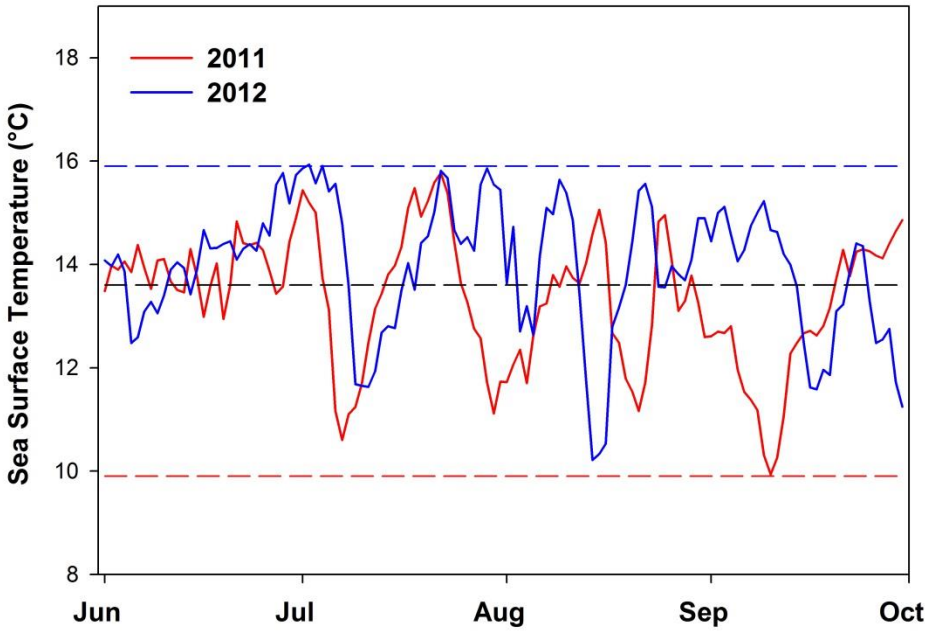


**Table B1** Diet proportions by month based on stomach contents of 208 subyearling Chinook salmon (*Oncorhynchus tshawytscha*).

| | | 2011 | | | 2012 | | |
|---|---|---|---|---|---|---|---|
| **Common name** | **Scientific name** | Jun-Jul | Jul-Aug | Aug-Sep | Jun-Jul | Jul-Aug | Aug-Sep |
| Insect | Insecta | 0.160 | 0.276 | 0.085 | 0.143 | 0.019 | 0.183 |
| Pteropod | Pteropoda | | | | | | 0.015 |
| Cladoceran | Cladocera | | | | | 0.297 | |
| Ostracod | Ostracoda | 0.001 | | | | | |
| Copepod | Copepoda | 0.022 | | | | | 0.003 |
| Isopod | Isopoda | | | | | | 0.014 |
| Amphipod | Amphipoda | 0.490 | 0.306 | 0.142 | 0.436 | 0.157 | 0.066 |
| Mysid | Mysidacea | 0.097 | | | 0.033 | | |
| Krill | Euphausiidae | | 0.216 | | 0.119 | | 0.032 |
| Shrimp larvae | Pandalidae | 0.053 | | | | 0.019 | 0.169 |
| Crab larvae | *Metacarcinus magister* and *Cancer* spp. | 0.176 | 0.003 | 0.109 | 0.124 | | 0.329 |
| Northern anchovy | *Engraulis mordax* | | 0.025 | 0.394 | | 0.254 | 0.034 |
| Unidentified fish | Osteichthyes | | 0.175 | 0.270 | 0.144 | 0.254 | 0.155 |

**Table B2** Energy density (J $g^{-1}$) of prey for input into the bioenergetics model, including indigestible percentages and references.

| | 2011 | | | 2012 | | | | |
|---|---|---|---|---|---|---|---|---|
| **Common name** | Jun-Jul | Jul-Aug | Aug-Sep | Jun-Jul | Jul-Aug | Aug-Sep | % Indigestible | Reference |
| Insect | 3511 | 3511 | 3511 | 3511 | 3511 | 3511 | 3.33 | 3 |
| Pteropod | 2612 | 2612 | 2630 | 2612 | 2612 | 2630 | 8.50 | 2 |
| Cladoceran | 2514 | 2514 | 2514 | 2514 | 2514 | 2514 | 10.00 | 1 |
| Ostracod | 2586 | 2586 | 2586 | 2586 | 2586 | 2586 | 10.00 | 1 |
| Copepod | 2623 | 2623 | 2623 | 2623 | 2623 | 2623 | 9.00 | 3 |
| Isopod | 2460 | 2460 | 2460 | 2460 | 2460 | 2460 | 50.00 | 3 |
| Amphipod | 3606 | 3606 | 3606 | 3606 | 3606 | 3606 | 15.12 | 3 |
| Mysid | 4208 | 4208 | 4208 | 4208 | 4208 | 4208 | 11.83 | 3 |
| Krill | 3190 | 3190 | 3190 | 3190 | 3190 | 3190 | 0.00 | 4 |
| Shrimp larvae | 3959 | 3959 | 3959 | 3959 | 3959 | 3959 | 0.00 | 4 |
| Crab larvae | 3658 | 4343 | 5027 | 3733 | 3514 | 3295 | 0.00 | 4 |
| Northern anchovy | 2345 | 3257 | 2892 | 2345 | 2764 | 3103 | 0.00 | 4 |
| Unidentified fish | 4104 | 4104 | 4104 | 4104 | 4104 | 4104 | 13.67 | 3 |
| **Total Diet** | **3314** | **3274** | **3367** | **3298** | **2894** | **3394** | | |

[1] Boldt and Haldorson 2004
[2] Beauchamp et al. 2007
[3] Marin Jarrin 2012
[4] This study