A COMPILATION AND META-ANALYSIS OF SALMON DIET DATA FROM THE NORTH PACIFIC OCEAN

by

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B.A., Grinnell College, 2016

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Oceans and Fisheries)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

August 2020

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A compilation and meta-analysis of salmon diet data from the North Pacific Ocean

submitted by Caroline Graham in partial fulfillment of the requirements for

the degree of Master of Science

in Oceans and Fisheries

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Abstract

Salmon migrate thousands of kilometers through dynamic ecosystems of the North Pacific Ocean, however, their open ocean life phase is poorly understood with limited research comparing salmon trophic ecology across the entire basin. Understanding the marine trophic ecology of salmon has the potential to reveal information about ocean conditions, competition, prey abundance, as well as salmon health and survival. The first goal of this research was to build an open-access database to centralize Pacific salmon diet data using a standardized format ('North Pacific Marine Salmon Diet Database'). This database was then populated with an initial data set that came from 62 sources identified through a systematic literature review, targeting peer reviewed and gray literature from time periods with high research activity: 1959–1969 and 1987–1997. The second goal was to examine spatial and interspecies differences in diet and trophic niche for chum, pink and sockeye salmon across the North Pacific between 1959 and 1969, a period during a negative phase of the Pacific Decadal Oscillation and prior to significant hatchery enhancement. In the Western Subarctic, all species tended to consume zooplankton and prey availability was higher than the Eastern Subarctic. In the Gulf of Alaska and Eastern Subarctic, interspecies differences in diet were most apparent with chum and sockeye specializing on zooplankton and micronekton, respectively, while pink ate a mixture of zooplankton and micronekton. In the Bering Sea chum ate zooplankton while sockeye and pink alternated between zooplankton and micronekton. In addition to the large-scale trophic patterns, these data revealed novel fine-scale spatial trophic patterns, including latitudinal, onshore-offshore, and cross-gyre gradients. These results showed that pink were more generalist consumers, and their diets may be a better reflection of overall prey presence and abundance in the environment. Conversely, chum and sockeye were more specialist consumers, and their diets may be a better reflection of interspecies dynamics and/or specific prey presence and abundance of zooplankton and micronekton, respectively. Overall, this research provides an open-access database that can help address gaps in ecological understanding of the North Pacific, as well as complementary data analyses to further understanding of salmon marine ecology.

Lay Summary

Salmon spend at least 50% of their lives in the ocean, but this part of their life is not well understood. One way we can learn about the lives of salmon is by studying what they eat. This information can tell us what food is available, whether this food is healthy and nutritious, and whether there may be competition for food. There is some historic data on salmon feeding, but these data are scattered throughout many sources and countries. To help other researchers, this study initiated consolidation of these diet data into a database that is publicly available. This research also analyzed the data within this database and found that different salmon species have different feeding patterns across the vast North Pacific Ocean that are determined by the environmental conditions that they encounter and the competition that they meet. This information can help us understand what challenges salmon face.

Preface

This thesis is the original, unpublished work of Caroline Graham. The research was designed by Dr. Brian P. V. Hunt, Dr. Evgeny A. Pakhomov and Caroline Graham. Caroline Graham conducted the systematic literature review. Data were extracted and standardization by Caroline Graham, as well as by research assistants Dr. Marina Espinasse, Nicole Link, and Carmen Manuel. Caroline Graham designed the database and conducted all analyses. The North Pacific Marine Salmon Diet Database is publicly available on GitHub: https://github.com/mcarolinegraham/North_Pacific_Marine_Salmon_Diet_Database.

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List of Abbreviations

BS	Bering Sea
ES	Eastern Subarctic
GoA	Gulf of Alaska
NPMSDD	North Pacific Marine Salmon Diet Database
PDO	Pacific Decadal Oscillation
SoJ	Sea of Japan
SoO	Sea of Okhotsk
WS	Western Subarctic

Acknowledgements

This project would not have been possible without the financial support of the Ambrose Monell and G. Unger Vetlesen Foundations, the University of British Columbia, and the Tula Foundation. I would also like to acknowledge the donors behind the W. H. Mathews Scholarship and the COSMOS International Graduate Travel Award that helped me pursue this research.

I would like to extend my heartfelt gratitude to Dr. Brian Hunt for taking me on as a student. You have an incredible dedication and drive to everything you do that is very inspiring. You have been instrumental in improving my scientific abilities while also encouraging me to be a well-rounded scientist and person. Thank you for always being supportive of my other interests and projects and trusting me to juggle everything appropriately. Thanks to you I am able to walk away with new skills that I did not anticipate from a fulfilling graduate student experience. I would also like to thank Dr. Evgeny Pakhomov for being the connection between the NPAFC and UBC that led me to this program and for his insightful comments and expertise throughout the process. Also, thank you to Dr. William Cheung for contributing valuable perspectives and feedback on this work.

Thank you to the many people that were instrumental in my research process. This includes Dr. Raymond Ng who guided me through the database design process and Sally Taylor who helped me understand the art of systematic literature reviews. Thank you to Kyoko Adachi and Tim Spesivy for their assistance with source translations. And thank you to Svetlana Naydenko, Alexey Khoruzhiy and Alexei Somov for helping to track down Russian data sources.

Thank you to my incredible labmates and other friends that have helped me every step of the way. This would not have been possible without all of you. I would especially like to thank Dr. Tim Cashion who was an extremely patient teacher and helped me tackle the daunting world

of R, as well as the other Deep Sea Data Squad members that mentored me along the way. I would also like to thank Vanessa Zahner for keeping me motivated and on track through the final months in the midst of a pandemic. Thank you to all my friends that have been there for the ups and downs, especially GP, providing moral support through evening swims, beach days, phone calls, and cooking nights. And thank you to my partner, for coaxing laughs out of me even in my most stressful moments. Your endless support and patience helped me push through and I am grateful for you every day.

And finally, thank you to my family, especially my parents, who never once doubted me and who have always encouraged me to dream big, even when that means moving far away. I am forever grateful for all the opportunities you have given me.

To my family

Chapter 1: Introduction

In the North Pacific, salmon are iconic and valuable keystone species that play important roles in terrestrial, freshwater and marine environments. Anadromous salmon nourish freshwater and surrounding terrestrial ecosystems by bringing nutrients from the marine environment back to their natal rivers when they return to spawn and die (Helfield and Naiman, 2001; Naiman et al., 2002; Verspoor et al., 2011). They also provide food to many organisms along the way, including bears, birds, and orcas (Gende et al., 2002; Hanson et al., 2010; Payne and Moore, 2006). Salmon are of great cultural importance in the North Pacific, especially for some Indigenous Peoples for whom salmon shape their ways of life and are of immeasurable cultural value (Colombi and Brooks, 2012; Garner and Parfitt, 2006). Salmon have even been defined as a "cultural keystone species" due to their foundational role in the cultures of some Indigenous Peoples (Garibaldi and Turner, 2004). Salmon are also economically valuable, providing food, revenue, jobs and tourism opportunities in North Pacific countries, such as Canada, Japan, Korea, Russia and the United States (Criddle and Shimizu, 2014; Gislason et al., 2017). Developing a better understanding of salmon life histories and the factors impacting their survival is critical for the continued existence and prosperity of culturally, ecologically, and economically valuable Pacific salmon.

The six major anadromous Pacific salmon species—Chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), sockeye (*O. nerka*), pink (*O. gorbuscha*), chum (*O. keta*) and steelhead (*O. mykiss*)—have been studied widely by individual countries of the North Pacific rim with a focus on the freshwater and early marine phases of their life cycles. However, the late marine phase of their life cycle, during which they migrate thousands of kilometers through the open ocean, is not well understood (Groot and Margolis, 1991). During their epic migrations, they cross international boundaries and encounter many other species and stocks from across the North Pacific. For example, chum salmon from Japan have been found to migrate all the way to the Gulf of Alaska, where stocks from Canada and the United States also intermix (Beacham et al., 2009; Myers et al., 2007). On the western side of the North Pacific, salmon from both Japan and Russia rear in the Sea of Okhotsk and Western Subarctic (Myers et al., 2007; Urawa et al., 2004). To the north, Asian and North American salmon meet in the Bering Sea (Myers et al., 2007; Ruggerone et al., 2003; Seeb et al., 2004). Although some coordinated international efforts have been made to study salmon in the open ocean, mainly through the International North Pacific Fisheries Commission and the North Pacific Anadromous Fish Commission, more efforts are needed to address this international phase of the salmon life cycle (Davis et al., 2009, 1996; Myers and Aydin, 1996; Walker et al., 2005). The late marine phase is difficult to study due to the logistical challenges of open ocean research in a vast and dynamic region, however, there are important questions that need to be addressed.

Although salmon face many challenges throughout their life cycle from both natural and human-induced pressures, the challenges they face during their marine phase are the least understood. These include changing ocean conditions, such as temperature, ocean acidification, stratification, and circulation patterns. The North Pacific has long been subjected to natural shifts in ocean conditions, including multidecadal shifts, such as those measured by the Pacific Decadal Oscillation Index and the North Pacific Gyre Oscillation Index, as well as interannual shifts, such as those measured by the El Niño Southern Oscillation Index (Di Lorenzo et al., 2008; Hare and Mantua, 2000; Mantua and Hare, 2002; Ware, 1995). However, human-induced climate change is a more recent phenomenon that contributes to changing ocean conditions, causing overall warmer temperatures, increased ocean acidification, increased stratification and changing circulation patterns, among other impacts (Doney et al., 2012). Climate change is expected to shrink available salmon habitat in the North Pacific, especially in more southern regions, in accordance with species' thermal tolerances (Abdul-Aziz et al., 2011). While some salmon species and stocks may experience new habitat opening up in northern regions, not all salmon will be able to take advantage of this habitat. Climate change is also expected to change prey distributions and abundances. For example, studies have shown that squid, a common oceanic prey for several Pacific salmon species, have a distinct lower temperature threshold and their distribution is therefore heavily influenced by environmental conditions (Kawabata et al., 2006; Tian et al., 2013). As another example, in the northeast Pacific, a switch from warmer to cooler ocean temperatures has been found to increase zooplankton biomass in the more southern regions and shift community composition to larger, boreal copepod species (Batten and Welch, 2004; Peterson and Schwing, 2003; Brodeur and Ware, 1992). The opposite is true when conditions shift from cooler to warmer. These are just a few examples of the ways in which changing ocean conditions can affect salmon, but this is not the only threat they face during their marine phase.

Another threat to salmon during the marine phase is related to density-dependent factors caused by rising numbers of Pacific salmon. The overall abundance of salmon in the North Pacific is considered to have reached a record high, based on available historic data. This has largely been attributed to favorable ocean conditions in more northern and offshore areas and increased hatchery production of mainly chum and pink salmon (Francis and Hare, 1994; Hare and Mantua, 2000; Irvine and Fukuwaka, 2011; Kim et al., 2017; Ruggerone and Irvine, 2018). This has raised questions about competition and the overall carrying capacity for salmon in the North Pacific. Some research has pointed to the early marine phase as a critical time in the life history of salmon, partially attributed to density-dependent factors, like food availability (Beamish and Mahnken, 2001). Fukuwaka and Suzuki (2000) found that in the waters of coastal Japan, when the density of juvenile chum increased, the weight of their stomach contents decreased. Ruggerone and Goetz (2004) found that juvenile Chinook has reduced first-year growth and survival in years of high pink salmon abundance. Other research has speculated that density-dependent factors could play a role in the late marine phase as well, however, this is not as well understood. Evidence for density-dependence during the late marine phase largely comes from research on salmon marine ecology during years of high versus low pink salmon abundance. There is some evidence of reduced marine growth for chum, Chinook and sockeye salmon during years when pink salmon are more abundant in the ocean (Bugaev et al., 2001; Ruggerone et al., 2005, 2003). Additionally, studies have found that chum salmon may prey-switch during the late marine phase and feed on less nutritious prey, such as gelatinous zooplankton, when more pink salmon are present (Andrievskaya, 1966; Kaga et al., 2013; Tadokoro et al., 1996). In order to gain a holistic understanding of the challenges salmon face today, we need to focus efforts towards the least understood marine phase of the salmon life cycle.

Diet data can provide important insight into the lives of organisms—especially those like salmon that are challenging to observe and track—and diets have been used to examine many different organisms and ecosystems. Diet data can help to address scientific questions regarding evolution, competition, spatial and temporal dynamics, ecosystem changes and organism health, among others. For example, diets have been used to study the evolution of humans, along with organisms such as bats, fish, and other primates (Dean et al., 2007; DeCasien et al., 2017; Luca et al., 2010; Perry et al., 2007; Schondube et al., 2001). Diet studies have also revealed important competition dynamics between species ranging from krill and copepods, to dingoes and foxes, to sharks and dolphins (Cupples et al., 2011; Heithaus, 2001; Stige et al., 2018). Diets can even reveal ecosystem-level changes, such as the shift from larger epipelagic fish to smaller mesopelagic species in the eastern tropical Pacific Ocean, as revealed by the diets of yellowfin tuna (Olson et al., 2014). In the California Current system, the diets of marine birds have indicated important changes in marine communities, such as changing abundances of rockfish and euphausiids that correspond to shifting climatic conditions (Sydeman et al., 2001). Across the North Pacific, salmon diets have been used to address many similar research questions.

Salmon are size-selective consumers and are often considered ecosystem samplers whose diets can reveal what is available in the surrounding environment (Brodeur, 1990; Groot and Margolis, 1991). They consume a variety of prey, from zooplankton, like copepods, euphausiids and pteropods, to micronekton, including small fish and squid. Salmon diet studies have been used to address questions regarding salmon health and competition during their late marine phase. Salmon diets can reveal insight into salmon health because some prey items are more nutritious than others in terms of caloric value and lipid content (Daly et al., 2010; Davis et al., 1998). Davis et al. (1998) found that species of cnidarians had some of the lowest caloric values among potential salmon prey items, while copepods, euphausiids, fish and squid species had some of the highest. Lipid composition is important to salmon health as well since lipids are sources of energy for fish growth, reproduction, and migration (Tocher, 2003). Fish and crustacean zooplankton have been found to have higher lipid content compared to non-crustacean zooplankton, and varying consumption of these prey can affect salmon lipid composition (Bailey et al., 1995; Daly et al., 2010; Kaga et al., 2013). For salmon, essential fatty acids include docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA), and salmon prey items have been found to contain varying quantities of these fatty acids (Daly et al., 2010). Besides providing insight into salmon health, studying diets can reveal potential competition between species or stocks which can be observed through prey-switching behavior which may indicate less resource availability. Chum salmon in particular have been found to exhibit this behavior when they switch to feeding on less nutritious prey, such as gelatinous zooplankton (Andrievskaya, 1966; Kaga et al., 2013; Tadokoro et al., 1996).

Salmon diet studies have also been used to answer questions regarding temporal and spatial ecosystem dynamics in the North Pacific Ocean, but studies have often been limited in either time or space. Although many studies show that temporal ecosystem changes have occurred across the North Pacific, especially over multidecadal time scales, salmon diets have rarely been studied over these time scales (Anderson and Piatt, 1999; Irvine et al., 2009; Kim et al., 2017; Mantua et al., 1997). In one multidecadal study, Brodeur et al. (2007a) found that the proportion of pteropods and copepods in juvenile coho diets was higher during weak upwelling or warm years, while the proportion of euphausiids was higher during strong upwelling and high productivity years in the California Current system. Kaeriyama et al., (2004) also examined diets over a multidecadal time scale in the Gulf of Alaska and found that squid composition of most salmon species' diets decreased during La Niña events. In addition to temporal changes, studies have also revealed large-scale spatial diet differences within the eastern North Pacific and within the western North Pacific (Brodeur et al., 2007b; Hertz et al., 2015; Karpenko et al., 2007). However, very few studies have looked across the entire basin, even though salmon can migrate between the east and west during their impressive journeys (Myers et al., 2007; Qin and Kaeriyama, 2016). Studies have shown that the eastern and western Subarctic Pacific have distinct features and the western side is characterized by higher cholorphyll, higher zooplankton and lower temperatures, while the eastern side is characterized by lower chlorophyll, lower zooplankton and higher temperatures (Harrison et al., 1999; Polovina et al., 2011; Saito et al., 2011; Sugimoto and Tadokoro, 1997). More robust temporal and spatial research is needed to understand the marine phase of the salmon life cycle in the past in order to predict what may happen in the future.

Salmon diet data have been collected since the early 1900s by researchers across the North Pacific, however, these data have remained scattered in different publications, databases, and grey literature, making it difficult to find and utilize (Wilbert McLeod Chapman, 1936; Silliman, 1941). The process to collate these disparate data into a useable format presents many challenges considering that the data have been reported using a variety of methods, metrics and languages. However, collating and providing these data to all interested parties is of high importance if researchers are to begin to better understand the complex marine phase of the salmon life cycle. Open science is on the rise around the world and this concept involves ensuring that data, code, collaborative platforms and scientific findings are available to everyone (Fecher and Friesike, 2014). As the ocean faces a period of rapid change and salmon face an uncertain future, it is more important than ever to adopt open science principles (Tai and Robinson, 2018). This will allow research to happen quickly, efficiently and collaboratively to address growing concerns about salmon productivity in the North Pacific.

The purpose of this thesis was to collate and analyze historic marine salmon diet data from across the North Pacific Ocean, to better understand the complex dynamics of the marine phase of the salmon life cycle. Chapter 2 details the creation of the "North Pacific Marine Salmon Diet Database", which is an open-access relational database built to house different types of salmon diet data from their ocean phase. This chapter also details the initial collection of data, which includes stomach content data from time periods with high research activity that were identified through a systematic literature review process. In Chapter 3, diet data from the North Pacific Marine Salmon Diet Database were analyzed to study spatial and interspecies differences in diet and trophic niche between the three most abundant salmon species: pink, chum and sockeye. Very few studies have compared salmon trophic ecology across the eastern and western North Pacific and this research examines both diet and trophic niche during a negative Pacific Decadal Oscillation phase before the effects of hatchery enhancement were significant. In conclusion, this research presents a new open-access tool for researchers and the first application of this tool to begin to piece together the understudied marine phase of the salmon life cycle.

Chapter 2: A salmon diet database for the North Pacific Ocean

2.1 Introduction

Even though salmon spend 1-6 years of their life in the marine environment, this phase of their life cycle is poorly understood compared to their freshwater phase (Groot and Margolis, 1991). There are limited data on how salmon are distributed, what they feed on, and what threats to survival they may face during this phase, which includes nearshore and offshore components. The marine phase is hypothesized to contain salmon population bottlenecks (Beamish and Mahnken, 2001), and research has shown that salmon smolt to adult survival rates can be less than 1% for some stocks in the North Pacific (Bradford, 1995). There is also evidence that Pacific salmon marine survival has been declining over the past several decades in certain areas, especially more southern stocks (Mueter et al., 2003; Zimmerman et al., 2015). Therefore, it is becoming urgent that researchers understand what is happening to salmon during the marine phase of their life cycle, especially after they have moved offshore, because this phase tends to be data-poor compared to the early marine coastal phase.

One of the most important factors affecting salmon survival is the presence and abundance of suitable prey. Although it is difficult to assess prey distribution across ocean basins, information on prey presence and abundance can be derived from salmon diets. Marine diet data has the potential to give insight into food webs, niche overlap among species/stocks, competition, health, and changing ocean conditions (Dale et al., 2017; Davis et al., 2009; Qin and Kaeriyama, 2016). Since the early 1900s, researchers have been examining the diets of Pacific salmon to provide information on species biology and the conditions that salmon face in the ocean (W. M. Chapman, 1936; Silliman, 1941). Although there have been some reviews of salmon diet data in the North Pacific, these have been limited in time and space and the data are not normally made publicly available (Brodeur, 1990; Brodeur et al., 2007a; Davis et al., 2009; Kaeriyama et al., 2004; Karpenko et al., 2007; Qin and Kaeriyama, 2016; Starovoytov, 2007).

Salmon diet data have been collected using a variety of methodologies employed by researchers from countries across the North Pacific. These data are scattered across the peer reviewed and gray literature, making collation challenging. However, there is high value in collating these data, considering the costliness and difficulty of conducting fieldwork in the open ocean. Synthesizing these data can reveal important information about salmon open ocean life history experience and further understanding of the potential impacts of changing oceans on salmon productivity. Additionally, more comprehensive, accurate and robust diet data will be an asset to ecosystem models, which are increasingly being applied in ecosystem-based management (Jamieson et al., 2010). As salmon face an uncertain future with climate change (Healey, 2011; Erik R Schoen et al., 2017), this is a critical time to consolidate available knowledge in order to advance research on salmon marine ecology.

The goal of this project was to develop an open-access database framework for collating marine salmon diet data, alongside available salmon biological data, prey biological data, and environmental data. An initial contribution of salmon stomach content diet data from offshore areas was compiled through a systematic literature review, followed by quality control and standardization procedures for two time periods: 1959–1969 and 1987–1997. These decades were selected partially because they are time periods in which there are a larger quantity of data available on salmon diets. This database will continue to grow as more sources are identified and added and can be used as a tool by researchers to study salmon marine survival and North Pacific ecosystem dynamics.

2.2 Methods

2.2.1 Systematic literature review

In order to identify sources that contained salmon diet data, in the form of stomach contents, a systematic literature review was performed using database keyword searches of ProQuest: Aquatic Sciences and Fisheries Abstracts, Web of Science: Core Collection and Web of Science: Zoological Record (Clarivate Analytics, n.d., n.d.; Food and Agriculture Organization of the United Nations, n.d.). Not all salmon diet studies are part of the peer-reviewed literature and many North Pacific researchers have published data through the North Pacific Anadromous Fish Commission (NPAFC) and the defunct International North Pacific Fisheries Commission (INPFC). Therefore, database search results were supplemented with relevant INPFC documents and bulletins (North Pacific Anadromous Fish Commission, n.d.), NPAFC documents (North Pacific Anadromous Fish Commission, n.d.) and bulletins (North Pacific Anadromous Fish Commission, n.d.), and relevant bibliographic references found within these documents and bulletins (Table 2.1).

The database keyword searches identified 591 unique sources. Sources were filtered for relevance and excluded based on the following criteria:

(i) the source did not have salmon stomach content diet data from between 1959–1969 or 1987–1997 for the marine environment, as defined by the area beyond the Riverine Coastal Domain (~15 km) (Carmack et al., 2015) (556 sources);

(ii) the source did not have extractable diet data and authors did not respond to inquiries (1 source);

(iii) the source was a review, in which case the original sources were used, if possible and relevant, to extract data (2 sources);

(iv) the source overlapped completely with another source, i.e., the data were reported using the exact same metrics for the same samples as another source (2 sources).

The database search was supplemented with sources that met the same criteria from the INPFC documents and bulletins and the NPAFC documents and bulletins, bringing the total number of unique sources to 62 (Table A1).

2.2.2 Data extraction

For each salmon diet sample, we extracted the following data (if available): source metadata (e.g., publication year, title, authors) (Table A2), salmon capture method (Table A3), site information (time, location), salmon information (e.g., taxonomy, life stage, sex), salmon replicates, type of diet data (e.g., percent weight of prey, total number of prey), and prey information (e.g., taxonomy, life stage, quantity) (Table A4). A diet sample is defined as a distinct sample in time and space from a specific source and is entered into the database exactly as it is reported in the source. A sample can contain diet data from one salmon or more than one salmon when individuals were grouped together for diet analysis (up to 2,215 salmon in this data compilation). If different diet metrics were reported for the same diet sample (e.g., number of prey and volume of prey), then all metrics were entered into the database. If the data were not available in table format, but figure format only, then the data were extracted using WebPlotDigitizer (Rohatgi, 2019).

For each source, we extracted data as they were presented in the sources in almost all cases and therefore it was extracted according to the data resolution of the source. For example, if the sample location was presented as a station, it was extracted as a station with specific geographical coordinates, but if it was presented as a transect or area, then it was extracted as a transect or area with latitude and/or longitude minimums and maximums. If geographical coordinates were not specified, then they were estimated based on survey maps or descriptions present in the source. Prey taxonomy was reported to different resolutions across sources (e.g., Copepoda versus *Neocalanus cristatus*). In order to keep the lowest data resolution reported in the source while also being able to compare across sources, each prey item was reported at all possible taxonomic levels (kingdom, phylum, class, order, family, genus, species). In addition to the salmon diet data, if the source presented additional related data for salmon biological parameters (i.e., variables) (Table A5), prey biological parameters (Tables A6–A7), or environmental parameters (Table A8), these data were extracted as well. For detailed information about the different types of data extracted and the extraction methodology see Tables A2–A8. Data were visualized using R statistical software v3.6.1 (R Core Team, 2019).

2.2.3 Database framework

We built an open-access relational database in MySQL v8.0.18 called the "North Pacific Marine Salmon Diet Database" ("MySQL," 2019). The North Pacific Marine Salmon Diet Database contains all of the extracted data noted above: diet data, salmon biological data, prey biological data, and environmental data. This database also allows for inclusion of prey biological data that are not associated with a salmon sample. For example, if a researcher conducted a zooplankton tow for potential prey and they have biological data for these potential prey (e.g., length, weight), these data can be added to the database. In this database, all data are linked by site, which has both a temporal and spatial component. All data are also related to a source in order to distinguish related data and trace its origins. While the database was built specifically to house North Pacific salmon data from the marine environment, the database structure was designed to easily be applied to other predator and prey interactions with only slight modifications, hence the predator-prey terminology used (Figure 2.1).

2.3 Data records

The North Pacific Marine Salmon Diet Database currently contains 6,869 diet observations from 6,305 unique diet samples of over 69,942 salmon. Types of diet data included percent weight of prey, absolute weight of prey, average weight of prey, percent volume of prey, percent number of prey, absolute number of prey, average number of prey, frequency of occurrence (numerical and percent), stomach content index, index of fullness, and index of relative importance. The database also houses 11,965 observations of salmon biological parameters for 6,172 unique salmon samples. One observation means one biological parameter measured for one sample of salmon, which can contain one or many fish. Salmon biological parameters include length, weight, daily ration, empty stomachs, male/female ratio and many others. Additionally, the database includes 238 observations of prey biological parameters from 112 unique prey taxonomic categories. Prey biological parameters include body length, body weight, body width and size index. Finally, the database contains 2,790 observations of environmental parameters. Environmental parameters include temperature, salinity and others.

2.3.1 Spatial and temporal coverage

Diet samples were collected at 751 unique spatial locations, which included areas (polygons), transects, and point locations across the North Pacific from the California Current to the Sea of Japan (Figure 2.2). Salmon biological data were collected from 709 locations, prey biological data from 4 locations, and environmental data from 446 locations. Salmon biological data were reported across the entire North Pacific, while prey biological data were sparsely reported from a few locations in the Gulf of Alaska and the Sea of Okhotsk/Kuril Islands. Environmental data were mainly available from the eastern and central North Pacific Ocean. Since our search was focused on specific time periods, most of the data we collected fell within our specified decadal periods: 1959–1969 and 1987–1997 (Figure 2.3). However, some sources reported data from other time periods and these data were also included in the database. While diet data and salmon biological data were consistently reported across the temporal range, environmental data and prey biological data were inconsistently reported.

2.3.2 Salmon and prey species coverage

Sockeye (*Oncorhynchus nerka*), pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) were reported most frequently in our database, while coho (*Oncorhynchus kisutch*), Chinook (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) were reported less frequently (Figure 2.4). The most commonly reported prey groups were amphipods, fish (Class Actinopterygii), euphausiids, cephalopods (Subclass Coleoidea), and copepods (Fig. 3). The category 'miscellaneous' was also commonly reported, although it usually made up just a small percentage of the diets. Within the diet data reported in the database, there are 186 unique prey taxa, meaning the lowest taxonomic classifications of prey items. Only 18.5% of salmon diet data were reported to the species level, while the majority were reported to higher taxonomic levels (e.g., Amphipoda, Decapoda, Euphausiacea).

2.4 Technical validation

Standardization procedures were used to verify and collate the data. Since some of the taxonomic records were outdated, the taxonomies were verified and updated using the World Register of Marine Species (Horton et al., 2019). For types of diet data that should add to a cumulative percentage of 100 (e.g., percent weight, percent volume), diet samples were excluded if the cumulative percent of prey was above 105% or below 95%. If the cumulative percentage did not add to 100 but still fell within this range, diet data values for that sample were rescaled to add to 100. For other metrics, including absolute and average weight and number of prey, as well as numerical frequency of occurrence, we consulted a salmon diet expert to determine if our highest values were reasonable to find in adult salmon stomachs (V. Zahner, pers. comm.).

2.5 Usage notes

The database, as well as associated documentation and code, are available in the North Pacific Marine Salmon Diet Database GitHub repository, which will be updated as more historic data are digitized and made available by the Pelagic Ecosystems Laboratory at the University of British Columbia (Graham et al., 2020). The North Pacific Marine Salmon Diet Database is publicly available and can be used under the license of CC BY, meaning that the work can be distributed, remixed, adapted and built upon with acknowledgement of authors.

2.6 Tables

Table 2.1. The number of salmon diet data sources identified from a systematic literature review. A keyword search was used to identify sources in three online databases (Proquest: Aquatic Sciences and Fisheries Abstracts, Web of Science: Core Collection, Web of Science: Zoological Record), which contained most of the peer-reviewed literature. The former steelhead species name “*Salmo gairdneri*”, when included as a search term, did not provide any more relevant sources that met our criteria. A manual search through the NPAFC and INPFC documents and bulletins provided most of the gray literature. A total of 62 unique sources met the qualifications for database entry.

Search terms	Source	Results before filtering	Results after filtering
(Chinook OR "Oncorhynchus tshawytscha" OR coho OR "Oncorhynchus kisutch" OR sockeye OR "Oncorhynchus nerka" OR pink OR "Oncorhynchus gorbuscha" OR chum OR "Oncorhynchus keta" OR steelhead OR "Oncorhynchus mykiss") AND (marine OR ocean* OR coast* OR "Gulf of Alaska" OR "Bering Sea") AND (stomach OR gut* OR "prey composition" OR "diet* composition" OR "composition of diet" OR "composition of prey") AND (diet* OR prey OR food)	Proquest: Aquatic Sciences and Fisheries Abstracts	410	23
	Web of Science: Core Collection	182	6
	Web of Science: Zoological Record	142	12
	North Pacific Anadromous Fisheries Commission Documents		23
	North Pacific Anadromous Fisheries Commission Bulletins		16
	International North Pacific Fisheries Commission Documents		5
	International North Pacific Fisheries Commission Bulletins		6
			Total = 62

2.7 Figures

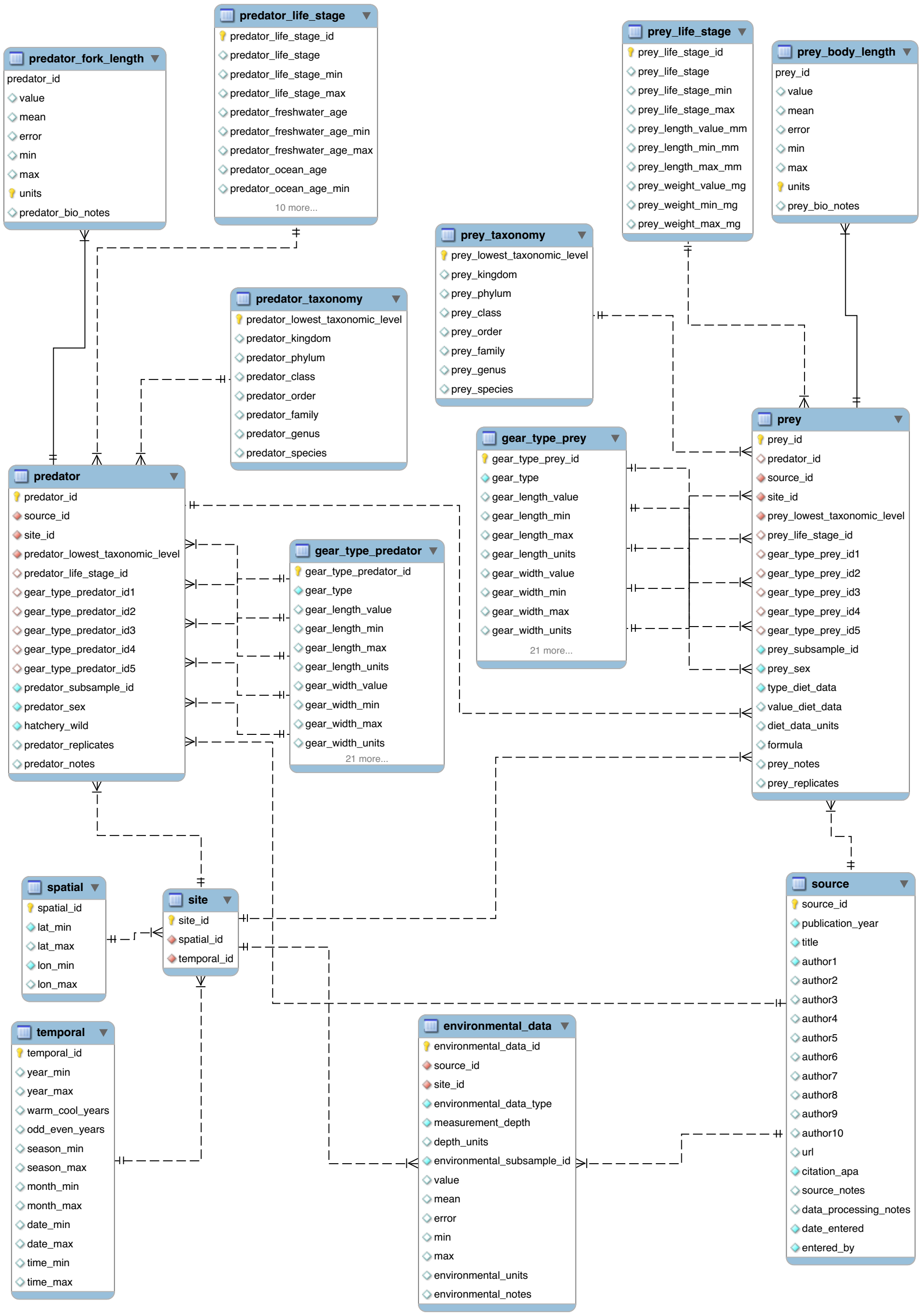


Figure 2.1. The relational model for the North Pacific Marine Salmon Diet Database. The yellow symbols represent the primary key, red represents foreign keys, and blue represents not NULL attributes. Not all predator and prey biological parameter relations are displayed in the diagram. Just one example is given for one predator and one prey biological parameter.

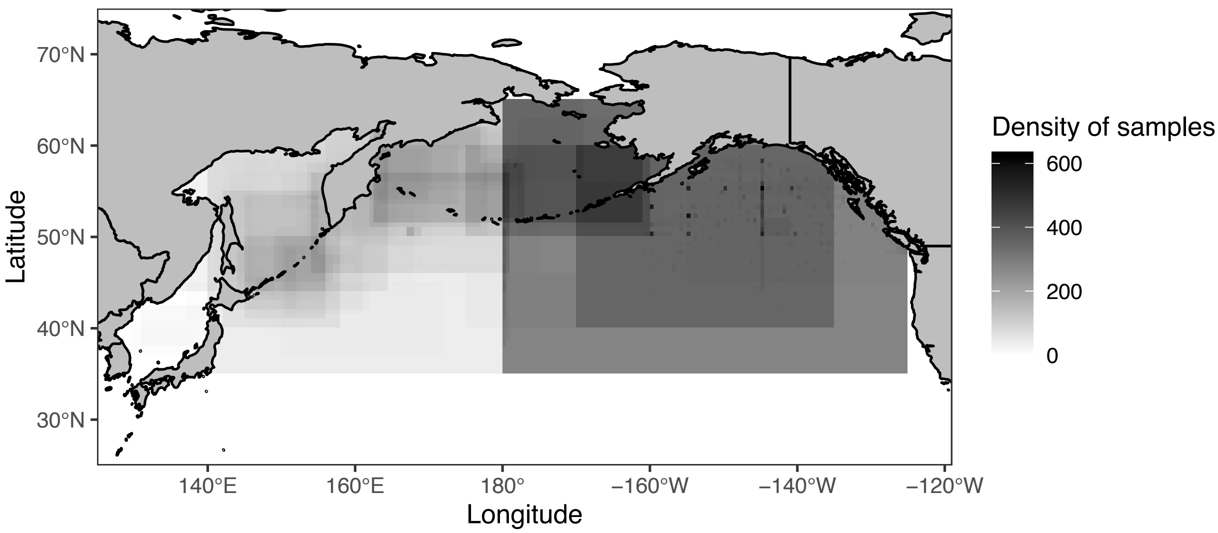


Figure 2.2. The spatial distribution of diet samples across the North Pacific Ocean. The density of diet samples, in the form of points, lines, and polygons (rectangles) based on the latitude and longitude minimum and maximum values.

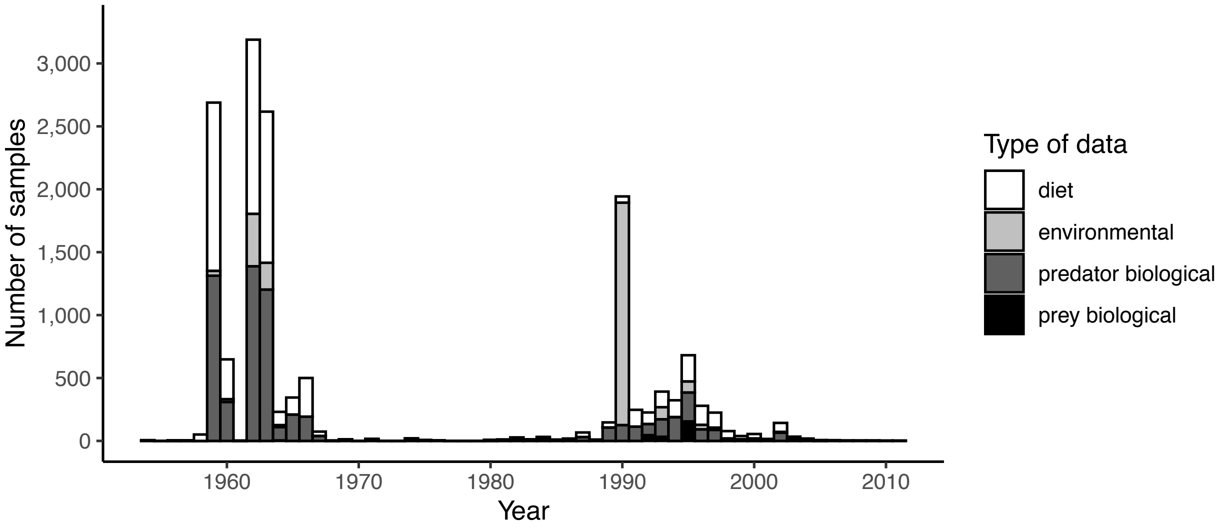


Figure 2.3. The number of samples for each type of data reported across the temporal range 1950–2011. If a single sample consisted of data from multiple years, then the median year was selected to represent the sample and half years were rounded down.

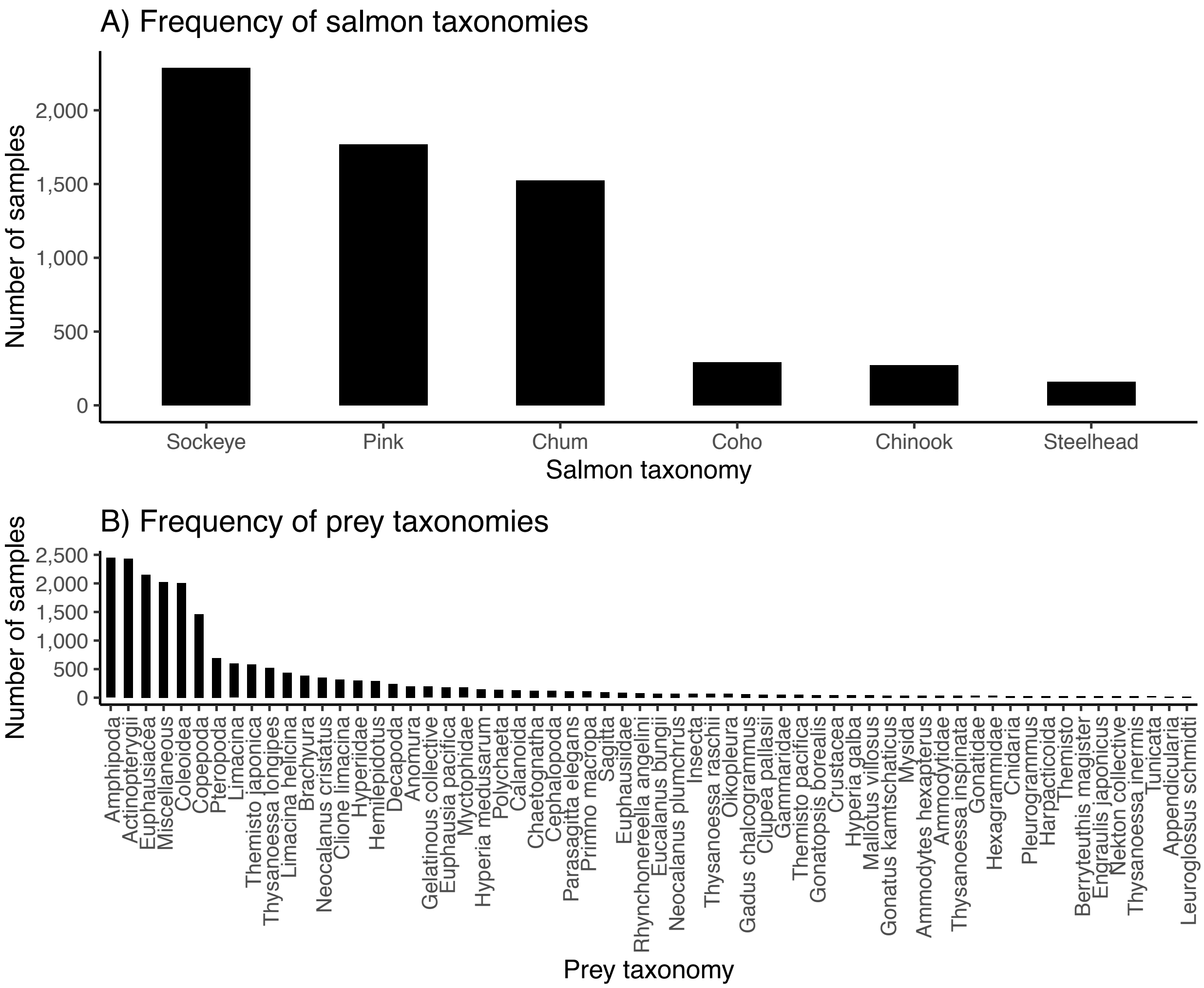


Figure 2.4. The number of diet samples that contain each salmon and each prey taxonomic classification. (A) The number of diet samples in the database for each species of salmon. (B) The number of samples containing each prey taxonomy. Prey taxonomy refers to the lowest taxonomic level identified by the source. Prey taxonomies that were reported in less than 20 samples were excluded.

Chapter 3: Salmon trophic ecology reveals spatial and interspecies dynamics across the North Pacific

3.1 Introduction

Pacific salmon spend at least 50% of their life cycle as post juveniles in the coastal or open ocean, yet this phase of their life cycle is the least understood (Groot and Margolis, 1991). The marine phase is of increasing concern due to unanswered questions about the carrying capacity of the North Pacific, including how it may be impacted by climate change and long-term hatchery enhancement (Beamish, 2017; Beamish and Mahnken, 2001; Ruggerone and Irvine, 2018; Ruggerone and Nielsen, 2004; Erik R. Schoen et al., 2017). Even though total numbers of Pacific salmon are increasing, many stocks are in decline, especially in more southern regions, and all salmon face an unpredictable future with climate change (Abdul-Aziz et al., 2011; Healey, 2011; Irvine et al., 2009; Irvine and Fukuwaka, 2011; Ruggerone and Irvine, 2018). Studying salmon foraging ecology can provide insight into salmon health, ocean conditions, and interspecies interactions, illuminating the challenges that salmon may face during the marine phase. Furthermore, understanding historic salmon spatial and interspecies dynamics in the marine environment can help to improve understanding of the past, present and future of salmon production in the North Pacific.

The abundance of the three most common salmon species in the North Pacific—pink (*Oncorhynchus gorbuscha*), chum (*O. keta*) and sockeye (*O. nerka*)—is estimated to have nearly tripled from less than 300 million adults during the 1960s to approximately 800 million adults in 2009 (Ruggerone and Irvine, 2018). These species all rear in off-shelf regions and their substantial increase has been partially attributed to hatchery enhancement, especially of chum salmon, which started to climb in the 1970s. This culminated in hatcheries contributing 60% of chum, 15% of pink and 4% of sockeye produced in the North Pacific between 1990 and 2015 (Ruggerone and Irvine, 2018). Furthermore, increases in salmon production have also been attributed to favorable ocean conditions in specific regions and during certain time periods. For example, multi-decadal climate shifts related to the Pacific Decadal Oscillation (PDO) have been discussed as important drivers of salmon productivity, producing distinct warm and cool conditions across the North Pacific (Irvine et al., 2009; Kim et al., 2017; Mantua et al., 1997). In the eastern Pacific, the regime shift of 1977, from positive to negative PDO phase, led to warmer than normal conditions in the east and increased salmon production in more northern regions while production decreased in more southern regions (Anderson and Piatt, 1999; Mantua et al., 1997). In the western Pacific, Russian salmon productivity was negatively correlated with the PDO index, while Japanese and Korean salmon productivity was positively correlated (Kim et al., 2017). North Pacific ecosystems have also been impacted by climate change which has caused rising temperatures, increasing ocean acidification, growing oxygen minimum zones and changing circulation patterns, among other impacts (Doney et al., 2012). While coastal ecosystems are particularly affected by climate change, offshore areas are also experiencing changes that impact salmon. Changing ocean conditions can affect foraging conditions available to salmon due to shifts in the types, distributions and biomass of prey species (Atcheson et al., 2012; Healey, 2011; Welch et al., 1998). It is thus critical to obtain historical baseline data on salmon foraging ecology that can help in understanding intra- and inter-specific salmon species responses to changing ocean conditions and increased hatchery production.

Salmon are size-selective consumers that have often been thought of as ecosystem samplers, consuming whatever prey is available in their environment (Brodeur, 1990; Karpenko et al., 2007). However, salmon are not completely indiscriminate consumers and different species have been found to have different dietary trophic niches. Chum have been shown to mostly consume zooplankton and are often considered to have a unique trophic niche due to their high consumption of gelatinous zooplankton (Brodeur, 1990; Dulepova and Dulepov, 2003; Myers and Aydin, 1996; Welch and Parsons, 1993). Sockeye and pink salmon diets are largely comprised of crustacean zooplankton and micronekton, in varying proportions (Ito, 1964; Kaeriyama et al., 2004; Qin and Kaeriyama, 2016). It has been hypothesized that competitive interactions exist between salmon, especially in years where pink salmon are abundant (Karpenko et al., 2007; Ruggerone et al., 2003; Ruggerone and Nielsen, 2004; Tadokoro et al., 1996). Evidence for this competition is found during years of high pink salmon abundance in the form of reduced salmon growth, reduced abundances of large phytoplankton and copepods, and chum salmon prey-switching to less nutritious prey (Andrievskaya, 1966; Batten et al., 2018; Ruggerone et al., 2005, 2003; Tadokoro et al., 1996). Improved understanding of the diets and trophic niche width and overlap of different salmon species can give insight into their degree of specialization, potential for competition, and vulnerability to changing conditions in the North Pacific. Furthermore, as ecosystem samplers, salmon diets provide insights into the effect of changing ocean conditions on zooplankton and micronekton, and the information gained in this way can be better qualified with a detailed knowledge of salmon trophic ecology.

The North Pacific Ocean is composed of a mosaic of dynamic ecosystems and regions, which include the Gulf of Alaska, Bering Sea, Sea of Okhotsk, Sea of Japan and the Subarctic Pacific (Figure 3.1). Diverse geomorphology and oceanographic processes in these regions lead to different levels of productivity and communities of plankton and nekton (Table 3.1). Although the diets of Pacific salmon in the open ocean have been studied since the early 1900s, there are very few quantitative studies comparing the diets of salmon species and their trophic niches across all regions of the dynamic North Pacific basin. However, salmon diets and trophic niche have been found to vary spatially across certain parts of the North Pacific. Research has revealed onshore to offshore changes in salmon diets (Auburn and Ignell, 2000; Carlson et al., 1996), intra-regional spatial differences (Davis et al., 2009; Fukataki, 1967; Kanno and Hamai, 1971; Starovoytov, 2007), as well as inter-regional differences (Brodeur et al., 2007b; Hertz et al., 2015; Karpenko et al., 2007; Qin and Kaeriyama, 2016; Takeuchi, 1972). Comparisons between the eastern and western North Pacific, specifically for post-juvenile salmon in off-shelf areas, have been limited, with the exception of Qin and Kaeriyama (2016) who compared spatially patchy salmon diet data in the Gulf of Alaska, Bering Sea and Western Subarctic Gyre from an unspecified time period. They found evidence that pink and sockeye predominantly consumed squid in the Gulf of Alaska and zooplankton in other areas, while chum consumed different zooplankton species throughout these three regions. Qin and Kaeriyama (2016) also examined overall trophic niche overlap for the entire North Pacific basin and reported high overlap for chum, pink and sockeye. However, the question of how trophic niche varies spatially is still unresolved. Since the migratory pathways of salmon span vast regions of the North Pacific, analysis of spatial diet data from across the basin can further understanding of the complex marine phase of the salmon life cycle.

Here we use the North Pacific Marine Salmon Diet Database (Graham et al., 2020) to investigate spatial and interspecies differences in diet and trophic niche between the three most abundant salmon species (chum, pink and sockeye) across the North Pacific Ocean during a baseline period. The spatial data used are from 1959–1969, during which time there was a lot of interest in studying salmon on the high seas and salmon diet data were collected with relatively good spatial coverage. The 1959–1969 time period was during a negative Pacific Decadal

Oscillation phase, meaning cooler conditions than normal in the eastern Pacific and warmer conditions than normal in the central and western Pacific (Mantua and Hare, 2002), and preceded the major effects of hatchery enhancement (Ruggerone and Irvine, 2018). This study establishes a historic baseline from which researchers can compare cross-basin changes in diet and trophic niche for chum, pink and sockeye salmon that furthers understanding of salmon production and the impact of ocean conditions across the North Pacific.

3.2 Methods

3.2.1 Data extraction and standardization

We extracted all pink, chum, and sockeye stomach content diet data between the years 1959 and 1969 from the North Pacific Marine Salmon Diet Database, as well as associated source, predator, and site information (Graham et al., 2020). Diet data for other salmon species did not have good spatial coverage and are therefore not included. If data were collected over a range of years that fell at least partially outside of this time period, then the latter data were excluded from the analysis. We eliminated the data that were not reported as weight or volume diet data because these were by far the most common diet metrics reported in the database and thus were the most comparable across the North Pacific. If data were reported as raw prey weight or volume, then they were converted to proportional data. Weight and volume data were combined for the analysis since they are closely related metrics and duplicated data were removed.

Since salmon are size-selective feeders, to standardize the data we only used diet data for salmon that were ocean age 1 and above. If the source provided the maturity of the salmon then immature, maturing, mature, and kelt were all included. If the source provided lengths or weights for the salmon then we used diet data from fish greater than 30 cm (Beamish, 2018) or greater than 289 g, based on the length-weight relationship for the genus *Oncorhynchus* from FishBase (Binohian and Pauly, 2000). If the samples included a mixture of juveniles (< ocean age 1) and post-juveniles, then these samples were excluded. If the source did not provide any information about salmon life stage but the data were collected from an offshore environment, then the samples were assumed to consist of post-juvenile salmon and were used in the analysis.

Most data were reported as summary statistics of diet data from multiple salmon of the same species and life stage collected by the same source from a certain time and spatial location with a certain gear type. However, where data were reported as raw data for individual fish, this information was averaged for each source, salmon species, salmon life stage, time, spatial location, and gear type. In order to compare diet data across multiple sources, we determined the prey taxonomic level of the analysis based on the level of detail reported in most cases for prey taxonomic groups. Since most studies reported to higher taxonomic levels (e.g., order – Decapoda, Amphipoda, subclass – Copepoda), we decided to use the following prey taxonomic categories in our analysis: amphipod, cephalopod, copepod, decapod, euphausiid, fish, and gastropod. Prey taxa that did not fit into these categories was grouped into an 'other' category. For this study, the 'other' category included prey taxonomies such as cnidarians, ctenophores, chaetognaths, polychaetes, ostracods, and larvaceans. To avoid false zeros, sources were eliminated if we had reason to believe they did not examine or report all of the prey categories listed above (1 source).

In addition to the diet data, we extracted average 8-daily total chlorophyll concentration data across the North Pacific between 1997–2010 from the Giovanni online data system [SeaWiFS SeaWiFS_L3m_CHL_8d v2018] (Acker and Leptoukh, 2007). These data were used to visualize spatial differences in productivity across the North Pacific. There is very limited chlorophyll data from the 1959–1969 time period, however, previous research supports the large-scale inter-regional trends in productivity reflected in the 1997–2010 data as long-term trends (Mackas and Tsuda, 1999; Saito et al., 2011; Sugimoto and Tadokoro, 1997).

3.2.2 Data analysis

We examined diet and trophic niche differences among different regions of the North Pacific: the Bering Sea, Sea of Okhotsk, Sea of Japan, Gulf of Alaska/Eastern Subarctic Pacific and the Western Subarctic Pacific (Figure 3.1). The Bering Sea was defined as the region north of the Aleutian Islands and Alaska Peninsula, south of the Bering Strait, west of Alaska, and east of Russia. The Sea of Okhotsk was defined as the region east of Sakhalin, north of the Kuril Islands and Hokkaido, and west of the Kamchatka Peninsula. The Sea of Japan was defined as the region between the Japanese archipelago, Sakhalin, Korea and the Russian mainland. The Gulf of Alaska/Eastern Subarctic was defined as the region south of the Bering Sea, east of -165°E and west of Southeast Alaska and British Columbia. The Western Subarctic was defined as the region south of the Bering Sea, west of -165°E and east of the Kamchatka Peninsula and Kuril Islands. If a sampling area overlapped with two regions, then the sampling area was assigned to the region where the majority of the sampling area lay.

To examine the differences between salmon species diets, we first performed two-dimensional non-metric multidimensional scaling (NMDS) based on a Bray-Curtis dissimilarity matrix of the arcsine square root transformed proportional diet data (Legendre and Legendre, 2012). The Bray-Curtis dissimilarity matrix is frequently used with community data that contain lots of zeros and this dissimilarity measure gives more weight to abundant species than rare species (Bray and Curtis, 1957; Legendre and Legendre, 2012). The arcsine square root transformation is commonly used for proportional data and can handle many zero values that are common in diet data (Sokal and Rohlf, 1995). This transformation is used to spread out the distribution of values while reducing the influence of the most common and most rare taxonomic groups. NMDS uses a dissimilarity matrix to rank differences between samples and reproduce those differences in a reduced number of dimensions. The NMDS analysis produces a measure of stress that represents the differences in distance between samples in reduced dimensional space versus complete multidimensional space, and that stress value should not exceed 0.2 for community data (Clarke, 1993). When visualizing the results, samples that are plotted closer together are more similar. Prey taxonomic category vectors, calculated by performing a version of Clarke and Ainsworth's (1993) BIOENV analysis, were projected onto the ordination plot to show how prey categories correlated with sample differences (Oksanen et al., 2016).

Pairwise analyses of similarity (ANOSIM) were then performed to test for differences in diet between species pairs. The ANOSIM test produces an R value between 0 and 1, which indicates whether species diets are more similar (closer to 0) or different (closer to 1), based on a comparison of within-group and between-group Bray-Curtis dissimilarities. To further interrogate species differences, we used a similarity percentages test (SIMPER) to determine the contribution of each prey taxonomic category to the average between-group Bray-Curtis dissimilarity (Clarke, 1993).

To assess spatial diet patterns across the North Pacific, we used Ward’s clustering method to analyze a Bray-Curtis dissimilarity matrix of the arcsine square rooted transformed proportional diet data. Ward’s method is an agglomerative hierarchical clustering method that merges objects by minimizing the within group sum-of-squares (Ward, 1963). Although the sum-of-squares calculation is technically based on a Euclidean model, this method still produces meaningful clusters for non-Euclidean data (Borcard et al., 2018). We also tried average linkage agglomerative hierarchical clustering and it produced similar clusters, so the results are not included.

We clustered data separately for each salmon species and determined an appropriate number of clusters by optimizing the silhouette coefficients and plots. Silhouette coefficients are a measure of a sample's similarity to its own cluster compared to other clusters and can range from -1 to 1, with a higher value signaling that the sample fits well within its own cluster (Rousseeuw, 1987). We examined average silhouette coefficients and silhouette plots for a range of cluster numbers from 2 to 9 for sockeye, pink and chum. To further illuminate spatial diet patterns, we calculated Spearman's rank correlation coefficients to determine how well each prey taxonomic group correlated with latitude and longitude midpoints. Spearman rank correlation is a nonparametric method for assessing how well the relationship between two variables can be described with either a linear or non-linear function.

To understand how trophic niche overlap between salmon species changed spatially across the North Pacific based on their diets, we used Schoener's index, defined by:

$$P_{ab} = \left[\sum_{i=1}^{n} (\min p_{ia}, p_{ib})\right] \times 100$$

where P_{ab} is the percentage overlap between species a and b, p_{ia} (and p_{ib}) are the percentage of all the prey taxonomic categories used by species a (or b) that is prey taxonomic category i, and n is the total number of prey taxonomic categories found in the diets. This is a common and simple index to examine percentage niche overlap with proportional data that are not sensitive to how prey items are grouped (Krebs, 1999; Schoener, 1970). Previous studies have considered niche overlap values of greater than 60% to be biologically significant (Wallace, 1981; Zaret and Rand, 1971). Other niche overlap indices, like Pianka's index, gave similar results so they are not included here. We also calculated average trophic niche overlap by species for the entire North Pacific and by region. Only samples where all three species were found at the same time and place were included in the trophic niche overlap calculations.

We also examined how trophic niche width, based on their diets, changed spatially for each salmon species using Levin's measure, defined by: $B = 1/\sum p_i^2$, where p is the proportion of diet consisting of prey taxonomic category i. We report the standardized index which is: $B_s = (B - 1)/(n - 1)$, where *n* represents the total number of prey taxonomic categories. Levin's measure gives relatively more weight to the abundant species as opposed to the rare species and it can be used with proportional data (Krebs, 1999; Levins, 1968). Novakowski et al. (2008) considered niche width values to be low if they were less than 0.4, moderate if they were less than 0.4 and greater than 0.6 and high if they were greater than 0.6. Other niche width indices, like the Shannon-Weiner index, gave similar results so they are not included here. Additionally, we calculated average trophic niche width by species for the entire North Pacific during this time period and by region. Only samples where all three species were found at the same time and place were included in the trophic niche width calculations.

We compared trophic niche width with trophic niche overlap between salmon species using beta regression with a logit link function. Beta regression is used to model relationships between variables that have values between 0 and 1 (Ferrari and Cribari-Neto, 2004). We tried other link functions, but they performed similarly to the logit link function based on the Akaike Information Criteria values, therefore these results are not included. Width and overlap data were transformed prior to regression using the following equation to remove values of exactly 0 or 1: $(y \cdot (n - 1) + 0.5)/n$, where *n* is sample size (Smithson and Verkuilen, 2006). We also calculated a pseudo R^2 value, which is the squared correlation of the linear predictor and link-transformed response.

All statistical analyses were conducted in R statistical software v3.6.1 (R Core Team, 2019) with multivariate analyses performed using the "vegan" package (Oksanen et al., 2016). The "cluster" package was used to calculate silhouette coefficients (Maechler et al., 2019), the "spaa" package was used to calculate niche width and niche overlap indices (Zhang, 2016) and the "betareg" package was used to perform beta regression analyses (Cribari-Neto and Zeileis, 2010). Results were visualized using R statistical software v3.6.1 (R Core Team, 2019).

3.3 Results

A total of 9 sources were used in the final diet data spatial meta-analysis and these sources provided data from the Sea of Japan, Sea of Okhotsk, Subarctic Pacific, Bering Sea, and the Gulf of Alaska between the years 1959 and 1969 (Table 3.2). Most available data were collected from the Subarctic Pacific, Bering Sea, and the Gulf of Alaska, while minimal data were collected from the Sea of Japan and Sea of Okhotsk.

3.3.1 Species differences in diet composition

Species differences in diet were apparent between sockeye, chum and pink salmon with the most abundant prey items being 'other' for chum, fish for pink and cephalopods for sockeye (Figure 3.2). A non-metric multidimensional scaling ordination in two-dimensional space (stress = 0.199) confirmed differences in diet among the salmon species (Figure 3.3). This was also supported by ANOSIM tests which showed significant differences between all pairwise comparisons of species — chum and sockeye ($R = 0.185$, $p < 0.001$), chum and pink ($R = 0.161$, $p < 0.001$), as well as sockeye and pink ($R = 0.037$, $p < 0.001$). Prey taxonomic classification vectors overlaid on the NMDS ordination plot showed the prey taxonomic category of 'other' mainly driving differences between chum and other species, while several different prey species, including fish and cephalopods, drove differences between pink and sockeye (Figure 3.3). A SIMPER analysis revealed that the prey taxonomic categories contributing most to dissimilarity between pink and sockeye salmon were fish (14.6%), cephalopods (13.9%), amphipods (13.2%) and euphausiids (12.2%). Fish made up 22.8% of prey in both pink and sockeye diets. Cephalopods made up 11.0% of pink diets and 26.6% of sockeye diets. Amphipods made up 21.1% of pink diets and 18.0% of sockeye diets. And finally, euphausiids made up 17.6% of pink diets and 17.9% of sockeye diets. The category of 'other' contributed the most to dissimilarity between chum and other species (18.8% for pink, 19.1% for sockeye), while other prey taxonomic categories did not come close to 'other' in percent contribution (Table 3.3). The category of 'other' made up 41.6% of prey in chum diets, 6.2% of prey in pink diets and 5.3% of prey in sockeye diets.

3.3.2 Spatial differences in diet composition

Cluster analyses produced 6 clusters for chum (silhouette coefficient = 0.49), 6 for pink (silhouette coefficient = 0.35), and 4 for sockeye (silhouette coefficient = 0.41) (Figure 3.4). Based on the clusters, there appeared to be some spatial patterns for chum, pink and sockeye, to varying degrees (Figure 3.5). Spatial differences in diet were also supported by Spearman rank correlations between latitude, longitude and the different prey taxonomic categories (Table 3.4).

The cluster analysis revealed a distinct feeding behavior for chum in the Gulf of Alaska and Eastern Subarctic, where they consumed a high proportion of prey items classified into the 'other' taxonomic category (Cluster 2). While this dietary pattern was also present to some extent in the Western Subarctic, it was minimal in the Bering Sea. Spearman rank correlations revealed a significant positive correlation between longitude and 'other' ($\rho = 0.445$, $p < 0.001$)

while there was a weak negative, non-significant correlation between latitude and ‘other’ ($\rho = -0.039$, $p = 0.418$). From the cluster analysis, chum appeared to consume more amphipods and copepods in the Bering Sea and the northern Gulf of Alaska/Eastern Subarctic compared to other areas (Cluster 3). Amphipods showed a significant negative correlation with longitude ($\rho = -0.255$, $p < 0.001$), while copepods showed a weak, non-significant negative correlation ($\rho = -0.086$, $p = 0.078$). In the Western Subarctic, chum seemed to consume a mixture of mainly euphausiids, gastropods and ‘other’ (Clusters 1, 2, & 4). Euphausiids ($\rho = -0.308$, $p < 0.001$) and gastropods ($\rho = -0.515$, $p < 0.001$) had significant negative correlations with longitude, while ‘other’ ($\rho = 0.445$, $p <0.001$) had a significant positive correlation with longitude. In the Sea of Okhotsk, chum consumed mostly cephalopods (Cluster 5), but the sample size was limited and confined to a relatively small spatial area. Cephalopods did show a significant negative correlation with longitude ($\rho = -0.365$, $p < 0.001$) and a weaker, but still significant, negative correlation with latitude ($\rho = -0.141$, $p = 0.004$).

For pink salmon diets, the cluster analysis revealed evidence of an onshore to offshore gradient in the Gulf of Alaska/Eastern Subarctic where they consumed more gastropods closer to shore, specifically off the coast of Southeast Alaska and Canada (Cluster 5). This trend was not apparent in the Spearman rank correlations, likely because this spatial pattern only occurred in a small area of the North Pacific. From the cluster analysis, pink salmon also appeared to consume more euphausiids, copepods and ‘other’ in the Subarctic Pacific (Clusters 3 & 6), compared to the Bering Sea. However, only copepods showed a significant negative correlation with latitude ($\rho = -0.285$, $p <0.001$) while euphausiids and ‘other’ showed weak, non-significant negative correlations ($\rho = -0.010$, $p = 0.844$; $\rho = -0.052$, $p = 0.279$). Euphausiids did show a negative correlation with longitude ($\rho = -0.198$, $p < 0.001$) and were more common prey in the western

North Pacific (Cluster 3). Amphipods (Cluster 1) and fish (Cluster 4) were common in pink diets across the North Pacific, but amphipods were more common in the western North Pacific ($\rho = -0.271$, $p < 0.001$) and fish were more common in the northern North Pacific ($\rho = 0.208$, $p < 0.001$). In the Sea of Okhotsk and Sea of Japan there were few samples, but amphipods dominated these samples (Cluster 1).

Based on the cluster analysis, sockeye diets showed some evidence of a latitudinal gradient in the Gulf of Alaska/Eastern Subarctic where they appeared to consume more fish in the north and more cephalopods in the south. Spearman rank correlations supported this pattern, with fish having a strong positive correlation with latitude ($\rho = 0.184$, $p < 0.001$) and cephalopods having a strong negative correlation with latitude ($\rho = -0.2$, $p < 0.001$). In the Bering Sea, the cluster analysis revealed potential longitudinal patterns which included sockeye consuming more fish in the eastern Bering Sea (Cluster 4), more cephalopods in the central Bering Sea (Cluster 2) and a variety of mainly zooplankton in the western Bering Sea (Cluster 1). When looking across the entire North Pacific, the cluster analysis showed that sockeye consumed more zooplankton in the Western Subarctic (Clusters 1 & 3) and more micronekton in the Bering Sea and Gulf of Alaska/Eastern Subarctic (Clusters 2 & 4). These patterns were not always apparent in the Spearman rank correlations, likely because they were not strictly latitudinal or longitudinal gradients. The Spearman rank correlations showed significantly lower consumption of cephalopods in the north ($\rho = -0.2$, $p < 0.001$) and a higher consumption of fish in the north and west ($\rho = 0.184$, $p < 0.001$). Additionally, Spearman rank correlations showed higher consumption of euphausiids and amphipods in the west ($\rho = -0.117$, $p < 0.008$; $\rho = -0.258$, $p < 0.001$). Prey taxonomic categories such as decapod, copepod, gastropod and ‘other’ did show significant correlations with latitude or longitude but made up a relatively small percent of sockeye diets (Table 3.4).

3.3.3 Species differences in trophic niche overlap and trophic niche width

Schoener's index of niche overlap revealed spatial patterns in trophic niche overlap for all three species interactions (chum/pink, chum/sockeye, and pink/sockeye) (Figure 3.6). Overall, trophic niche overlap did not exceed the 60% threshold for biological significance for any of the species pairs. The highest trophic niche overlap across the North Pacific was between pink and sockeye (46.6%), followed by chum and pink (31.8%), and lastly by chum and sockeye (30.9%). This pattern was consistent for the Gulf of Alaska and Eastern and Western Subarctic, but in the Bering Sea, overlap between chum and sockeye was higher than overlap between chum and pink. In general, trophic niche overlap was higher in the Western Subarctic for all species pairs, followed by the Bering Sea and then the Gulf of Alaska/Eastern Subarctic. Chum and pink overlap as well as chum and sockeye overlap appeared to follow similar spatial patterns with patches of high trophic niche overlap in the western portion of the Eastern Subarctic and in the Western Subarctic, especially near the Aleutian Islands. Pink and sockeye overlap was more spatially homogenous.

Levin's standardized measure of trophic niche width revealed spatial patterns in niche width for chum, pink and sockeye (Figure 3.7). Overall, niche width was low for all species. Chum had the narrowest niche width (0.108), followed by sockeye (0.129) and then pink (0.138). However, this pattern was not consistent across the spatial regions. Trophic niche width was highest in the Western Subarctic for all species, compared to other regions. Pink and sockeye seemed to follow similar spatial patterns in trophic niche width, while chum appeared to have a lower niche width in the central portion of the Gulf of Alaska/Eastern Subarctic compared to other areas. Beta regression of trophic niche width and trophic niche overlap by species all resulted in positive slopes and relatively low R^2 values (Figure 3.8). The relationships with highest R^2 values were chum width compared to chum/pink overlap ($R^2 = 0.197$) and chum width compared to chum/sockeye overlap ($R^2 = 0.143$). Other relationships had much lower R^2 values (≤ 0.06).

3.4 Discussion

This study examined the trophic ecology of the three most abundant open ocean rearing North Pacific salmon species—sockeye, pink and chum—for the time period 1959–1969, a baseline period during a negative phase of the PDO and before the major growth of hatchery enhancement. We demonstrate differences in trophic ecology across the more data rich North Pacific regions, including the Gulf of Alaska/Eastern Subarctic, the Bering Sea and the Western Subarctic. In the Gulf of Alaska/Eastern Subarctic and the Bering Sea, salmon consumed a mixture of zooplankton and micronekton while in the Western Subarctic they consumed mostly zooplankton. Within regions, smaller-scale spatial trophic patterns were observed, including latitudinal, onshore-offshore, and cross-gyre gradients. These spatial patterns differed by species and chum, pink and sockeye salmon were found to have distinct feeding patterns in diverse regions of the North Pacific. Overall, chum had the most distinct foraging ecology, with high consumption of ‘other’—which likely consisted of mainly gelatinous prey, such as cnidarians and ctenophores—and consistent consumption of zooplankton across the North Pacific. Sockeye and pink had high trophic niche overlap and consumed more varied diets containing both zooplankton and micronekton, depending on the region. Sockeye tended to eat more micronekton than pink, while pink had more diverse diets in which they consumed a mixture of zooplankton and micronekton, giving them the largest trophic niche width among the three species. Below we discuss these finding in detail and their application in untangling the dynamic marine phase of the salmon life cycle.

Our findings on large-scale spatial patterns in interspecies diets and trophic niche largely agreed with previous findings for the North Pacific Ocean. In the Western Subarctic, chum, pink and sockeye diets were the most similar with all species consuming mainly zooplankton. This region had both the highest trophic niche overlap and niche width values. On the other side of the Pacific, in the Gulf of Alaska and Eastern Subarctic, interspecies diet differences were most apparent, with chum consuming mainly zooplankton while pink consumed a mixture of zooplankton and micronekton and sockeye consumed mostly micronekton. Niche overlap and niche width were lower in the Gulf of Alaska and Eastern Subarctic compared to the Western Subarctic in all cases. Although environmental and biological data from 1959–1969 were limited, previous research has found a long-term trend in which the western part of the Subarctic Pacific has been more productive, in terms of primary productivity and zooplankton biomass, compared to the eastern part (Table 3.1; Figure 3.9). Therefore, diet specialization in the eastern part may be due to more limited prey in this region. This could be attributed to a higher concentration of nutrients in the west than the east (Serno et al., 2014; Nishioka et al., 2020). In the Bering Sea, chum mostly consumed zooplankton while pink and sockeye consumed largely micronekton. Trophic niche overlap values were in the range of values calculated for the Subarctic Pacific/Gulf of Alaska and niche width was low for all species in this region. Qin and Kaeriyama (2016) found similar large-scale spatial patterns between these regions with some slight differences. They found chum, pink and sockeye salmon consumed mostly zooplankton in the Western Subarctic and Bering Sea, while they mainly consumed micronekton, specifically squid, in the Gulf of Alaska, except for chum which consumed largely zooplankton in all regions. These differences could be due to the time period in which they collected their samples, however, the sampling dates in that study were not noted which makes comparisons difficult. Our results also included some data from other regions, like the Sea of Okhotsk and Sea of Japan, however, data from these regions were limited, making it difficult to draw any conclusions about the trophic ecology of salmon in these areas.

In addition to large-scale trophic patterns, our data revealed some fine-scale spatial diet patterns by species. One of these fine-scale patterns was the consumption of gastropods by pink salmon in the eastern Gulf of Alaska. Other studies have shown gastropods to be important prey for juvenile and adult pink salmon near southeast Alaska (Orsi et al., 1997; Sturdevant et al., 2012; Sturdevant and Ignell, 1997), suggesting that this is a consistent feature of the region. In the Gulf of Alaska, sockeye salmon showed latitudinal differences in diet, consuming more fish in the north and more cephalopods in the south. Cephalopods have previously been shown to make up a large component of salmon diets in the Gulf of Alaska/Eastern Subarctic (Kaeriyama et al., 2004; Qin and Kaeriyama, 2016). The prevalence of cephalopods in the diets of sockeye in the south, likely reflects their temperature-dependent growth and distributions, with greater abundance in the warmer southern Gulf of Alaska/Eastern Subarctic than the cooler northern Gulf of Alaska/Eastern Subarctic (Fiscus and Mercer, 1982; Forsythe, 2004). These findings highlight the potential importance of ocean conditions in determining salmon diet, and the need for a better understanding of how factors such as temperature, salinity, stratification and circulation impact North Pacific ecosystems and foraging conditions for salmon.

In addition to the fine-scale diet patterns, our robust spatial data pointed to some novel, fine-scale trophic niche patterns, a metric that is normally reported for salmon only at coarse spatial scales. With regards to trophic niche overlap, while pink and sockeye showed fairly consistent spatial overlap across the North Pacific, chum revealed certain hotspots of niche overlap with both pink and sockeye. These areas included the perimeter of the Alaskan Gyre, in addition to the area directly south of the Aleutian Islands. In these areas, niche width was also relatively high for chum. These fine-scale patterns in trophic niche may be attributed to all salmon species feeding on abundant prey that accumulate at the edges of the Alaskan Gyre and the Western Subarctic Gyre compared to lower prey biomass in the middle of these gyres (Mackas and Tsuda, 1999). We found a positive relationship between niche overlap values and niche width values, and this relationship was particularly apparent for chum niche width and chum niche overlap with sockeye and pink salmon. This supports the idea that in areas where prey are abundant and diverse, such as the edges of these gyres, chum salmon are consuming the same prey that pink and sockeye are consuming, and these areas may provide a refuge from competition. However, when chum migrate away from these areas and prey become less abundant, competition increases and chum begin to specialize, causing them to have both low niche overlap and width values.

Our findings support previous research showing that chum salmon have a distinct foraging ecology compared to other species of salmon and we provide new evidence in support of chum specializing due to competition with other salmon species. Chum have been found to specialize on zooplankton and types of prey not usually consumed by other species, specifically gelatinous prey, such as cnidarians and ctenophores (Brodeur, 1990; Dulepova and Dulepov, 2003; Myers and Aydin, 1996; Welch and Parsons, 1993). Chum have been shown to have anatomical differences compared to pink and sockeye which may be related to their specialization on gelatinous prey that is generally considered lower quality compared to other zooplankton and micronekton prey (Davis et al., 1998). For example, chum salmon have large and highly acidic stomachs, which allow for rapid digestion of large prey items, and a small spleen, which may force chum to adopt less active feeding strategies (Azuma, 1995; Welch, 1997). In our analysis, we examined historic diet data that were coarse in taxonomic resolution; however, the ‘other’ category that was often consumed by chum and rarely by other species has been identified by previous studies as likely comprising mainly gelatinous prey that is quickly digested and difficult to identify during stomach content analyses (Brodeur, 1990; Davis, 2003). Our research found that chum were not always consuming gelatinous prey across the North Pacific and they were found to disproportionately consume large amounts of ‘other’ in the Gulf of Alaska/Eastern Subarctic, an area with relatively low productivity (Table 3.1; Figure 3.9). Our trophic niche spatial comparison revealed that in areas where chum salmon were consuming large amounts of ‘other’ they had very low niche overlap with pink and sockeye and they also had low niche width. This suggests that chum specialization on prey not usually consumed by other species may be a way of avoiding competition in areas of lower productivity. Limited previous research supports the idea that chum salmon may change their diets in response to increases in the abundance of other salmon species which can cause competition (Andrievskaya, 1966; Kaga et al., 2013; Tadokoro et al., 1996).

Our findings support previous research showing that pink and sockeye salmon have similar diets and trophic niche, however, our results suggest that there are important interspecies spatial differences to consider as well. Pink and sockeye diets were the most similar and had the highest trophic niche overlap, both alternating between zooplankton and micronekton prey. However, these species showed spatial differences in diets reflected in variable consumption of micronekton. Sockeye had a tendency to consume more micronekton compared to pink, especially in the Gulf of Alaska/Eastern Subarctic where they consumed a high percentage of cephalopods. This tendency of sockeye to consume at a slightly higher trophic level compared to pink is supported by stable isotope analyses, even though their diets are usually considered to be very similar (Welch and Parsons, 1993; Johnson and Schindler, 2009; Kaeriyama et al., 2000; Qin and Kaeriyama, 2016). Sockeye also had less diverse diets than pink and chum, with the fewest number of clusters and the lowest niche width among species, indicating that they may specialize on micronekton when they are available. Qin and Kaeriyama (2016) also hypothesized that sockeye selectively feed on squids when they are available. Pink salmon showed the greatest niche width among species and alternated between zooplankton and micronekton more than both chum and sockeye. This is in contrast to the results of Qin and Kaeriyama (2016) who found chum to have the highest trophic niche width, however, our results do show similar niche width for pink, chum and sockeye when averaged across all spatial areas. It is possible that this similarity in trophic niche was due to the coarseness of the diet information and it is important to analyze higher-resolution taxonomic data that could yield different results.

When comparing the diets of sockeye, pink and chum salmon we found that they fell into a gradient of specialist to generalist consumers, and that this gradient had a spatial component. Chum salmon were found to be the most specialized consumers due to their high consumption of ‘other’, likely gelatinous prey, and this may be due to competition with other salmon species. Sockeye salmon were also found to be more specialist consumers, specializing on micronekton, and more specifically cephalopods, compared to other species. Pink salmon, in contrast, were more generalist consumers, alternating between a diverse array of zooplankton and micronekton across the North Pacific. Our results suggest that different species may be able to provide different information about the dynamic marine phase of the salmon life cycle based on their tendencies to be specialists versus generalists. Generalists, like pink salmon, may better reflect overall prey presence and abundance in the environment, while specialists like chum and sockeye may better reflect interspecies dynamics (competition) and/or specific prey presence and abundance—micronekton for sockeye and zooplankton for chum.

The information gained from the diets of each salmon species provide important insights into the marine phase of the salmon life cycle that can help in understanding the future of salmon production and North Pacific ecosystems. A robust spatial comparison with more recent data on salmon diets may help in understanding the carrying capacity of the North Pacific by revealing whether competition has increased with increased salmon production over the past half-century. If this is true, we might expect chum salmon to consume more gelatinous prey. The data used in this study were collected during a negative phase of the PDO, during which conditions were cooler than average in the east and warmer than average in the central and the west. Comparison of these data with a positive phase of the PDO could yield valuable insights into the effect of a shift on ocean conditions on salmon prey fields, competition and production, including the effects of warming in the eastern Pacific. For example, we would expect climate driven ocean warming to cause changing prey distributions and abundance, potentially leading to increased abundance of prey that prefer warmer waters, like squids and decreased abundance of prey that prefer cooler waters, such as certain fish and copepods (Batten and Welch, 2004; Peterson and Schwing, 2003). Finally, it should be noted that improved taxonomic data in diet studies could make an important contribution to improved understanding of ocean warming impacts on salmon trophic ecology. For example, such data can be used to estimate the nutritional quality of prey, an important aspect for salmon production that can only be coarsely examined with low taxonomic resolution data.

3.5 Conclusion

Overall, this study provided a novel and robust cross-basin comparison of salmon diet and trophic niche during a negative PDO phase in the north Pacific (1959–1969). While supporting limited previous research on large-scale spatial and interspecies salmon diet differences, this study also revealed novel fine-scale patterns that point to the importance of sub-mesoscale oceanographic features in Pacific salmon foraging ecology. Our findings suggest that the spatial trophic ecology of chum, pink and sockeye salmon may provide unique insights into challenges salmon face from changing ocean conditions and interspecies interactions. Studying the diets of specialist consumers, like chum and sockeye salmon, may further understanding of competition, productivity, and ocean conditions relevant to specific prey items, like gelatinous organisms in the case of chum and micronekton in the case of sockeye. Studying the diets of pink salmon, which tend to be generalist consumers, may further understanding of overall prey presence, abundance and diversity, which can help in understanding ecosystem responses to changing ocean conditions. In the future, salmon may face increased challenges from climate change and rising hatchery production and studying both the large-scale and fine-scale spatial trophic ecology of different salmon species can provide insight into these challenges. Future research should address how interspecies and spatial trophic dynamics have changed over time in order to inform questions related to salmon production in a rapidly changing world.

3.6 Tables

Table 3.1. Oceanographic and biological information for each region of the North Pacific Ocean. The regions correspond to the shaded areas in Figure 3.1. Sea surface temperatures were calculated using time averaged reconstructed monthly sea surface temperatures from the NOAA Extended Reconstructed Sea Surface Temperature (ERSST) model (version 4). Chlorophyll concentrations were calculated using time averaged 8-daily total chlorophyll concentrations from the Giovanni online data system, developed and maintained by the NASA Goddard Earth Sciences Data and Information Services Center [SeaWiFS SeaWiFS_L3m_CHL_8d v2018]. For sea surface temperatures, chlorophyll concentrations, and zooplankton concentrations, the years that were averaged are listed in parenthesis. Results reflect available long-term regional averages as much as possible because data were sparse for the 1959–1969 time period, with the exception of reconstructed temperature data for which the 1959–1969 data reflected the same long-term inter-regional differences shown in the table. The errors listed are standard deviations.

Region	Sea ice dominated ecosystem	Large continental shelf	Sea surface temperature (°C)	Chlorophyll concentration (mg/m^3)	Zooplankton concentration (mg/m^3)	Common zooplankton species	Common nekton species
Gulf of Alaska/Eastern Subarctic (Alaskan Gyre)	No	No	9.89 ± 2.13 (1950-2019)[1]	0.700 ± 1.410 (1997-2010)[2]	243.03 ± 283.49 (1960-1994)[3]	*Neocalanus* spp., *Thysanoessa spinifera*, *T. longipes*[4]	*Pseudopentaceros wheeleri*[5]; *Pandalus borealis*, *Theragra chalcogramma*, *Hippoglossoides elassodon*[6]; *Berryteuthis anonychus*[7]
Western Subarctic (Western Subarctic Gyre)	No	No	7.88 ± 2.25 (1950-2019)[1]	0.558 ± 0.368 (1997-2010)[2]	355.69 ± 356.63 (1954-1994)[3]	*Neocalanus* spp., *Parasagitta elegans*[8]	*Cololabis saira*, *Todarodes pacificus*[5]
Bering Sea	Yes	Yes	4.25 ± 1.13 (1950-2019)[1]	1.722 ± 1.447 (1997-2010)[2]	Western Bering Sea: 923.35 (1984-2006)[8] Eastern Bering Sea: 492.37 ± 448.12 (1955-1994)[3]	Western Bering Sea: *Eucalanus bungii*, *Neocalanus plumchrus*, *Parasagitta elegans*[8] Eastern Bering Sea: *Calanus* spp., *Parasagitta elegans*, *Aglantha digitale*[9]	Western Bering Sea: *Boreoteuthis borealis*, *Stenobrachius leucopsarus*, *Pleurogrammus monopterygius*, *Theragra chalcogramma*[10] Eastern Bering Sea: *T. chalcogramma*, *Clupea pallasi*, *Mallotus villosus*[11]

Region	Sea ice dominated ecosystem	Large continental shelf	Sea surface temperature (°C)	Chlorophyll concentration (mg/m^3)	Zooplankton concentration (mg/m^3)	Common zooplankton species	Common nekton species
Sea of Okhotsk	Yes	Yes	4.15 ± 0.78 (1950-2019)[1]	1.766 ± 1.522 (1997-2010)[2]	1104.15 (1984-2006)[8]	*Thysanoessa raschii, Metridia okhotensis, Parasagitta elegans*[8]	*Theragra chalcogramma, Clupea pallasii, Leuroglossus schmidti*[12]
Sea of Japan	No	No	13.19 ± 3.26 (1950-2019)[1]	0.761 ± 0.879 (1997-2010)[2]	49.05 ± 22.18 (1966-1990)[13]	*Calanus* spp., *Oithona* spp.[14]; *Metridia pacifica*[13]	*Todarodes pacificus, Theragra chalcogramma*[15]

[1] Huang, B., Banzon, V.F., Freeman, E., Lawrimore, J., Liu, W., Peterson, T.C., Smith, T.M., Thorne, P.W., Woodruff, S.D., Zhang, H.-M., 2015. Extended reconstructed sea surface temperature version 4 (ERSST.v4). Part I : Upgrades and intercomparisons. American Meterological Society 28, 911–930.

[2] Acker, J.G., Leptoukh, G., 2007. Online analysis enhances use of NASA earth science data. Eos Transactions American Geophysical Union 88(2), 14,17.

[3] Sugimoto, T., Tadokoro, K., 1997. Interannual-interdecadal variations in zooplankton biomass, chlorophyll concentration and physical environment in the subarctic Pacific and Bering Sea. Fisheries Oceanography 6(2), 74–93.

[4] Mackas, D.L., Tsuda, A., 1999. Mesozooplankton in the eastern and western subarctic Pacific: Community structure, seasonal life histories, and interannual variability. Progress in Oceanography 43, 335–363.

[5] Brodeur, Richard D., McKinnell, S., Nagasawa, K., Pearcy, W., Radchenko, V., Takagi, S., 1999. Epipelagic nekton of the North Pacific Subarctic and Transition zones. Progress in Oceanography 43, 365–397.

[6] Anderson, P.J., Piatt, J.F., 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecology Progress Series 189, 117–123.

[7] Jorgensen, E.M., 2007. Identification, distribution and relative abundance of paralarval gonatid squids (Cephalopoda: Oegopsida: Gonatidae) from the Gulf of Alaska, 2001–2003. Journal of Molluscan Studies 73, 155–165.

[8] Volkov, A.F., 2008. Mean annual characteristics of zooplankton in the Sea of Okhotsk, Bering Sea and Northwestern Pacific (Annual and seasonal biomass values and predominance). Russian Journal of Marine Biology 34(7), 437–451.

[9] Eisner, L.B., Napp, J.M., Mier, K.L., Pinchuk, A.I., Andrews, A.G., 2014. Climate-mediated changes in zooplankton community structure for the eastern Bering Sea. Deep-Sea Research Part II: Topical Studies in Oceanography 109, 157–171.

[10] Somov, A.A., 2017. The seasonal dynamics of the abundance and species composition of nekton in the upper epipelagic layer of the Western Bering Sea. Russian Journal of Marine Biology 43(7), 535–554.

[11] Brodeur, Richard D, Wilson, M.T., Walters, G.E., Melnikov, I. V, 1999. Forage fishes in the Bering Sea: Distribution, species associations, and biomass trends, in: Loughlin, T.R., Ohtani, K. (Eds.), Dynamics of the Bering Sea. University of Alaska Sea Grant, Fairbanks, U.S.A., pp. 509–580.

[12] Sukhanov, V. V., Ivanov, O.A., 2012. Biocenotic zoning in the Sea of Okhotsk based on the species structure of nekton. Russian Journal of Marine Biology 38(4), 299–309.

[13] Hirota, Y., Hasegawa, S., 1999. The zooplankton biomass in the Sea of Japan. Fisheries Oceanography 8(4), 274–283.

[14] Ashjian, C.J., Davis, C.S., Gallager, S.M., Alatalo, P., 2005. Characterization of the zooplankton community, size composition, and distribution in relation to hydrography in the Japan/East Sea. Deep Sea Research II 52, 1363–1392.

[15] Zhang, C.I., Lee, J.B., Seo, Y. Il, Yoon, S.C., Kim, S., 2004. Variations in the abundance of fisheries resources and ecosystem structure in the Japan/East Sea. Progress in Oceanography 61, 245–265.

Table 3.2. The sources from the North Pacific Marine Salmon Diet Database included in the analysis. Sources are listed in order of their source_id number, which corresponds to their source_id in the database.

Source ID	Reference
1	Andrievskaya, L. D. (1966). Food relationships of the Pacific salmon in the sea. Voprosy Ikhtiologii, 6(1), 84–90.
8	Fukataki, H. (1967). Stomach contents of the pink salmon, Oncorhynchus gorbuscha (Walbaum), in the Japan Sea during the spring season of 1965. Bull. Jap. Sea Reg. Fish. Res. Lab., 17, 49–66.
10	Ito, J. (1964). Food and feeding habits of Pacific salmon (genus Oncorhynchus) in their oceanic life. Bulletin of the Hokkaido Regional Fisheries Research Laboratory, 29, 85–97.
13	Kanno, Y., & Hamai, I. (1972). Food of salmonid fish in the Bering Sea in summer of 1966. Bulletin Faculty of Fisheries Hokkaido University, 22, 107–128.
14	Karpenko, V. I., Volkov, A. F., & Koval, M. V. (2007). Diets of Pacific salmon in the Sea of Okhotsk, Bering Sea, and northwest Pacific Ocean. North Pacific Anadromous Fish Commission Bulletin, 4, 105–116.
18	Takeuchi, I. (1972). Food animals collected from the stomachs of three salmonid fishes (Oncorhynchus) and their distribution in the natural environments in the northern North Pacific. Bull. Hokkaido Reg. Fish. Res. Lab, 38, 1–119.
44	Lebrasseur, R. J., & Doidge, D. A. (1966). Stomach contents of salmonids caught in the Northeastern Pacific Oean - 1963 & 1964. Fisheries Research Board of Canada, 5(23).
45	Lebrasseur, R. J., & Doidge, D. A. (1966). Stomach contents of salmonids caught in the Northeastern Pacific Ocean - 1962. Fisheries Research Board of Canada, 4(22), 80 pp.
46	LeBrasseur, R. J., & Doidge, D. A. (1966). Stomach contents of salmonids caught in the Northeastern Pacific Ocean - 1959 & 1960. Fisheries Research Board of Canada, 3(21), 67 pp.

Table 3.3. The percent contribution of prey taxonomic categories to the average Bray-Curtis dissimilarity between sockeye, pink and chum salmon in the North Pacific Ocean, as determined by SIMPER analysis.

Prey taxonomic category	Sockeye/Chum	Pink/Chum	Pink/Sockeye
Amphipod	10.9	11.9	13.2
Cephalopod	13.9	8.2	13.9
Copepod	5.3	6.2	5.6
Decapod	1.8	1.6	2.1
Euphausiid	11.4	11.0	12.2
Fish	12.9	12.6	14.6
Gastropod	6.4	9.3	7.2
Other	19.1	18.8	5.6

Table 3.4. Spearman rank correlations between latitude, longitude and prey taxonomic categories for chum, pink and sockeye. Latitude and longitude midpoints were calculated for spatial polygons. Longitude was assessed on a scale from 0° to 360° with lower values in the west and higher values in the east. Negative correlations are red and positive values are blue with darker colors representing stronger correlations. Significant correlations ($p < 0.05$) are denoted by asterisks.

	Prey taxonomic category	Chum	Pink	Sockeye
Latitude	Amphipod	-0.012	-0.080	-0.017
	Cephalopod	-0.141*	-0.138*	-0.200*
	Copepod	0.046	-0.285*	-0.082
	Decapod	0.069	0.071	0.154*
	Euphausiid	-0.090	-0.010	0.156*
	Fish	0.0876	0.208*	0.184*
	Gastropod	-0.142*	-0.057	-0.028
	Other	-0.039	-0.052	-0.012
Longitude	Amphipod	-0.255*	-0.271*	-0.258*
	Cephalopod	-0.365*	-0.372*	0.063
	Copepod	-0.086	-0.335*	-0.192*
	Decapod	0.007	0.056	-0.078
	Euphausiid	-0.308*	-0.198*	-0.117*
	Fish	-0.142*	-0.051	-0.129*
	Gastropod	-0.515*	0.006	-0.262*
	Other	0.445*	-0.135*	-0.098*

3.7 Figures

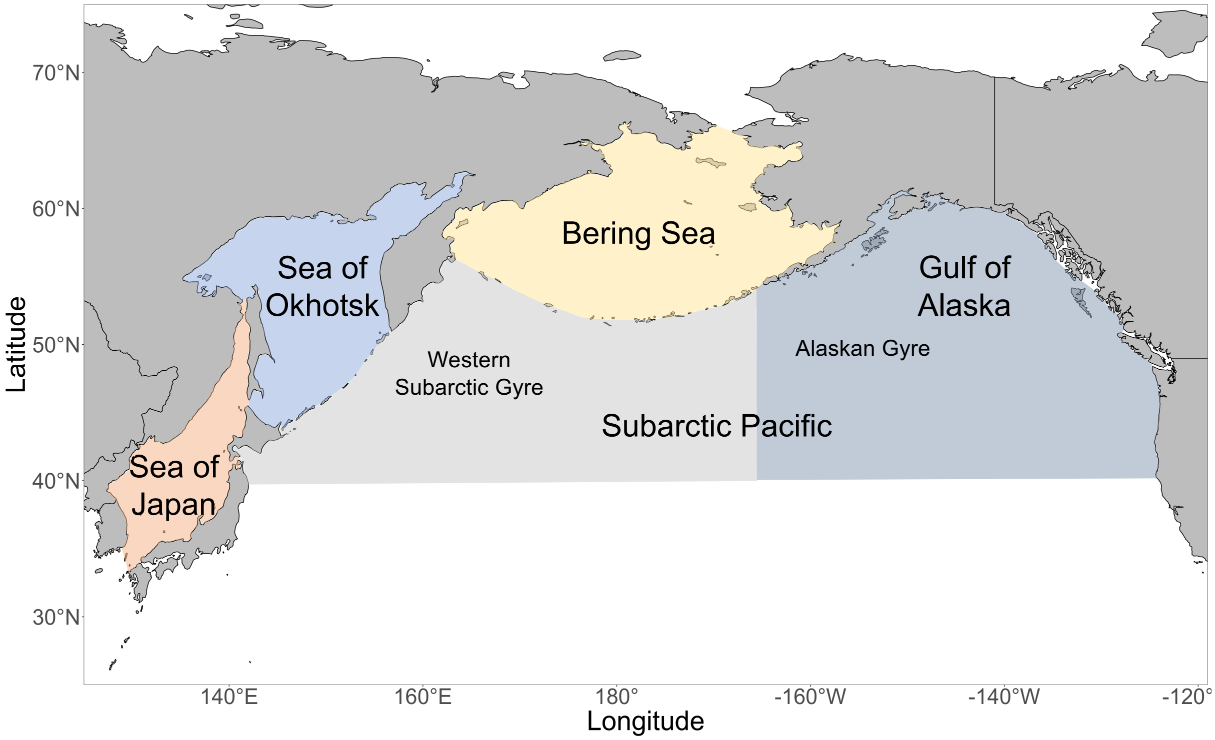


Figure 3.1. A map of the regions in the North Pacific Ocean. The colors in the Subarctic Pacific represent the Gulf of Alaska/Eastern Subarctic (blue, right) and the Western Subarctic (gray, left).

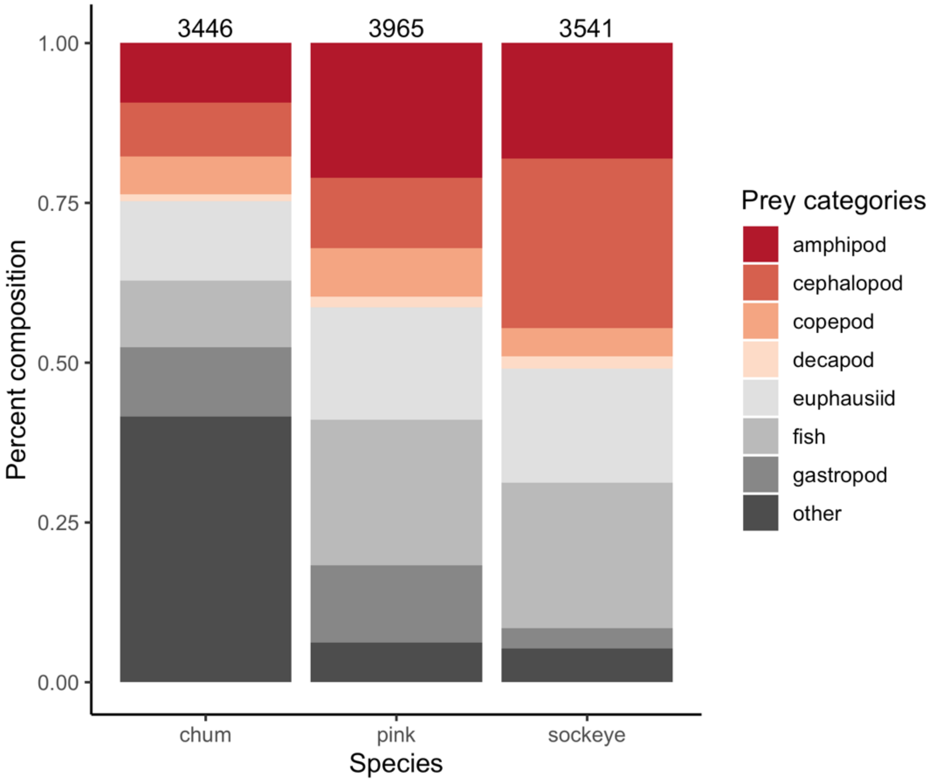


Figure 3.2. Average proportional diet composition by species across the North Pacific. Known sample sizes (total number of salmon) are displayed above each bar. These numbers are an underestimate of the actual sample size since it was not always reported in the source.

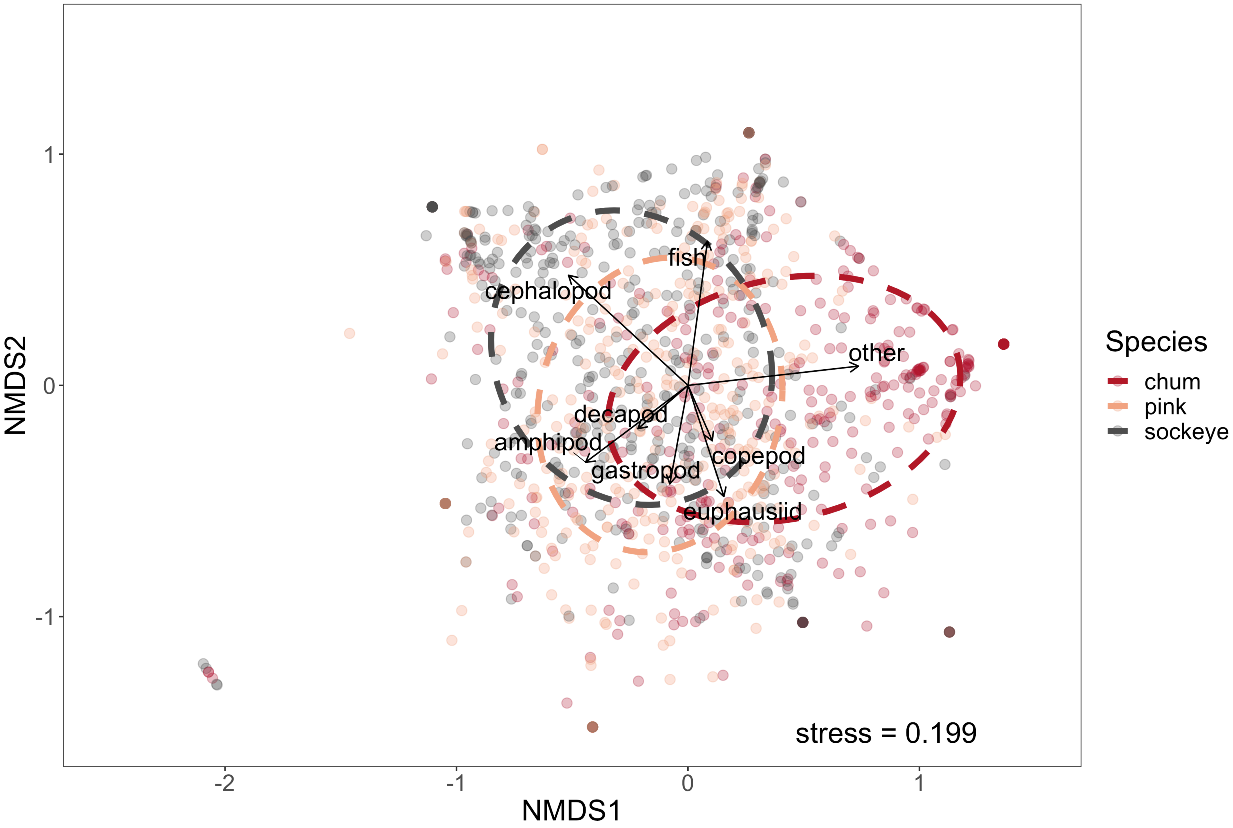
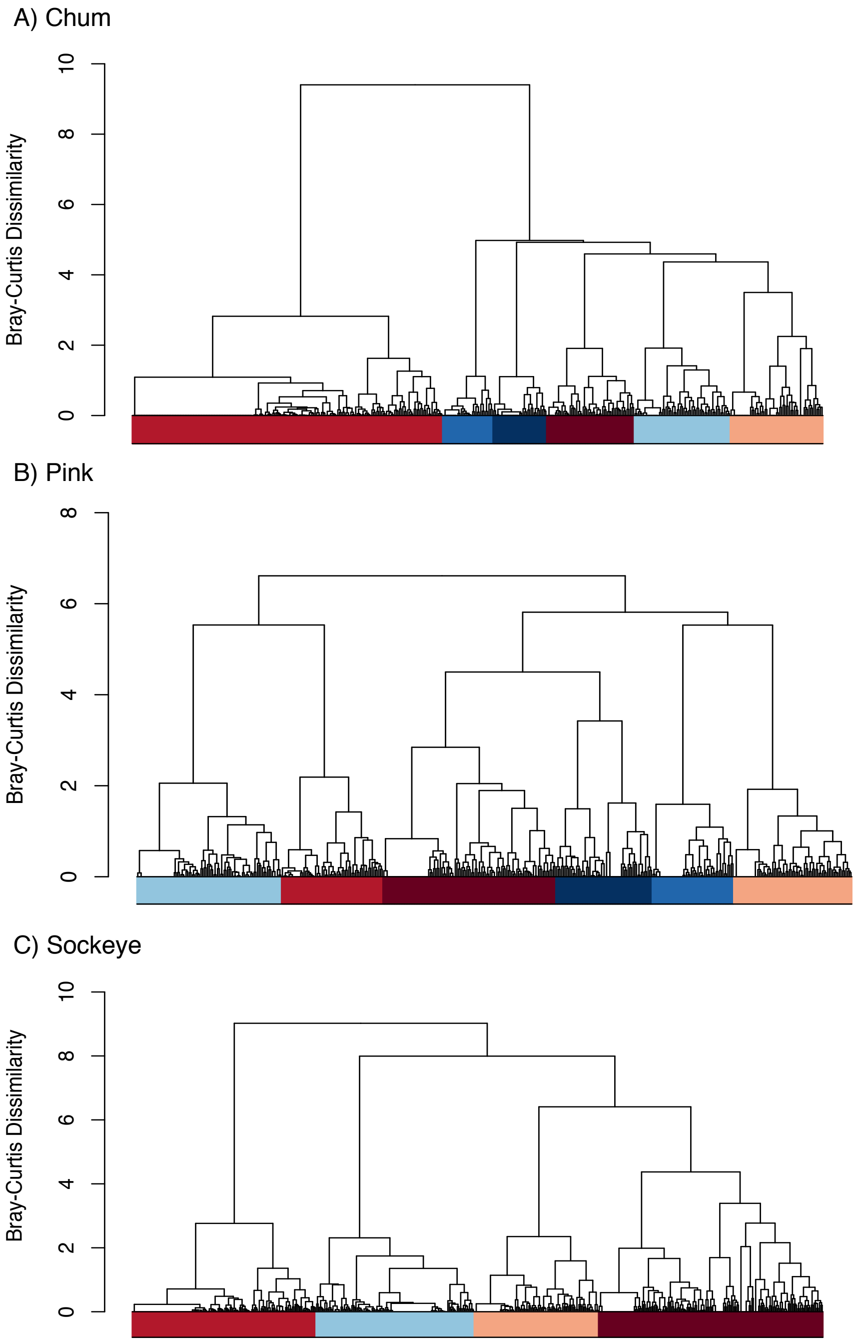


Figure 3.3. Non-metric multidimensional scaling ordination of Bray-Curtis dissimilarities between arcsine square root transformed proportional weight/volume data for prey taxonomic classifications of chum, pink and sockeye stomach content data. Prey taxonomic classification vectors are overlaid on the ordination to show how prey taxonomic groups relate to species differences in diet composition. Ellipses represent standard deviation.

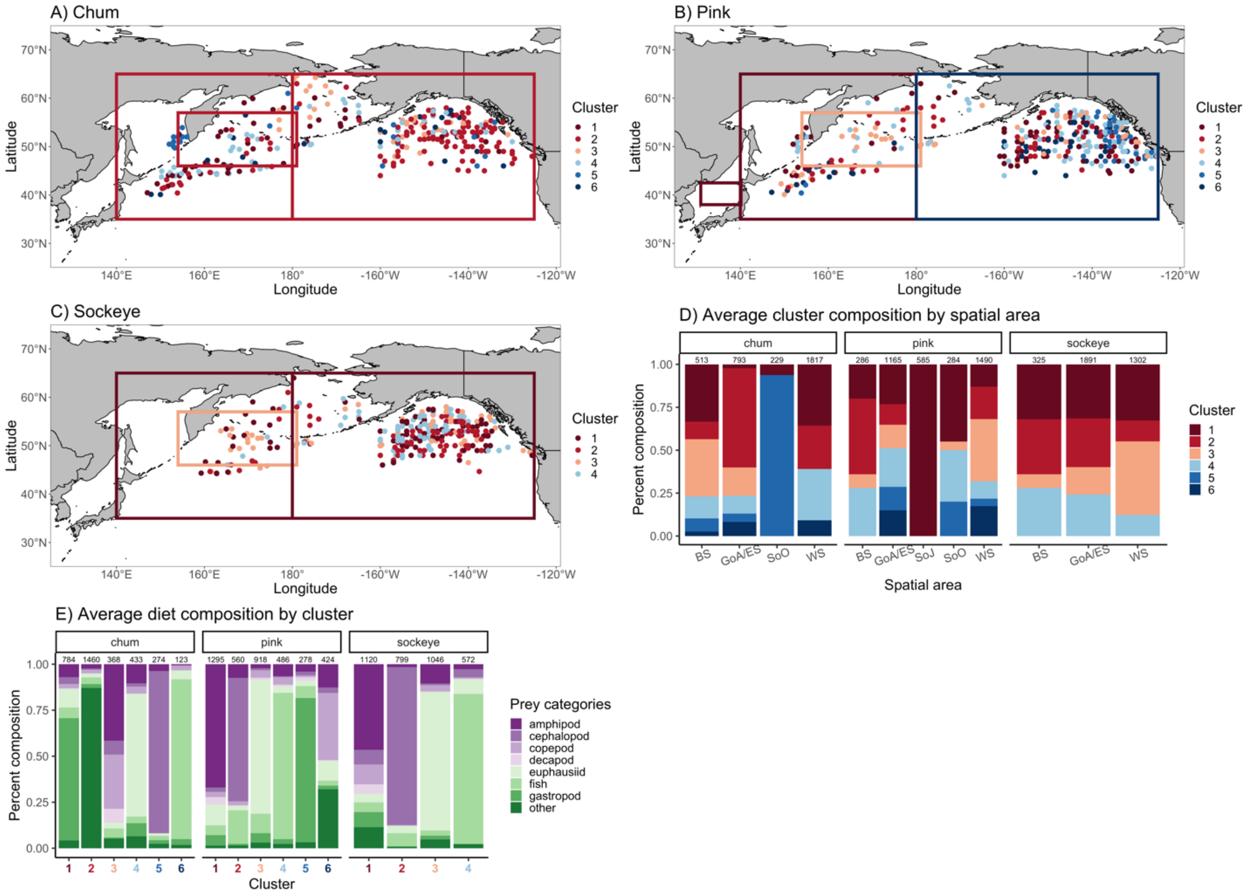


A) Chum

B) Pink

C) Sockeye

Figure 3.4. Dendrograms of a cluster analysis performed on Bray-Curtis dissimilarities between arcsine square root transformed proportional weight/volume diet data for (A) chum, (B) sockeye and (C) pink salmon. Colored bars below dendrograms denote different clusters. Ward's clustering method was performed separately for each salmon species. Silhouette coefficients and plots were used to determine the number of clusters.


A) Chum

B) Pink

C) Sockeye

D) Average cluster composition by spatial area

E) Average diet composition by cluster

Figure 3.5. Spatial representation of a cluster analysis performed on Bray-Curtis dissimilarities between arcsine square root transformed proportional weight/volume diet data of (A) chum, (B) sockeye and (C) pink salmon. Ward’s clustering method was performed separately for each salmon species. Silhouette coefficients and plots were used to determine the number of clusters. The proportional cluster composition for each species and spatial area (BS = Bering Sea, GoA/ES = Gulf of Alaska/Eastern Subarctic, SoJ = Sea of Japan, SoO = Sea of Okhotsk, WS = Western Subarctic) is displayed (D) with known samples sizes (total number of salmon) above each bar. The average proportional diet composition of each cluster and species is displayed (E) with known sample sizes above each bar. The sample sizes displayed are an underestimate of the actual sample sizes since these values were not always reported in the source. Cluster colors correspond to the color-coding scheme from Figure 3.4.

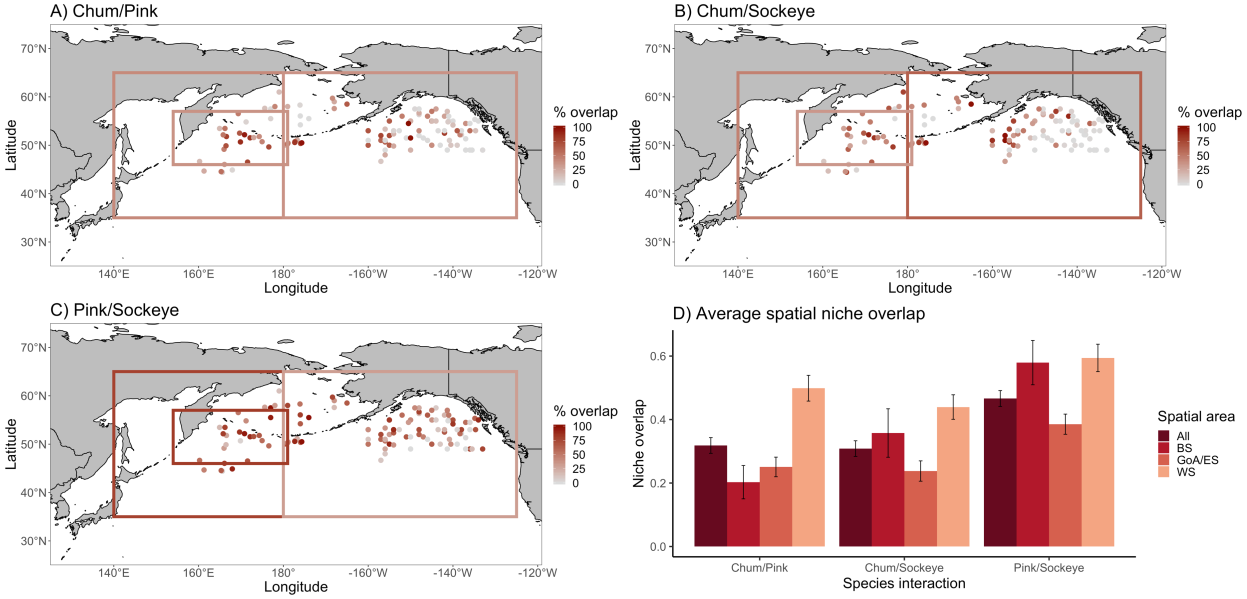


Figure 3.6. A spatial map of trophic niche overlap, measured using Schoener's index of niche overlap, for (A) chum/pink, (B) chum/sockeye and (C) pink/sockeye calculated for each site where chum, sockeye and pink were collected together at the same time. Additionally, the average spatial niche overlap for the entire North Pacific (All) and broken down by three regions (BS = Bering Sea, GoA/ES = Gulf of Alaska/Eastern Subarctic, WS = Western Subarctic) are displayed with standard error bars (D).

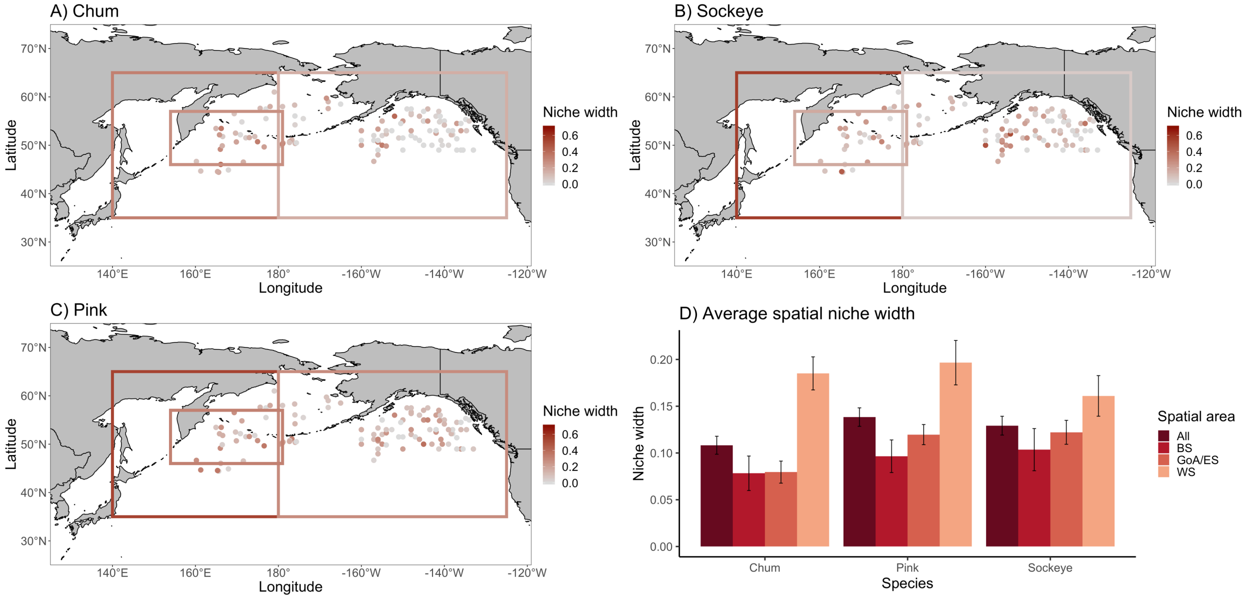


Figure 3.7. A spatial map of trophic niche width, reported using Levin's standardized measure, for (A) chum, (B) sockeye and (C) pink calculated for each site where chum, sockeye and pink were collected together at the same time. Additionally, the average spatial niche overlap for the entire North Pacific (All) and broken down by three regions (BS = Bering Sea, GoA/ES = Gulf of Alaska/Eastern Subarctic, WS = Western Subarctic) are displayed with standard error bars (D).

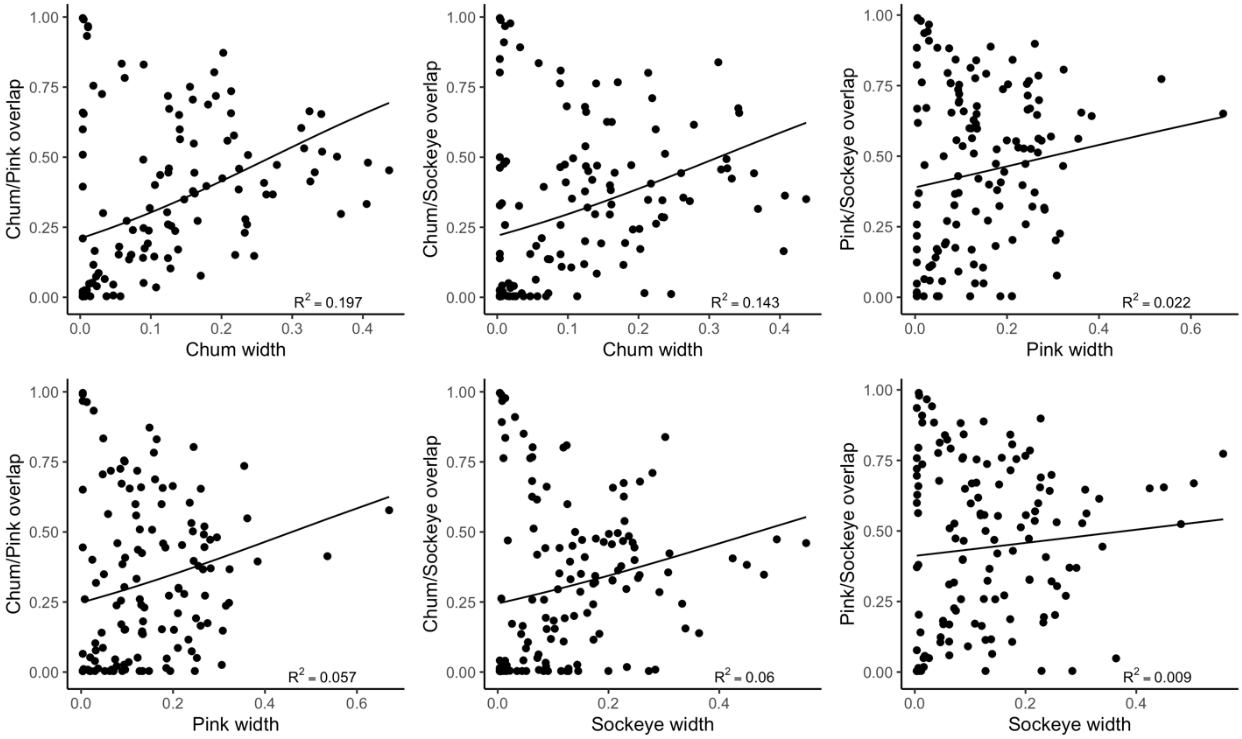


Figure 3.8. The relationships between trophic niche width for salmon species and trophic niche overlap between species pairs fitted using beta regression with a logit link function. Prior to regression, data were transformed using $(y \cdot (n - 1) + 0.5)/n$, where n is sample size, to remove values of 0 and 1. The R^2 value represents the pseudo-R^2 value, which is calculated by squaring the correlation of the linear predictor and link-transformed response.

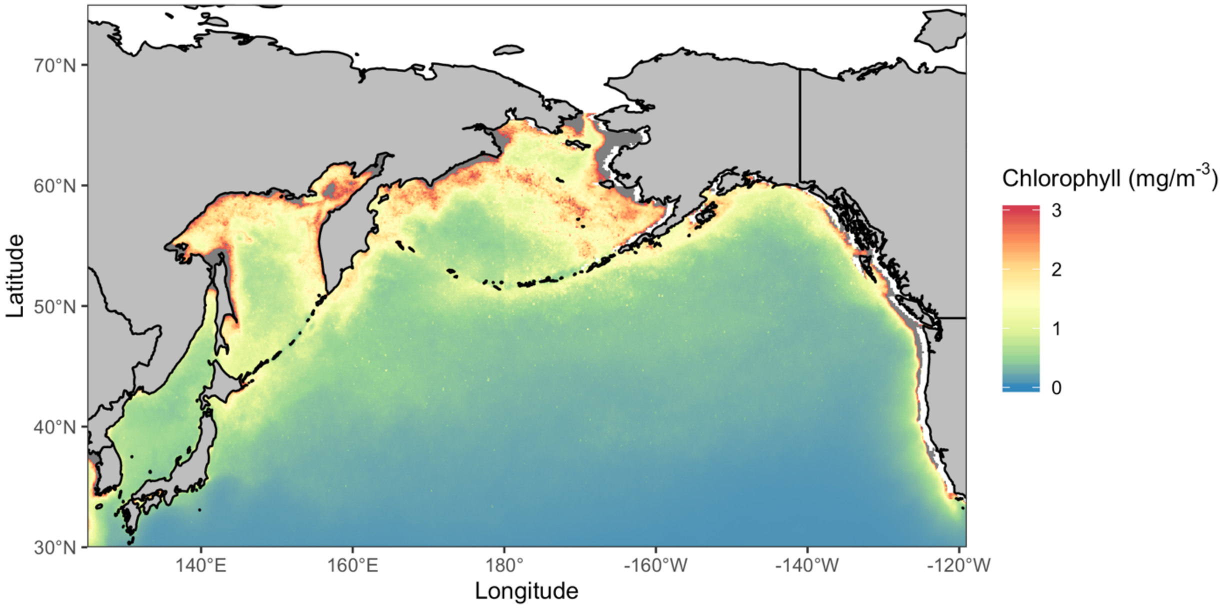


Figure 3.9. Time averaged 8-daily total chlorophyll concentration (mg/m^3) at 9 km x 9 km resolution across the North Pacific from 1997-2010. Values above 3 mg/m^3 are gray. Source: Giovanni online data system, developed and maintained by the NASA Goddard Earth Sciences Data and Information Services Center [SeaWiFS SeaWiFS_L3m_CHL_8d v2018].

Chapter 4: Conclusion

Pacific salmon are facing an increasingly unpredictable future as they are exposed to threats at all stages of their dynamic life cycle. The least understood threats to salmon occur during their marine phase and the high seas portion of their life cycle in particular is not well understood. This is likely because it is challenging to study, due to the inaccessibility of the open ocean and the high cost of this research. However, increasingly questions are arising about the effects of climate change on this phase and about the carrying capacity of the North Pacific as total salmon abundance reaches a record high (Ruggerone and Irvine, 2018). Salmon diets have been studied for decades and they can help to answer some of these questions by revealing information about salmon health, potential competition, and changing ocean ecosystems. This research arose from a need to 1) collate and make available historic salmon diet data from the marine phase and 2) gain a better understanding of baseline spatial and interspecies trophic dynamics across the North Pacific Ocean.

Prior to the development of the North Pacific Marine Salmon Diet Database, it was very time-intensive to find and analyze salmon diet data from the marine environment at the North Pacific basin scale. Even though salmon diets have been studied for decades, these data have previously only been available in disparate peer-reviewed and gray literature from the countries of Korea, Japan, Russia, Canada and the United States. This new database tool will be instrumental in facilitating international collaboration on issues that are pertinent to salmon during their dynamic marine phase, when they cross international boundaries and interact with stocks from different countries (Beacham et al., 2009; Myers et al., 2007; Ruggerone et al., 2003; Urawa et al., 2004). Chapter 2 presented the initial compilation of data for the database that were identified through a systematic literature review process. However, the database will continue to grow and was built to house all types of salmon diet information—from stomach contents, to stable isotopes, to fatty acids—as well as associated predator and prey biological information and environmental data. This resource is available to everyone and our hope is that it will encourage researchers to consider standardizing the format of their data to allow for easy incorporation into the database and to encourage the release of data that are currently being held in inaccessible institutional archives.

In Chapter 3, a subset of the initial compilation of data from the North Pacific Marine Salmon Diet Database, presented in Chapter 2, were analyzed to study baseline spatial and interspecies salmon dynamics across the North Pacific Ocean. This study presented a robust, cross-basin spatial analysis of salmon trophic ecology from a baseline period 1959–1969, during a negative Pacific Decadal Oscillation phase when the effects of hatchery enhancement were minimal. Data on chum, pink and sockeye salmon diets revealed both large- and fine-scale spatial patterns and interspecies differences in trophic ecology. These findings supported limited previous research by Qin and Kaeriyama (2016) on large-scale spatial and interspecies diet differences in the North Pacific, such as higher consumption of zooplankton in the more productive Western Subarctic compared to the less productive Eastern Subarctic/Gulf of Alaska where certain species like pink and sockeye consumed more micronekton. This research also supported previous studies showing overall interspecies differences in the trophic ecology of chum, pink and sockeye, with chum consuming more zooplankton while pink and sockeye alternated more between zooplankton and micronekton. However, these findings revealed novel fine-scale interspecies trophic patterns, that were not revealed by previous coarser and/or region-specific spatial studies. For example, chum salmon were found to have higher trophic niche width and overlap with pink and sockeye at the edges of the Subarctic gyres, which may be due to an abundance of diverse prey in these areas that could provide relief from competition. Overall, interspecies differences suggested that chum, pink and sockeye can help reveal unique and important spatial information about the changing North Pacific Ocean. Pink, the more generalist consumers, may better reflect overall prey presence and abundance in the environment, while chum and sockeye, the more specialist consumers, may better reflect interspecies dynamics and/or specific prey presence and abundance of gelatinous prey and micronekton, respectively.

This study provided information on baseline spatial and interspecies trophic dynamics for chum, pink and sockeye, however, further research is required to understand how these dynamics have changed over time and will continue to change with increased hatchery production and varying environmental conditions, such as those brought on by climate change. Numerous studies have shown that environmental conditions affect the composition of North Pacific ecosystems and in turn affect the diets and trophic ecology of salmon (Anderson and Piatt, 1999; Batten and Welch, 2004; Brodeur et al., 2007a; Kaeriyama et al., 2004; Kim et al., 2017; Mantua et al., 1997; Peterson and Schwing, 2003). There is less evidence linking increased salmon abundance to changes in salmon trophic ecology, however, fluctuations in numbers of pink salmon have been correlated with ecosystem-level changes, including diet shifts for chum salmon (Andrievskaya, 1966; Karpenko et al., 2007; Ruggerone et al., 2003; Ruggerone and Nielsen, 2004; Springer and Van Vliet, 2014; Tadokoro et al., 1996). Based on fluctuations in pink abundance, Connors et al. (2020) found that spatial considerations are of high importance when trying to understand the combined effects of hatchery enhancement and climate change on salmon production. By understanding past spatial and interspecies salmon trophic ecology, we can better understand the present and future of salmon in the North Pacific.

In conclusion, this study presents a new tool for North Pacific researchers and an example of how this tool can be used to address questions about the understudied marine phase of the salmon life cycle. Studying salmon diets can not only help further understanding of salmon life histories but can also help further understanding of North Pacific ecosystems more broadly and promote better management practices. For example, diet information is an important component of ecosystem models, which are becoming critical tools in ecosystem-based management (Jamieson et al., 2010). However, in order to increase understanding of the dynamic and vast North Pacific Ocean, people must work together at an international level to study these ecosystems and share data that are critical to the management of salmon and other North Pacific species. We hope that this research encourages collaboration in a time of rapid, human-induced change.

References

Abdul-Aziz, O.I., Mantua, N.J., Myers, K.W., Bradford, M., 2011. Potential climate change impacts on thermal habitats of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean and adjacent seas. Canadian Journal of Fisheries and Aquatic Sciences 68, 1160–1680.

Acker, J.G., Leptoukh, G., 2007. Online analysis enhances use of NASA earth science data. Eos Transactions American Geophysical Union 88(2), 14,17.

Anderson, P.J., Piatt, J.F., 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecology Progress Series 189, 117–123.

Andrievskaya, L.D., 1966. Food relationships of the Pacific salmon in the sea. Voprosy Ikhtiologii 6 (38), 84–90 (Translation by U.S. Joint Publications Research Service for Bureau of Commercial Fisheries, Seattle, U.S.A, 11 pp).

Atcheson, M.E., Myers, K.W., Beauchamp, D.A., Mantua, N.J., 2012. Bioenergetic response by steelhead to variation in diet, thermal habitat, and climate in the North Pacific Ocean. Transactions of the American Fisheries Society 141, 1081–1096.

Auburn, M.E., Ignell, S.E., 2000. Food habits of juvenile salmon in the Gulf of Alaska July–August 1996. North Pacific Anadromous Fish Commission Bulletin 2, 89–97.

Azuma, T., 1995. Biological mechanisms enabling sympatry between salmonids with special reference to sockeye and chum salmon in oceanic waters. Fisheries Research 24, 291–300.

Bailey, T.G., Youngbluth, M.J., Owen, G.P., 1995. Chemical composition and metabolic rates of gelatinous zooplankton from midwater and benthic boundary layer environments off Cape Hatteras, North Carolina, USA. Marine Ecology Progress Series 122, 121–134.

Batten, S.D., Ruggerone, G.T., Ortiz, I., 2018. Pink salmon induce a trophic cascade in plankton populations in the southern Bering Sea and around the Aleutian Islands. Fisheries Oceanography 27, 548–559.

Batten, S.D., Welch, D.W., 2004. Changes in oceanic zooplankton populations in the north-east Pacific associated with the possible climatic regime shift of 1998/1999. Deep-Sea Research Part II: Topical Studies in Oceanography 51, 863–873.

Beacham, T.D., Candy, J.R., Sato, S., Urawa, S., Le, K.D., Wetklo, M., 2009. Stock origins of chum salmon (Oncorhynchus keta) in the Gulf of Alaska during winter as estimated with microsatellites. North Pacific Anadromous Fish Commission Bulletin 5, 15–23.

Beamish, R.J. (Ed.), 2018. The Ocean Ecology of Pacific Salmon and Trout. American Fisheries Society, Bethesda, U.S.A.

Beamish, R.J., 2017. What the past tells us about the future of Pacific salmon research. Fish and Fisheries 18(6), 1161–1175.

Beamish, R.J., Mahnken, C., 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography 49, 423–437.

Binohian, C., Pauly, D., 2000. The LENGTH-WEIGHT Table, in: Froese, R., Pauly, D. (Eds.), FishBase 2000: Concepts, Design and Data Sources. ICLARM, Los Baños, Laguna, Philippines, pp. 131–133.

Borcard, D., Gillet, F., Legendre, P., 2018. Numerical Ecology with R, 2nd ed. Springer International Publishing AG, Cham, Switzerland.

Bradford, M.J., 1995. Comparative review of Pacific salmon survival rates. Canadian Journal of

Fisheries and Aquatic Sciences 52(6), 1327–1338.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27(4), 325–349.

Brodeur, R.D., 1990. A synthesis of the food habits and feeding ecology of salmonids in marine waters of the North Pacific (INPFC Doc.; FRI-UW-9016). Fisheries Research Institute, University of Washington, Seattle, U.S.A., 38 pp.

Brodeur, R.D., Daly, E.A., Schabetsberger, R.A., Mier, K.L., 2007a. Interannual and interdecadal variability in juvenile coho salmon (Oncorhynchus kisutch) diets in relation to environmental changes in the northern California Current. Fisheries Oceanography 16(5), 395–408.

Brodeur, R.D., Daly, E.A., Sturdevant, M. V, Miller, T.W., Moss, J.H., Thiess, M.E., Trudel, M., Weitkamp, L.A., Armstrong, J., Norton, E.C., 2007b. Regional comparisons of juvenile salmon feeding in coastal marine waters off the west coast of North America. American Fisheries Society Symposium 57, 183–203.

Brodeur, R.D., Ware, D.M., 1992. Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. Fisheries Oceanography 1(1), 32–38.

Bugaev, V.F., Welch, D.W., Selifonov, M.M., Grachev, L.E., Eveson, J.P., 2001. Influence of the marine abundance of pink (Oncorhynchus gorbuscha) and sockeye salmon (O. nerka) on growth of Ozernaya River sockeye. Fisheries Oceanography 10(1), 26–32.

Carlson, H.R., Myers, K.W., Farley, E. V, Jaenicke, H.W., Haight, R.E., Guthrie, C.M., 1996. Cruise report of the F/V Great Pacific survey of young salmon in the North Pacific—Dixon entrance to Western Aleutians—July–August 1996 (NPAFC Doc. 222.) Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Juneau, U.S.A, 50 pp.

Carmack, E., Winsor, P., Williams, W., 2015. The contiguous panarctic Riverine Coastal Domain: A unifying concept. Progress in Oceanography 139, 13–23.

Chapman, W.M., 1936. The pilchard fishery of the state of Washington in 1936 with notes on the food of the silver and Chinook salmon off the Washington coast (Biological Report No. 36C). State of Washington, Division of Scientific Research, Department of Fisheries, Olympia, U.S.A., 20 pp.

Clarivate Analytics, n.d. Web of Science: Core Collection. URL www.webofknowledge.com (accessed 4.9.19).

Clarivate Analytics, n.d. Web of Science: Zoological Record. URL www.webofknowledge.com (accessed 4.9.19).

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18, 117–143.

Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. Marine Ecology Progress Series 92, 205–219.

Colombi, B.J., Brooks, J.F. (Eds.), 2012. Keystone nations: Indigenous Peoples and salmon across the North Pacific. School for Advanced Research Press, Santa Fe, U.S.A.

Connors, B., Malick, M.J., Ruggerone, G.T., Rand, P., Adkison, M., Irvine, J.R., Campbell, R., Gorman, K., 2020. Climate and competition influence sockeye salmon population dynamics across the Northeast Pacific Ocean. Canadian Journal of Fisheries and Aquatic Sciences 77, 943–949.

Cribari-Neto, F., Zeileis, A., 2010. Beta regression in R. Journal of Statistical Software 34(2), 1–

24.

Criddle, K.R., Shimizu, I., 2014. The economic importance of wild Pacific salmon, in: Woo, P.T.K., Noakes, D.J. (Eds.), Salmon: Biology, Ecological Impacts and Economic Importance. Nova Science Publishers Inc., New York, U.S.A., pp. 269–306.

Cupples, J.B., Crowther, M.S., Story, G., Letnic, M., 2011. Dietary overlap and prey selectivity among sympatric carnivores: Could dingoes suppress foxes through competition for prey? Journal of Mammalogy 92(3), 590–600.

Dale, K.E., Daly, E.A., Brodeur, R.D., 2017. Interannual variability in the feeding and condition of subyearling Chinook salmon off Oregon and Washington in relation to fluctuating ocean conditions. Fisheries Oceanography 26(1), 1–16.

Daly, E.A., Benkwitt, C.E., Brodeur, R.D., Litz, M.N.C., Copeman, L.A., 2010. Fatty acid profiles of juvenile salmon indicate prey selection strategies in coastal marine waters. Marine Biology 157, 1975–1987.

Davis, N.D., 2003. Feeding ecology of Pacific salmon (Oncorhynchus spp.) in the Central North Pacific Ocean and Central Bering Sea. 1991-2000. Hokkaido Univeriesty, PhD thesis.

Davis, N.D., Myers, K.W., 1998. Caloric value of high-seas salmon prey organisms and simulated salmon ocean growth and prey consumption. North Pacific Anadromous Fish Commission Bulletin 1, 146–162.

Davis, N.D., Takahashi, M., Ishida, Y., 1996. The 1996 Japan-U.S. cooperative high-seas salmon research cruise of the Wakatake maru and a summary of 1991–1996 results (NPAFC Doc. 194; FRI-UW-9617). Fisheries Research Institute, University of Washington, Seattle, U.S.A; National Research Institute of Far Seas Fisheries, Shimizu, Japan, 45 pp.

Davis, N.D., Volkov, A. V, Efimkin, A.Y., Kuznetsova, N.A., Armstrong, J.L., Sakai, O., 2009. Review of BASIS salmon food habits studies. North Pacific Anadromous Fish Commission Bulletin 5, 197–208.

Dean, M.N., Bizzarro, J.J., Summers, A.P., 2007. The evolution of cranial design, diet, and feeding mechanisms in batoid fishes. Integrative and Comparative Biology 47(1), 70–81.

DeCasien, A.R., Williams, S.A., Higham, J.P., 2017. Primate brain size is predicted by diet but not sociality. Nature Ecology and Evolution 1, 0112.

Di Lorenzo, E., Schneider, N., Cobb, K.M., Franks, P.J.S., Chhak, K., Miller, A.J., McWilliams, J.C., Bograd, S.J., Arango, H., Curchitser, E., Powell, T.M., Rivière, P., 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophysical Research Letters 35, L08607.

Doney, S.C., Ruckelshaus, M., Emmett Duffy, J., Barry, J.P., Chan, F., English, C.A., Galindo, H.M., Grebmeier, J.M., Hollowed, A.B., Knowlton, N., Polovina, J., Rabalais, N.N., Sydeman, W.J., Talley, L.D., 2012. Climate change impacts on marine ecosystems. Annual Review of Marine Science 4(1), 11–37.

Dulepova, E.P., Dulepov, V.I., 2003. Interannual and interregional analysis of chum salmon feeding features in the Bering Sea and adjacent Pacific waters of Eastern Kamchatka (NPAFC Doc. 728). Pacific Research Fisheries Centre, TINRO-Centre, Vladivostok, Russia, 8 pp.

Fecher, B., Friesike, S., 2014. Open science: One term, five schools of thought, in: Bartling, S., Friesike, S. (Eds.), Opening Science: The Evolving Guide on How the Internet Is Changing Research, Collaboration and Scholarly Publishing. Springer, Heidelberg, Germany, pp. 17–48.

Ferrari, S.L.P., Cribari-Neto, F., 2004. Beta regression for modelling rates and proportions. Journal of Applied Statistics 31(7), 799–815.

Fiscus, C.H., Mercer, W., 1982. Squids taken in surface gillnets in the North Pacific Ocean by the Pacific Salmon Investigations Program 1955–72 (NOAA Technical Memorandum NMFS F/NWC-28). Seattle, U.S.A., 32 pp.

Food and Agriculture Organization of the United Nations, n.d. ProQuest: Aquatic Sciences and Fisheries Abstracts. URL https://search.proquest.com/asfa (accessed 4.9.10).

Forsythe, J.W., 2004. Accounting for the effect of temperature on squid growth in nature: From hypothesis to practice. Marine and Freshwater Research 55, 331–339.

Francis, R.C., Hare, S.R., 1994. Decadal-scale regime shifts in the large marine ecosystems of the North-east Pacific: A case for historical science. Fisheries Oceanography 3(4), 279–291.

Fukataki, H., 1967. Stomach contents of the pink salmon, Oncorhynchus gorbuscha (Walbaum), in the Japan Sea during the spring season of 1965. Bulletin of the Japan Sea Regional Fisheries Research Laboratory 17, 49–66. In Japanese: English abstract.

Fukuwaka, M., Suzuki, T., 2000. Density-dependence of chum salmon in coastal waters of the Japan Sea. North Pacific Anadromous Fish Commission Bulletin 2, 75–81.

Garibaldi, A., Turner, N., 2004. Cultural keystone species: Implications for ecological conservation and restoration. Ecology and Society 9(3), 1.

Garner, K., Parfitt, B., 2006. First Nations, salmon fisheries and the rising importance of conservation. Pacific Fisheries Resource Conservation Council, Vancouver, Canada, 37 pp.

Gende, S.M., Edwards, R.T., Willson, M.F., Wipfli, M.S., 2002. Pacific Salmon in aquatic and terrestrial ecosystems. BioScience 52(10), 917.

Gislason, G., Lam, E., Gunnar, K., Guettabi, M., 2017. Economic impacts of Pacific salmon fisheries. Pacific Salmon Commission, Vancouver, Canada, 92 pp.

Graham, C., Pakhomov, E.A., Hunt, B.P.V., 2020. North Pacific Marine Salmon Diet Database [WWW Document]. URL https://github.com/mcarolinegraham/North_Pacific_Marine_Salmon_Diet_Database

Groot, C., Margolis, R.A. (Eds.), 1991. Pacific Salmon Life Histories. University of British Columbia Press, Vancouver, Canada.

Hanson, M.B., Baird, R.W., Ford, J.K.B., Hempelmann-Halos, J., Van Doornik, D.M., Candy, J.R., Emmons, C.K., Schorr, G.S., Gisborne, B., Ayres, K.L., Wasser, S.K., Balcomb, K.C., Balcomb-Bartok, K., Sneva, J.G., Ford, M.J., 2010. Species and stock identification of prey consumed by endangered southern resident killer whales in their summer range. Endangered Species Research 11, 69–82.

Hare, S.R., Mantua, N.J., 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47, 103–145.

Harrison, P.J., Boyd, P.W., Varela, D.E., Takeda, S., Shiomoto, A., Odate, T., 1999. Comparison of factors controlling phytoplankton productivity in the NE and NW Subarctic Pacific gyres. Progress in Oceanography 43, 205–234.

Healey, M., 2011. The cumulative impacts of climate change on Fraser River sockeye salmon (Oncorhynchus nerka) and implications for management. Canadian Journal of Fisheries and Aquatic Sciences 68, 718–737.

Heithaus, M.R., 2001. Predator-prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): A review. Journal of Zoology 253, 53–68.

Helfield, J.M., Naiman, R.J., 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. Ecology 82(9), 2403–2409.

Hertz, E., Trudel, M., Brodeur, R.D., Daly, E.A., Eisner, L., Farley, E. V., Harding, J.A., MacFarlane, R.B., Mazumder, S., Moss, J.H., Murphy, J.M., Mazumder, A., 2015. Continental-scale variability in the feeding ecology of juvenile Chinook salmon along the coastal Northeast Pacific Ocean. Marine Ecology Progress Series 537, 247–263.

Horton, T., *et al.,* 2019. World Register of Marine Species (WoRMS). URL http://www.marinespecies.org/ (accessed 10.30.19).

Huang, B., Banzon, V.F., Freeman, E., Lawrimore, J., Liu, W., Peterson, T.C., Smith, T.M., Thorne, P.W., Woodruff, S.D., Zhang, H.-M., 2015. Extended reconstructed sea surface temperature version 4 (ERSST.v4). Part I : Upgrades and intercomparisons. American Meterological Society 28, 911–930.

Irvine, J.R., Fukuwaka, M.A., 2011. Pacific salmon abundance trends and climate change. ICES Journal of Marine Science 68(6), 1122–1130.

Irvine, J.R., Fukuwaka, Masa-aki, Kaga, Toshiki, Park, J.-H., Baik Seong, K., Kang, Sukyung, Karpenko, Vladimir, Klovach, Natalia, Bartlett, Heather, Volk, Eric, Fukuwaka, M, Kaga, T, Park, J., Seong, K., Kang, S, Karpenko, V, Klovach, N, Bartlett, H, Volk, E, 2009. Pacific salmon status and abundance trends (NPAFC Doc. 1199). 153 pp.

Ito, J., 1964. Food and feeding habits of Pacific salmon (genus Oncorhynchus) in their oceanic life. Bulletin of the Hokkaido Regional Fisheries Research Laboratory 29, 85–97. In Japanese: English abstract.

Jamieson, G., Livingston, P., Zhang, C.-I., 2010. Report of Working Group 19 on Ecosystem-based Management Science and its Application to the North Pacific (PICES Scientific Report No. 37). North Pacific Marine Science Organization, Sidney, Canada, 184 pp.

Johnson, S.P., Schindler, D.E., 2009. Trophic ecology of Pacific salmon (Oncorhynchus spp.) in the ocean: A synthesis of stable isotope research. Ecological Research 24(4), 855–863.

Kaeriyama, M., Nakamura, M., Edpalina, R., Bower, J.R., Yamaguchi, H., Walker, R. V., Myers, K.W., 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (Oncorhynchus spp.) in the central Gulf of Alaska in relation to climate events. Fisheries Oceanography 13, 197–207.

Kaeriyama, M., Nakamura, M., Yamaguchi, M., Ueda, H., Anma, G., Takagi, S., Aydin, K.Y., Walker, R. V, Myers, K.W., 2000. Feeding ecology of sockeye and pink salmon in the Gulf of Alaska. North Pacific Anadromous Fish Commission Bulletin 2, 55–63.

Kaga, T., Sato, S., Azumaya, T., Davis, N.D., Fukuwaka, M.A., 2013. Lipid content of chum salmon Oncorhynchus keta affected by pink salmon O. gorbuscha abundance in the central Bering Sea. Marine Ecology Progress Series 478, 211–221.

Kanno, Y., Hamai, I., 1971. Food of salmonid fish in the Bering Sea in summer of 1966. Bulletin of the Faculty of Fisheries Hokkaido University 22, 107–128. In Japanese: English abstract.

Karpenko, V.I., Volkov, A.F., Koval, M. V, 2007. Diets of Pacific salmon in the Sea of Okhotsk, Bering Sea, and Northwest Pacific Ocean. North Pacific Anadromous Fish Commission Bulletin 4, 105–116.

Kawabata, A., Yatsu, A., Ueno, Y., Suyama, S., Kurita, Y., 2006. Spatial distribution of the Japanese common squid, Todarodes pacificus, during its northward migration in the western North Pacific Ocean. Fisheries Oceanography 15(2), 113–124.

Kim, S., Kang, S., Kim, J.K., Bang, M., 2017. Environmental variability and chum salmon production at the northwestern Pacific Ocean. Ocean Science Journal 52(4), 549–562.

Krebs, C.J., 1999. Ecological Methodology, 2nd ed. Addison-Welsey Educational Publishers, Inc., Menlo Park, U.S.A.

Legendre, P., Legendre, L., 2012. Numerical Ecology, 3rd ed. Elsevier, Amsterdam, Netherlands.

Levins, R., 1968. Evolution in changing environments. Princeton University Press, Princeton, U.S.A.

Luca, F., Perry, G.H., Di Rienzo, A., 2010. Evolutionary adaptations to dietary changes. Annual Reviews of Nutrition 30, 291–314.

Mackas, D.L., Tsuda, A., 1999. Mesozooplankton in the eastern and western subarctic Pacific: Community structure, seasonal life histories, and interannual variability. Progress in Oceanography 43, 335–363.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., 2019. cluster: Cluster Analysis Basics and Extensions. R package version 2.1.0.

Mantua, N.J., Hare, S.R., 2002. The Pacific Decadal Oscillation. Journal of Oceanography 58, 35–44.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78(6), 1069–1080.

Mueter, F.J., Peterman, R.M., Pyper, B.J., 2003. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (Oncorhynchus spp.) in northern and southern areas. Canadian Journal of Fisheries and Aquatic Sciences 60, 757–757.

Myers, K.W., Aydin, K.Y., 1996. The 1996 international cooperative salmon research cruise of the Oshoro maru and a summary of 1994–1996 results (NPAFC Doc. 195; FRI-UW-9613). University of Washington, Fisheries Research Institute, Seattle, U.S.A., 32 pp.

Myers, K.W., Klovach, N. V, Gritsenko, O.F., Urawa, S., Royer, T.C., 2007. Stock-specific distributions of Asian and North American salmon in the open ocean, interannual changes, and oceanographic conditions. North Pacific Anadromous Fish Commission Bulletin 4, 159–177.

MySQL, 2019. URL https://www.mysql.com/.

Naiman, R.J., Bilby, R.E., Schindler, D.E., Helfield, J.M., 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5, 399–417.

Nishioka, J., Obata, H., Ogawa, H., Ono, K., Yamashita, Y., Lee, K., Takeda, S., Yasuda, I., 2020. Subpolar marginal seas fuel the North Pacific through the intermediate water at the termination of the global ocean circulation. Proceedings of the National Academy of Sciences of the United States of America 117, 12665–12673.

North Pacific Anadromous Fish Commission, n.d. International North Pacific Fisheries Commission (1952–1992). URL https://npafc.org/inpfc/ (accessed 4.22.19).

North Pacific Anadromous Fish Commission, n.d. NPAFC Bulletins. URL https://npafc.org/bulletin/ (accessed 4.8.19).

North Pacific Anadromous Fish Commission, n.d. NPAFC Documents. URL https://npafc.org/npafc-documents/ (accessed 3.28.19).

Novakowski, G.C., Hahn, N.S., Fugi, R., 2008. Diet seasonality and food overlap of the fish assemblage in a pantanal pond. Neotropical Ichthyology 6(4), 567–576.

Oksanen, J., Blanchet, F.G., Fiendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2016.

vegan: Community Ecology Package. R package version 2.5.6.

Olson, R.J., Duffy, L.M., Kuhnert, P.M., Galván-Magaña, F., Bocanegra-Castillo, N., Alatorre-Ramírez, V., 2014. Decadal diet shift in yellowfin tuna Thunnus albacares suggests broad-scale food web changes in the eastern tropical Pacific Ocean. Marine Ecology Progress Series 497, 157–178.

Orsi, J.A., Murphy, J.M., Brase, A.L.J., 1997. Survey of juvenile salmon in the marine waters of Southeastern Alaska (NPAFC Doc. 277). Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Juneau, U.S.A., 27 pp.

Payne, L.X., Moore, J.W., 2006. Mobile scavengers create hotspots of freshwater productivity. Oikos 115, 69–80.

Perry, G.H., Dominy, N.J., Claw, K.G., Lee, A.S., Fiegler, H., Redon, R., Werner, J., Villanea, F.A., Mountain, J.L., Misra, R., Carter, N.P., Lee, C., Stone, A.C., 2007. Diet and the evolution of human amylase gene copy number variation. Nature Genetics 39(10), 1256–1260.

Peterson, W.T., Schwing, F.B., 2003. A new climate regime in northeast pacific ecosystems. Geophysical Research Letters 30(17), 1–4.

Polovina, J.J., Dunne, J.P., Woodworth, P.A., Howell, E.A., 2011. Projected expansion of the subtropical biome and contraction of the temperate and equatorial upwelling biomes in the North Pacific under global warming. ICES Journal of Marine Science 68(6), 986–995.

Qin, Y., Kaeriyama, M., 2016. Feeding habits and trophic levels of Pacific salmon (Oncorhynchus spp.) in the North Pacific Ocean. North Pacific Anadromous Fish Commission Bulletin 6, 469–481.

R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rohatgi, A., 2019. WebPlotDigitizer. URL https://automeris.io/WebPlotDigitizer/.

Rousseeuw, P.J., 1987. Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. Journal of Computational and Applied Mathematics 20, 53–65.

Ruggerone, G.T., Farley, E., Nielsen, J., Hagen, P., 2005. Seasonal marine growth of Bristol Bay sockeye salmon (Oncorhynchus nerka) in relation to competition with Asian pink salmon (O. gorbuscho) and the 1977 ocean regime shift. Fishery Bulletin 103(2), 355–370.

Ruggerone, G.T., Goetz, F.A., 2004. Survival of Puget Sound chinook salmon (Oncorhynchus tshawytscha) in response to climate-induced competition with pink salmon (Oncorhynchus gorbuscha). Canadian Journal of Fisheries and Aquatic Sciences 61, 1756–1770.

Ruggerone, G.T., Irvine, J.R., 2018. Numbers and biomass of natural- and hatchery-origin pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean, 1925–2015. Marine and Coastal Fisheries 10(2), 152–168.

Ruggerone, G.T., Nielsen, J.L., 2004. Evidence for competitive dominance of pink salmon (Oncorhynchus gorbuscha) over other salmonids in the North Pacific Ocean. Reviews in Fish Biology and Fisheries 14, 371–390.

Ruggerone, G.T., Zimmermann, M., Myers, K.W., Nielson, J.L., Rogers, D.E., 2003. Competition between Asian pink salmon (Oncorhynchus gorbuscha) and Alaskan sockeye salmon (O. nerka) in the North Pacific Ocean. Fisheries Oceanography 12(3), 209–219.

Saito, R., Yamaguchi, A., Saitoh, S.I., Kuma, K., Imai, I., 2011. East-west comparison of the zooplankton community in the subarctic Pacific during summers of 2003–2006. Journal of

Plankton Research 33(1), 145–160.

Schoen, E.R., Wipfli, M.S., Trammell, E.J., Rinella, D.J., Floyd, L., Grunblatt, J., Mccarthy, M.D., Meyer, B.E., John, M., Powell, J.E., Prakash, A., Reimer, M.N., Svetlana, L., Toniolo, H., Wells, B.M., Witmer, F.D.W., Schoen, E.R., Wipfli, M.S., Trammell, E.J., Rinella, D.J., Floyd, L., Grunblatt, J., Mccarthy, M.D., Meyer, B.E., Morton, J.M., Powell, J.E., Prakash, A., Reimer, M.N., Stuefer, S.L., Toniolo, H., Wells, B.M., 2017. Future of Pacific salmon in the face of environmental change: Lessons from one of the world's remaining productive salmon regions. Fisheries 42(10), 538–553.

Schoener, T.W., 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51(3), 408–418.

Schondube, J.E., Herrera-M, L.G., Martínez del Río, C., 2001. Diet and the evolution of digestion and renal function in phyllostomid bats. Zoology 104, 59–73.

Seeb, L.W., Crane, P.A., Kondzela, C.M., Wilmot, R.L., Urawa, S., Varnavskaya, N. V, Seeb, J.E., 2004. Migration of Pacific Rim chum salmon on the high seas: Insights from genetic data. Environmental Biology of Fishes 69, 21–36.

Serno, S., Winckler, G., Anderson, R.F., Hayes, C.T., Ren, H., Gersonde, R., Haug, G.H., 2014. Using the natural spatial pattern of marine productivity in the Subarctic North Pacific to evaluate paleoproductivity proxies. Paleoceanography 29, 438–453.

Silliman, R.P., 1941. Fluctuations in the diet of the Chinook and silver salmons (Oncorhynchus tschawytscha and O. kisutch) off Washington, as related to the troll catch of salmon. Copeia 1941, 80–87.

Smithson, M., Verkuilen, J., 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. Psychological Methods 11(1), 54–71.

Sokal, R.R., Rohlf, F.J., 1995. Biometry: the principles and practice of statistics in biological research, 3rd ed. W. H. Freeman, New York, U.S.A.

Springer, A.M., Van Vliet, G.B., 2014. Climate change, pink salmon, and the nexus between bottom-up and top-down forcing in the subarctic Pacific Ocean and Bering Sea. Proceedings of the National Academy of Sciences of the United States of America 111(18), E1880–E1888.

Starovoytov, A.N., 2007. Trends in abundance and feeding of chum salmon in the Western Bering Sea. North Pacific Anadromous Fish Commission Bulletin 4, 45–51.

Stige, L.C., Kvile, K., Bogstad, B., Langangen, Ø., 2018. Predator-prey interactions cause apparent competition between marine zooplankton groups. Ecology 99(3), 632–641.

Sturdevant, M. V, Ignell, S.E., Morris, J., 1997. Diet of juvenile salmon off Southeastern Alaska, October–November 1995 (NPAFC Doc. 275). Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Juneau, U.S.A., 28 pp.

Sturdevant, M. V, Orsi, J.A., Fergusson, E.A., 2012. Diets and trophic linkages of epipelagic fish predators in coastal Southeast Alaska during a period of warm and cold climate years, 1997–2011 diets and trophic linkages of epipelagic fish predators and cold climate years, 1997–2011. Marine and Coastal Fisheries 4(1), 526–545.

Sugimoto, T., Tadokoro, K., 1997. Interannual-interdecadal variations in zooplankton biomass, chlorophyll concentration and physical environment in the subarctic Pacific and Bering Sea. Fisheries Oceanography 6(2), 74–93.

Sydeman, W.J., Hester, M.M., Thayer, J.A., Gress, F., Martin, P., Buffa, J., 2001. Climate change, reproductive performance and diet composition of marine birds in the southern California Current system, 1969–1997. Progress in Oceanography 49, 309–329.

Tadokoro, K., Ishida, Y., Davis, N.D., Ueyanagi, S., Sugimoto, T., 1996. Change in chum salmon (Oncorhynchus keta) stomach contents associated with fluctuation of pink salmon (O. gorbuscha) abundance in the central subarctic Pacific and Bering Sea. Fisheries Oceanography 5(2), 89–99.

Tai, T.C., Robinson, J.P.W., 2018. Enhancing climate change research with open science. Frontiers in Environmental Science 6, 115.

Takeuchi, I., 1972. Food animals collected from the stomachs of three salmonid fishes (Oncorhynchus) and their distribution in the natural environments in the northern North Pacific. Bulletin of the Hokkaido Regional Fisheries Research Laboratory 38, 1–119. In Japanese: English abstract.

Tian, Y., Nashida, K., Sakaji, H., 2013. Synchrony in the abundance trend of spear squid Loligo bleekeri in the Japan Sea and the Pacific Ocean with special reference to the latitudinal differences in response to the climate regime shift. ICES Journal of Marine Science 70(5), 968–979.

Tocher, D.R., 2003. Metabolism and functions of lipids and fatty acids in teleost fish. Reviews in Fisheries Science 11(2), 107–184.

Urawa, S., Seki, J., Kawana, M., Crane, P.A., Seeb, L.W., Gorbatenko, K., Fukuwaka, M., 2004. Juvenile chum salmon in the Okhotsk Sea: Their origins estimated by genetic and otolith marks. NPAFC Technical Report 5, 87–88.

Verspoor, J.J., Braun, D.C., Stubbs, M.M., Reynolds, J.D., 2011. Persistent ecological effects of a salmon-derived nutrient pulse on stream invertebrate communities. Ecosphere 2(2), 18.

Walker, R. V, Davis, N.D., Myers, K.W., Helle, J.H., 2005. New information from archival tags from Bering Sea tagging, 1998–2004. North Pacific Anadromous Fish Commission Technical Report 6, 38–40.

Wallace, R.K., 1981. An assessment of diet-overlap indexes. Transactions of the American Fisheries Society 110 (1), 72–76.

Ward, J.H., 1963. Hierarchical grouping to optimize an objective function. Journal of the American Statistical Association 58(301), 236–244.

Ware, D.M., 1995. A century and a half of change in the climate of the NE Pacific. Fisheries Oceanography 4(4), 267–277.

Welch, D.W., 1997. Anatomical specialization in the gut of Pacific salmon (Oncorhynchus): Evidence for oceanic limits to salmon production? Canadian Journal of Zoology 75, 936–942.

Welch, D.W., Ishida, Y., Nagasawa, K., 1998. Thermal limits and ocean migrations of sockeye salmon (Oncorhynchus nerka): Long-term consequences of global warming. Canadian Journal of Fisheries and Aquatic Sciences 55, 937–948.

Welch, D.W., Parsons, T.R., 1993. δ13C-δ15N values as indicators of trophic position and competitive overlap for Pacific salmon (Oncorhynchus spp.). Fisheries Oceanography 2(1), 11–23.

Zaret, T.M., Rand, A.S., 1971. Competition in tropical stream fishes: Support for the competitive exclusion principle. Ecology 52(2), 336–342.

Zhang, J., 2016. spaa: Species Association Analysis. R package version 0.2.2.

Zimmerman, M.S., Irvine, J.R., O’Neill, M., Anderson, J.H., Greene, C.M., Weinheimer, J., Trudel, M., Rawson, K., 2015. Spatial and temporal patterns in smolt survival of wild and hatchery coho salmon in the Salish Sea. Marine and Coastal Fisheries 7, 116–134.

Appendix

Table A1. The references included in the database. References are listed in order of their source ID number, which corresponds to their source ID in the North Pacific Marine Salmon Diet Database.

Source ID	Reference
1	Andrievskaya, L.D., 1966. Food relationships of the Pacific salmon in the sea. Voprosy Ikhtiologii 6 (38), 84–90 (Translation by U.S. Joint Publications Research Service for Bureau of Commercial Fisheries, Seattle, U.S.A, 11 pp).
2	Carlson, H.R., 1976. Foods of juvenile sockeye salmon, Oncorhynchus nerka, in the inshore coastal waters of Bristol Bay, Alaska, 1966-67. Fishery Bulletin 74, 458–462.
3	Chuchukalo, V.L., Volkov, A.F., Efimkin, A.Y., Kuznetsova, N.A., 1995. Feeding and daily rations of sockeye salmon (Oncorhynchus nerka) during the summer period (NPAFC Doc. 125). Pacific Research Institute of Fisheries Oceanography (TINRO), Vladivostok, Russia, 9 pp.
4	Davis, N.D., Takahashi, M., Ishida, Y., 1996. The 1996 Japan-U.S. cooperative high-seas salmon research cruise of the Wakatake maru and a summary of 1991–1996 results (NPAFC Doc. 194; FRI-UW-9617). Fisheries Research Institute, University of Washington, Seattle, U.S.A; National Research Institute of Far Seas Fisheries, Shimizu, Japan, 45 pp.
5	Davis, N.D., Aydin, K.Y., Ishida, Y., 1998. Diel feeding habits and estimates of prey consumption of sockeye, chum, and pink salmon in the Bering Sea in 1997 (NPAFC Doc. 363; FRI-UW-9816). Fisheries Research Institute, University of Washington, Seattle, U.S.A; National Research Institute of Far Seas Fisheries, Shimizu, Japan, 24 pp.
6	Davis, N.D., Aydin, K.Y., Ishida, Y., 2000. Diel catches and food habits of sockeye, pink, and chum salmon in the Central Bering Sea in summer. North Pacific Anadromous Fish Commission Bulletin 2, 99–109.
7	Dulepova, E.P., Dulepov, V.I., 2003. Interannual and interregional analysis of chum salmon feeding features in the Bering Sea and adjacent Pacific waters of Eastern Kamchatka (NPAFC Doc. 728). Pacific Research Fisheries Centre, TINRO-Centre, Vladivostok, Russia, 8 pp.
8	Fukataki, H., 1967. Stomach contents of the pink salmon, Oncorhynchus gorbuscha (Walbaum), in the Japan Sea during the spring season of 1965. Bulletin of the Japan Sea Regional Fisheries Research Laboratory 17, 49–66. In Japanese: English abstract.
9	Glebov, I.I., 1998. Chinook and coho salmon feeding habits in the Far Eastern seas in the course of yearly migration cycle (NPAFC Doc. 378). Pacific Research Fisheries Centre TINRO-Centre, Vladivostok, Russia, 57 pp.
10	Ito, J., 1964. Food and feeding habits of Pacific salmon (genus Oncorhynchus) in their oceanic life. Bulletin of the Hokkaido Regional Fisheries Research Laboratory 29, 85–97. In Japanese: English abstract.
11	Kaeriyama, M., Nakamura, M., Yamaguchi, M., Ueda, H., Anma, G., Takagi, S.,

Source ID	Reference
	Aydin, K.Y., Walker, R. V, Myers, K.W., 2000. Feeding ecology of sockeye and pink salmon in the Gulf of Alaska. North Pacific Anadromous Fish Commission Bulletin 2, 55–63.
12	Kaeriyama, M., Nakamura, M., Edpalina, R., Bower, J.R., Yamaguchi, H., Walker, R. V, Myers, K.W., 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (Oncorhynchus spp.) in the central Gulf of Alaska in relation to climate events. Fisheries Oceanography 13, 197–207.
13	Kanno, Y., Hamai, I., 1971. Food of salmonid fish in the Bering Sea in summer of 1966. Bulletin of the Faculty of Fisheries Hokkaido University 22, 107–128. In Japanese: English abstract.
14	Karpenko, V.I., Volkov, A.F., Koval, M. V, 2007. Diets of Pacific salmon in the Sea of Okhotsk, Bering Sea, and Northwest Pacific Ocean. North Pacific Anadromous Fish Commission Bulletin 4, 105–116.
15	Manzer, J.I., 1968. Food of Pacific salmon and steelhead trout in the Northeast Pacific Ocean. Journal of the Fisheries Research Board of Canada 25(5), 1085–1089.
16	Perry, R.I., Hargreaves, N.B., Waddell, B.J., Mackas, D.L., 1996. Spatial variations in feeding and condition of juvenile pink and chum salmon off Vancouver Island, British Columbia. Fisheries Oceanography 5(2), 73–88.
17	Tadokoro, K., Ishida, Y., Davis, N.D., Ueyanagi, S., Sugimoto, T., 1996. Change in chum salmon (Oncorhynchus keta) stomach contents associated with fluctuation of pink salmon (O. gorbuscha) abundance in the central subarctic Pacific and Bering Sea. Fisheries Oceanography 5(2), 89–99.
18	Takeuchi, I., 1972. Food animals collected from the stomachs of three salmonid fishes (Oncorhynchus) and their distribution in the natural environments in the northern North Pacific. Bulletin of the Hokkaido Regional Fisheries Research Laboratory 38, 1–119. In Japanese: English abstract.
19	Ueno, M., Kosaka, S., Ushiyama, H., 1969. Food and feeding behavior of Pacific salmon—II. Sequential change of stomach contents. Bulletin of the Japanese Society of Scientific Fisheries 35(11), 1060–1066.
20	Volkov, A.F., Chuchukalo, V.I., Efimkin, A.Y. 1995. Feeding of Chinook and coho salmon in the Northwestern Pacific Ocean (NPAFC Doc. 124). Pacific Research Institute of Fisheries Oceanography, Vladivostok, Russia, 12 pp.
21	Auburn, M.E., Ignell, S.E., 2000. Food habits of juvenile salmon in the Gulf of Alaska July–August 1996. North Pacific Anadromous Fish Commission Bulletin 2, 89–97.
22	Aydin, K.Y., 1998. Abiotic and biotic factors influencing food habits of Pacific salmon in the Gulf of Alaska, In: Myers, K.W. (Ed.), Workshop of Climate Change and Salmon Production Technical Report, Vancouver, Canada, March 27, 1998. North Pacific Anadromous Commission, pp. 39–40.
23	Brodeur, R.D., Daly, E.A., Schabetsberger, R.A., Mier, K.L., 2007. Interannual and interdecadal variability in juvenile coho salmon (Oncorhynchus kisutch) diets in relation to environmental changes in the northern California Current.

Source ID	Reference
	Fisheries Oceanography 16, 395–408.
24	Daly, E.A., Brodeur, R.D., 2015. Warming ocean conditions relate to increased trophic requirements of threatened and endangered salmon. PLoS One 10(12), e0144066.
25	Davis, N.D., Armstrong, J.L., Myers, K.W., 2003. Bering Sea salmon food habits: Diet overlap in fall and potential for interactions among salmon. Final Report to the Yukon River Drainage Fisheries Association (SAFS-UW-0311). Fisheries Research Institute, School of Aquatic and Fisheries Sciences, University of Washington, Seattle, U.S.A., 34 pp.
26	Kawamura, H., Miyamoto, M., Nagata, M., Hirano, K., 1998. Interaction between chum salmon and fat greenling juveniles in the coastal Sea of Japan off northern Hokkaido. North Pacific Anadromous Fish Commission Bulletin 1, 412–418.
27	Qin, Y., Kaeriyama, M., 2016. Feeding habits and trophic levels of Pacific salmon (Oncorhynchus spp.) in the North Pacific Ocean. North Pacific Anadromous Fish Commission Bulletin 6, 469–481.
28	Starovoytov, A.N., 2007. Trends in abundance and feeding of chum salmon in the Western Bering Sea. North Pacific Anadromous Fish Commission Bulletin 4, 45–51.
29	Ueno, Y., 1992. Deepwater migrations of chum salmon (Oncorhynchus keta) along the Pacific coast of northern Japan. Canadian Journal of Fisheries and Aquatic Sciences 49, 2307–2312.
30	Ueno, Y., Seki, J., Shimizu, I., P. Shershnev, A., 1992. Large juvenile chum salmon Oncorhynchus keta collected in coastal waters of Iturup Island. Nippon Suisan Gakkaishi 58(8), 1393–1397.
31	Waddell, B.J., Morris, J.F.T., Healey, M.C., 1992. The abundance, distribution, and biological characteristics of Chinook and coho salmon on the fishing banks off southwest Vancouver Island, May 18–30, 1989 and April 23–May 5, 1990. Canadian Technical Report of Fisheries and Aquatic Sciences 1891, 113 pp.
32	Andrievskaya, L.D., 1970. The feeding of Pacific salmon fry in the sea. Proceedings of the Pacific Research Institute of Fisheries and Oceanography 64, 73–80 (Fisheries Research Board of Canada Translation Series 1423: 1–16).
33	Atcheson, M.E., Myers, K.W., Beauchamp, D.A., Mantua, N.J., 2012. Bioenergetic response by steelhead to variation in diet, thermal habitat, and climate in the North Pacific Ocean. Transactions of the American Fisheries Society 141, 1081–1096.
34	Carlson, H.R., Myers, K.W., Farley, E. V, Jaenicke, H.W., Haight, R.E., Guthrie, C.M., 1996. Cruise report of the F/V Great Pacific survey of young salmon in the North Pacific—Dixon entrance to Western Aleutians—July–August 1996 (NPAFC Doc. 222.) Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Juneau, U.S.A, 50 pp.
35	Davis, N.D., Fukuwaka, M., Armstrong, J.L., Myers, K.W., 2005. Salmon food

Source ID	Reference
	habits studies in the Bering Sea, 1960 to present. North Pacific Anadromous Fish Commission Technical Report 6, 24–28.
36	Myers, K.W., Aydin, K.Y., 1996. The 1996 international cooperative salmon research cruise of the Oshoro maru and a summary of 1994–1996 results (NPAFC Doc. 195; FRI-UW-9613). University of Washington, Fisheries Research Institute, Seattle, U.S.A., 32 pp.
37	Myers, K.W., Walker, R. V, Davis, N.D., Patton, W.S., Aydin, K.Y., Pikitch, E.K., Burgner, R.L., 1995. Migrations, abundance, and origins of salmonids in offshore waters of the North Pacific – 1995 (NPAFC Doc. 152; FRI-UW-9613). University of Washington, Fisheries Research Institute, Seattle, U.S.A., 84 pp.
38	Sturdevant, M. V, Ignell, S.E., Morris, J., 1997. Diet of juvenile salmon off Southeastern Alaska, October–November 1995 (NPAFC Doc. 275). Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Juneau, U.S.A., 28 pp.
39	Walker, R. V, 1993. Summary of cooperative U.S.-Japan high seas salmonid research aboard the Japanese research vessel Oshoro Maru, 1993 (NPAFC Doc. 21). Fisheries Research Institute, University of Washington, Seattle, U.S.A., 16 pp.
40	Suzuki, T., Fukuwaka, M., Shimizu, I., Seki, J., Kaeriyama, M., Mayama, H., 1994. Feeding selectivity of juvenile chum salmon in the Japan Sea Coast of Northern Honshu. Scientific Reports of the Hokkaido Salmon Hatchery 48, 11–16. In Japanese: English abstract.
41	Shimazaki, K., Mishima, S., 1969. On the diurnal change of the feeding activity of salmon in the Okhotsk Sea. Bulletin of the Faculty of Fisheries Hokkaido University 20, 82–93. In Japanese: English abstract.
42	Weitkamp, L.A., 2004. Ocean conditions, marine survival, and performance of juvenile chinook (Oncorhynchus tshawytscha) and coho (O. kisutch) salmon in Southeast Alaska. University of Washington, PhD thesis.
43	Starovoytov, A.N., 2003. Chum salmon (Oncorhynchus keta (Walbaum)) in the Far East Seas—biological description of the species 2. Diet composition and trophic linkages of chum salmon in the Far East Seas and adjacent waters of the Northwest Pacific Ocean. Izvestiya TINRO 133, 3–34. In Russian.
44	LeBrasseur, R.J., Doidge, D.A., 1966. Stomach contents of salmonids caught in the Northeastern Pacific Ocean—1959 & 1960. Circular, Statistical series, Fisheries Research Board of Canada, Biological Station, Nanaimo, Canada, 21, Vol. 3, 67 pp.
45	Lebrasseur, R.J., Doidge, D.A., 1966. Stomach contents of salmonids caught in the Northeastern Pacific Ocean—1962. Circular, Statistical series, Fisheries Research Board of Canada, Biological Station, Nanaimo, Canada, 22, Vol. 4, 80 pp.
46	Lebrasseur, R.J., Doidge, D.A., 1966. Stomach contents of salmonids caught in the Northeastern Pacific Ocean—1963 & 1964. Circular, Statistical series, Fisheries Research Board of Canada, Biological Station, Nanaimo, Canada, 23,

Source ID	Reference
	Vol. 5, 80 pp.
47	Ishida, Y., Davis, N.D., 1999. Chum salmon feeding habits in relation to growth reduction. Salmon Report Series 47, 104–110.
48	Tamura, R., Shimazaki, K., Ueno, Y., 1999. Trophic relations of juvenile salmon (genus Oncorhynchus) in the Okhotsk Sea and Pacific waters off the Kuril Islands. Salmon Report Series 47, 138–168.
49	Seki, J., Shimizu, I., 1998. Diel migration of zooplankton and feeding behavior of juvenile chum salmon in the central Pacific coast of Hokkaido. Bulletin of the National Salmon Resources Center 1, 13–27. In Japanese: English abstract.
50	Suzuki, T., Fukuwaka, M., Kawana, M., Ohkuma, K., Seki, J., 1995. Investigation on survival mechanism of juvenile chum salmon during the early sea life in 1994, Salmon Database 3, 59–68. In Japanese.
51	Andrievskaya, L.D., 1974. The feeding of pink salmon in the wintering areas in the Sea of Japan. Izvestiya TINRO 90, 97–110. In Russian.
52	Andrievskaya, L.D., 1970. Feeding of Pacific salmon juveniles in the Sea of Okhotsk. Izvestiya TINRO 78, 105–115. In Russian.
53	Chuchukalo, V.I., Volkov, A.F., Efimkin, A.Y., Blagoderov, A.I., 1994. Distribution and feeding of the Chinook salmon (Oncorhynchus tschawytscha) in the northwest Pacific, Izvestiya TINRO, 137–141. In Russian.
54	Gorbatenko, K.M., 1996. Food and feeding habits of juvenile pink and chum salmons in the epipelagic zone of the Okhotsk Sea in winter. Izvestiya TINRO 199, 234–243. In Russian.
55	Kayev, A.M., Chupakhin, V.M., Fedotova, N.A., 1993. Feeding peculiarities and interrelationships between juvenile salmons in coastal waters of the Etorofu Island. Voprosy Ikhtiologii 33, 215–224. In Russian.
56	Klovatch, N. V, 2002. Ecological consequences of large-scale propagation of chum salmon (Oncorhynchus keta). VNIRO, PhD extended summary. In Russian.
57	Shershnev, A.P., Chupakhin, V.M., Rudnev, V.A., 1982. Some features of the ecology of young Sakhalin and Iturup pink salmon Oncorhynchus gorbuscha (Walbaum) (Salmonidae) during marine period of life. Voprosy Ikhtiologii 22(3), 441–448. In Russian.
58	Tutubalin, B.G., Chuchukalo, V.I., 1992. Feeding habits of Pacific salmon of the genus Oncorhynchus in the northern Pacific Ocean in the winter and spring. Biological Resources of the Pacific Ocean, VNIRO, Moscow, Russia, 77–85. In Russian.
59	Volkov, A.F., 1996. Food and feeding habits of young Pacific salmon in the Okhotsk Sea during the autumn-winter period. Okeanologiya 36(1), 80–85. In Russian.
60	Volkov, A.F., 1994. Food and feeding habits of pink, chum and sockeye salmon during their anadromous migrations. Izvestiya TINRO 116, 128–137. In Russian.
61	Fisheries Agency of Japan. 1966. Report on research by Japan for the

Source ID	Reference
	International North Pacific Fisheries Commission during the year 1965. International North Pacific Fisheries Commission Annual Report 1965, 42–55.
62	Davis, N.D, 1990. U.S.-Japan cooperative high seas salmonid research in 1990: Summary of research aboard the Japanese research vessel Hokuho Maru, 4 June to 19 July (FRI-UW-9010). Fisheries Research Institute, University of Washington, Seattle, 24 pp.

Table A2. The metadata extracted for each source.

Column	Explanation
source_id	A unique number that is generated and assigned to each source (e.g., 1, 2, 3…etc.)
publication_year	Publication year in the format: YYYY
title	Title of the source
author1	First author of the source in the following format: M. C. Graham or M. Graham (first and middle names are abbreviated by initials and a period while last names are completely spelled out)
author2	Second author of the source in the following format: M. C. Graham or M. Graham (first and middle names are abbreviated by initials and a period while last names are completely spelled out)
author3	Third author of the source in the following format: M. C. Graham or M. Graham (first and middle names are abbreviated by initials and a period while last names are completely spelled out)
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author5	Fifth author of the source in the following format: M. C. Graham or M. Graham (first and middle names are abbreviated by initials and a period while last names are completely spelled out)
author6	Sixth author of the source in the following format: M. C. Graham or M. Graham (first and middle names are abbreviated by initials and a period while last names are completely spelled out)
author7	Seventh author of the source in the following format: M. C. Graham or M. Graham (first and middle names are abbreviated by initials and a period while last names are completely spelled out)
author8	Eighth author of the source in the following format: M. C. Graham or M. Graham (first and middle names are abbreviated by initials and a period while last names are completely spelled out)
author9	Ninth author of the source in the following format: M. C. Graham or M. Graham (first and middle names are abbreviated by initials and a period while last names are completely spelled out)
author10	Tenth author of the source in the following format: M. C. Graham or M. Graham (first and middle names are abbreviated by initials and a period while last names are completely spelled out)

Column	Explanation
url	URL associated with source, if applicable
citation	The full citation for the source
source_notes	Any additional notes about the source; for example, if the data might be overlapping with another source, this is indicated in this attribute
data_processing_notes	Notes about how the data were processed – in the lab or field, were quantities measured using scales or visually estimated, etc.
date_entered	The date the source was added to the database
entered_by	The full name of the person who entered the data (e.g., Caroline Graham)

Table A3. The data extracted for each salmon gear type.

Column	Explanation
gear_type_predator_id	A unique number that is generated and assigned to each unique predator gear type for each source (e.g., 1, 2, 3…etc.)
gear_type	The most basic description of the type of gear given in the source (e.g., trawl, gillnet, longline)
gear_length_value	The gear length
gear_length_min	If there are a range of gear lengths, then this attribute represents the minimum length
gear_length_max	If there are a range of gear lengths, then this attribute represents the maximum length
gear_length_units	The units associated with the gear length; units are fully spelled and plural (e.g., meters instead of meter)
gear_width_value	The gear width
gear_width_min	If there are a range of gear widths, then this attribute represents the minimum width
gear_width_max	If there are a range of gear widths, then this attribute represents the maximum width
gear_width_units	The units associated with the gear width; units are fully spelled and plural (e.g., meters instead of meter)
gear_depth_value	The gear depth; if the gear is reported to be deployed at the surface then the depth value is assigned to 0
gear_depth_min	If there are a range of gear depths, then this attribute represents the minimum depth; if the gear is reported to be deployed at the surface then the depth value is assigned to 0
gear_depth_max	If there are a range of gear depths, then this attribute represents the maximum depth
gear_depth_units	The units associated with the gear depth; units are fully spelled and plural (e.g., meters instead of meter)
mesh_size_value	The gear mesh size
mesh_size_min	If there are a range of gear mesh sizes, then this attribute represents the minimum mesh size

Column	Explanation
mesh_size_max	If there are a range of gear mesh sizes, then this attribute represents the maximum mesh size
mesh_size_units	The units associated with the mesh size; units are fully spelled and plural (e.g., millimeters instead of millimeter)
fishing_depth_value	The fishing depth; if fishing is reported to be at the surface then the depth value is assigned to 0
fishing_depth_min	If there are a range of fishing depths, then this attribute represents the minimum fishing depth; if fishing is reported to be at the surface then the depth value is assigned to 0
fishing_depth_max	If there are a range of fishing depths, then this attribute represents the maximum fishing depth
fishing_depth_units	The units associated with the fishing depth; units are fully spelled and plural (e.g., meters instead of meter)
tow_speed_value	The gear tow speed
tow_speed_min	If there are a range of gear tow speeds, then this attribute represents the minimum tow speed
tow_speed_max	If there are a range of gear tow speeds, then this attribute represents the maximum tow speed
tow_speed_units	The units associated with the tow speed; units are fully spelled and plural (e.g., knots instead of knot)
duration_deployment_value	The gear duration of deployment
duration_deployment_min	If there are a range of gear durations of deployment, then this attribute represents the minimum duration of deployment
duration_deployment_max	If there are a range of gear durations of deployment, then this attribute represents the maximum duration of deployment
duration_deployment_units	The units associated with the duration of deployment; units are fully spelled and plural (e.g., minutes instead of minute)
gear_notes	Any additional comments on the gear

Table A4. The diet data extracted for each salmon predator.

Column	Explanation
predator_id	A unique number that is generated and assigned to each predator sample
source_id	This number corresponds with the source_id from the 'sources.csv' file
year_min	YYYY; if there is just one value for the year then it is found in this attribute; if there are a range of values for the year then the minimum value is found in this attribute
year_max	YYYY; if there are a range of values for the year then the maximum value is entered into this attribute
warm_cool_years	Either 'warm', 'cool' or NA; this attribute will only have a value if the samples are explicitly reported as being

Column	Explanation
	from a warm versus cool year(s) and can only be uniquely identified this way
odd_even_years	Either ‘odd, ‘even’ or NA; this attribute will only have a value if the samples are explicitly reported as being from an odd versus even year(s) and can only be uniquely identified this way
season_min	Either ‘spring’, ‘summer’, ‘autumn’, or ‘winter’; if there is just one value for the season then it is entered into this attribute; If there are a range of values for the season then the minimum value is entered into this attribute; this attribute will only have a value if there is no value for the month/date and the source explicitly defines the temporal sampling period by season
season_max	Either ‘spring’, ‘summer’, ‘autumn’, or ‘winter’; if there are a range of values for the season then the maximum value is entered into this attribute; this attribute will only have a value if there is no value for the month/date and the source explicitly defines the temporal sampling period by season
month_min	Month names are completely spelled out with the first letter capitalized; if there is just one value for the month then it is entered into this attribute; If there are a range of values for the month then the minimum value is found in this attribute
month_max	Month names are completely spelled out with the first letter capitalized; if there are a range of values for the month then the maximum value is found in this attribute
date_min	Expressed using year, month, and day; if there is just one value for the date then it is entered into this attribute; if there are a range of values for the date then the minimum value is found in this attribute
date_max	Expressed using year, month, and day; if there are a range of values for the date then the maximum value is found in this attribute
time_min	HH:MM:SS; if there is just one value for the time then it is found in this attribute; if there are a range of values for the time then the minimum value is found in this attribute
time_max	HH:MM:SS; if there are a range of values for the time then the maximum value is found in this attribute
lat_min	If there is just one value for the latitude then it is found in this attribute; If there are a range of values for the latitude then the minimum value is found in this attribute; values are in decimal degrees format

Column	Explanation
lat_max	If there are a range of values for the latitude then the maximum value is found in this attribute; values are in decimal degrees format
lon_min	If there is just one value for the longitude then it is entered into this attribute; If there are a range of values for the longitude then the minimum value is entered into this attribute; values are in decimal degrees format
lon_max	If there are a range of values for the longitude then the maximum value is found in this attribute; values are in decimal degrees format
predator_lowest_taxonomic_level	The lowest taxonomic level reported in the source; if a source reports to the species level then this attribute includes both the genus and species names (e.g., Oncorhynchus nerka); only scientific names are reported, not common names
predator_life_stage	Either 'juvenile', 'adult' or NA
predator_life_stage_min	If there are a mixture of juveniles and adults, then 'juvenile' is entered here
predator_life_stage_max	If there are a mixture of juveniles and adults, then 'adult' is entered here
predator_freshwater_age	An integer to indicate the number of years spent living in freshwater
predator_freshwater_age_min	If there are a mixture of freshwater ages, then this attribute represents the minimum age; an integer to indicate the number of years spent living in freshwater
predator_freshwater_age_max	If there are a mixture of freshwater ages, then this attribute represents the maximum age; an integer to indicate the number of years spent living in freshwater
predator_ocean_age	An integer to indicate the number of years spent living in the ocean
predator_ocean_age_min	If there are a mixture of ocean ages, then this attribute represents the minimum age; an integer to indicate the number of years spent living in the ocean
predator_ocean_age_max	If there are a mixture of ocean ages, then this attribute represents the maximum age; an integer to indicate the number of years spent living in the ocean
predator_maturity	Either 'juvenile', 'immature', 'maturing' 'mature', 'kelt' (for steelhead), or NA
predator_maturity_min	If there are a mixture of maturity levels, then the minimum maturity level is found here
predator_maturity_max	If there are a mixture of maturity levels, then the maximum maturity level is found here

Column	Explanation
predator_length_value_cm	The length of a predator in centimeters (could be either fork length or total length); only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_length_min_cm	The minimum length of a predator in centimeters (could be either fork length or total length) if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_length_max_cm	The maximum length of a predator in centimeters (could be either fork length or total length) if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_weight_value_g	The weight of a predator in grams; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_weight_min_g	The minimum weight of a predator in grams if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_weight_max_g	The maximum weight of a predator in grams if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_subsample_id	A unique number that is generated and assigned to predator samples if a source reports the diets of individual predators with no unique identifiers; values are assigned for each source starting from 1 and increasing by a value of 1 each time (e.g., 1,2,3…); if unique subsample_ids are not required then the default value is 0
predator_sex	Either ‘male’, ‘female’ or ‘unspecified’
hatchery_wild	Either ‘hatchery’, ‘wild’ or ‘unspecified’
predator_replicates	The total number of predator replicates per sample
predator_notes	Any additional comments on the predator

Column	Explanation
gear_type_predator_id1	This id number corresponds with the gear_type_predator_id from the ’gear_type_predator’ csv file
gear_type_predator_id2	This id number corresponds with the gear_type_predator_id from the ’gear_type_predator’ csv file; this attribute is required if there are at least 2 types of gear used to sample predators
gear_type_predator_id3	This id number corresponds with the gear_type_predator_id from the ’gear_type_predator’ csv file; this attribute is required if there are at least 3 types of gear used to sample predators
gear_type_predator_id4	This id number corresponds with the gear_type_predator_id from the ’gear_type_predator’ csv file; this attribute is required if there are at least 4 types of gear used to sample predators
gear_type_predator_id5	This id number corresponds with the gear_type_predator_id from the ’gear_type_predator’ csv file; this attribute is required if there are at least 5 types of gear used to sample predators
type_diet_data	The diet metric reported in the source (e.g., percent weight of prey, index of relative importance)
diet_data_units	The diet data units (e.g., percent); if the diet data are reported as a number then the units are left as blank
formula	The formula for the diet metric, if applicable; this is for metrics such as the index of relative importance or the stomach content index because they may be calculated differently in different sources
prey_lowest_taxonomic_level	The lowest taxonomic level reported in the source; if a source reports to the species level then this attribute should include both the genus and species names (e.g., Calanus pacificus); in some cases the lowest taxonomic level is not a scientific name – like ‘gelatinous’ or ‘zooplankton_collective’ or ‘miscellaneous’
prey_kingdom	The kingdom based on the lowest taxonomic level
prey_phylum	The phylum based on the lowest taxonomic level
prey_class	The class based on the lowest taxonomic level
prey_order	The order based on the lowest taxonomic level
prey_family	The family based on the lowest taxonomic level
prey_genus	The genus based on the lowest taxonomic level
prey_species	The species based on the lowest taxonomic level
value_diet_data	Diet data values for the specific prey item and the sample
prey_sex	Either ‘male’, ‘female’ or ‘unspecified’

Column	Explanation
prey_life_stage	The prey life stage
prey_life_stage_min	If there are a mixture of life stages, then this attribute represents the minimum life stage
prey_life_stage_max	If there are a mixture of life stages, then this attribute represents the maximum life stage
prey_length_value_mm	The length of prey in millimeters; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of prey data from a source
prey_length_min_mm	The minimum length of prey in millimeters if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of prey data from a source
prey_length_max_mm	The maximum length of prey in millimeters if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of prey data from a source
prey_weight_value_mg	The weight of prey in milligrams; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of prey data from a source
prey_weight_min_mg	The minimum weight of prey in milligrams if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of prey data from a source
prey_weight_max_mg	The maximum weight of prey in milligrams if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of prey data from a source
prey_notes	Any additional comments on prey

Table A5. The associated salmon biological data for each salmon sample.

Column	Explanation
predator_id	A unique number that is generated and assigned to each predator sample
source_id	This number corresponds with the source_id from the ‘sources.csv’ file

Column	Explanation
year_min	YYYY; if there is just one value for the year then it is found in this attribute; if there are a range of values for the year then the minimum value is found in this attribute
year_max	YYYY; if there are a range of values for the year then the maximum value is entered into this attribute
warm_cool_years	Either 'warm', 'cool' or NA; this attribute will only have a value if the samples are explicitly reported as being from a warm versus cool year(s) and can only be uniquely identified this way
odd_even_years	Either 'odd, 'even' or NA; this attribute will only have a value if the samples are explicitly reported as being from an odd versus even year(s) and can only be uniquely identified this way
season_min	Either 'spring', 'summer', 'autumn', or 'winter'; if there is just one value for the season then it is entered into this attribute; If there are a range of values for the season then the minimum value is entered into this attribute; this attribute will only have a value if there is no value for the month/date and the source explicitly defines the temporal sampling period by season
season_max	Either 'spring', 'summer', 'autumn', or 'winter'; if there are a range of values for the season then the maximum value is entered into this attribute; this attribute will only have a value if there is no value for the month/date and the source explicitly defines the temporal sampling period by season
month_min	Month names are completely spelled out with the first letter capitalized; if there is just one value for the month then it is entered into this attribute; If there are a range of values for the month then the minimum value is found in this attribute
month_max	Month names are completely spelled out with the first letter capitalized; if there are a range of values for the month then the maximum value is found in this attribute
date_min	Expressed using year, month, and day; if there is just one value for the date then it is entered into this attribute; if there are a range of values for the date then the minimum value is found in this attribute
date_max	Expressed using year, month, and day; if there are a range of values for the date then the maximum value is found in this attribute

Column	Explanation
time_min	HH:MM:SS; if there is just one value for the time then it is found in this attribute; if there are a range of values for the time then the minimum value is found in this attribute
time_max	HH:MM:SS; if there are a range of values for the time then the maximum value is found in this attribute
lat_min	If there is just one value for the latitude then it is found in this attribute; if there are a range of values for the latitude then the minimum value is found in this attribute; values are in decimal degrees format
lat_max	If there are a range of values for the latitude then the maximum value is found in this attribute; values are in decimal degrees format
lon_min	If there is just one value for the longitude then it is entered into this attribute; if there are a range of values for the longitude then the minimum value is entered into this attribute; values are in decimal degrees format
lon_max	If there are a range of values for the longitude then the maximum value is found in this attribute; values are in decimal degrees format
predator_lowest_taxonomic_level	The lowest taxonomic level reported in the source; if a source reports to the species level then this attribute includes both the genus and species names (e.g., Oncorhynchus nerka); only scientific names are reported, not common names
predator_life_stage	Either 'juvenile', 'adult' or NA
predator_life_stage_min	If there are a mixture of juveniles and adults, then 'juvenile' is entered here
predator_life_stage_max	If there are a mixture of juveniles and adults, then 'adult' is entered here
predator_freshwater_age	An integer to indicate the number of years spent living in freshwater
predator_freshwater_age_min	If there are a mixture of freshwater ages, then this attribute represents the minimum age; an integer to indicate the number of years spent living in freshwater
predator_freshwater_age_max	If there are a mixture of freshwater ages, then this attribute represents the maximum age; an integer to indicate the number of years spent living in freshwater
predator_ocean_age	An integer to indicate the number of years spent living in the ocean
predator_ocean_age_min	If there are a mixture of ocean ages, then this attribute represents the minimum age; an integer to indicate the number of years spent living in the ocean

Column	Explanation
predator_ocean_age_max	If there are a mixture of ocean ages, then this attribute represents the maximum age; an integer to indicate the number of years spent living in the ocean
predator_maturity	Either ‘juvenile’, ‘immature’, ‘maturing’ ‘mature’, ‘kelt’ (for steelhead), or NA
predator_maturity_min	If there are a mixture of maturity levels, then the minimum maturity level is found here
predator_maturity_max	If there are a mixture of maturity levels, then the maximum maturity level is found here
predator_length_value_cm	The length of a predator in centimeters (could be either fork length or total length); only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_length_min_cm	The minimum length of a predator in centimeters (could be either fork length or total length) if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_length_max_cm	The maximum length of a predator in centimeters (could be either fork length or total length) if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_weight_value_g	The weight of a predator in grams; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_weight_min_g	The minimum weight of a predator in grams if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_weight_max_g	The maximum weight of a predator in grams if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_subsample_id	A unique number that is generated and assigned to predator samples if a source reports the diets of individual predators with no unique identifiers; values are assigned

Column	Explanation
	for each source starting from 1 and increasing by a value of 1 each time (e.g., 1,2,3…); if unique subsample_ids are not required then the default value is 0
predator_sex	Either ‘male’, ‘female’ or ‘unspecified’
hatchery_wild	Either ‘hatchery’, ‘wild’ or ‘unspecified’
predator_replicates	The total number of predator replicates per sample
predator_notes	Any additional comments on the predator
gear_type_predator_id1	This id number corresponds with the gear_type_predator_id from the ’gear_type_predator’ csv file
gear_type_predator_id2	This id number corresponds with the gear_type_predator_id from the ’gear_type_predator’ csv file; this attribute is required if there are at least 2 types of gear used to sample predators
gear_type_predator_id3	This id number corresponds with the gear_type_predator_id from the ’gear_type_predator’ csv file; this attribute is required if there are at least 3 types of gear used to sample predators
gear_type_predator_id4	This id number corresponds with the gear_type_predator_id from the ’gear_type_predator’ csv file; this attribute is required if there are at least 4 types of gear used to sample predators
gear_type_predator_id5	This id number corresponds with the gear_type_predator_id from the ’gear_type_predator’ csv file; this attribute is required if there are at least 5 types of gear used to sample predators
biological_parameter	The predator biological parameter reported in the source (e.g., total length, fork length, body weight)
predator_bio_notes	Any additional comments on the predator biological parameters
value	The biological parameter value
mean	The biological parameter mean
error	The error associated with the biological parameter mean
min	If there are a range of values for the biological parameter this attribute represents the minimum value
max	If there are a range of values for the biological parameter this attribute represents the maximum value
units	The units associated with the biological parameter; units are fully spelled and plural (e.g., centimeters instead of centimeter)

Table A6. The data extracted for each prey gear type.

Column	Explanation
gear_type_prey_id	A unique number that is generated and assigned to each unique prey gear type for each source (e.g., 1, 2, 3…etc.)
gear_type	The most basic description of the type of gear given in the source (e.g., bongo net); if the prey is a diet item, then the gear_type is 'predator' to indicate that it was not collected from the environment but instead in a salmon stomach
gear_length_value	The gear length
gear_length_min	If there are a range of gear lengths, then this attribute represents the minimum length
gear_length_max	If there are a range of gear lengths, then this attribute represents the maximum length
gear_length_units	The units associated with the gear length; units are fully spelled and plural (e.g., meters instead of meter)
gear_width_value	The gear width
gear_width_min	If there are a range of gear widths, then this attribute represents the minimum width
gear_width_max	If there are a range of gear widths, then this attribute represents the maximum width
gear_width_units	The units associated with the gear width; units are fully spelled and plural (e.g., meters instead of meter)
gear_depth_value	The gear depth; if gear is reported to be deployed at the surface then the depth value is assigned to 0
gear_depth_min	If there are a range of gear depths, then this attribute represents the minimum depth; if gear is reported to be deployed at the surface then the depth value is assigned to 0
gear_depth_max	If there are a range of gear depths, then this attribute represents the maximum depth
gear_depth_units	The units associated with the gear depth; units are fully spelled and plural (e.g., meters instead of meter)
mesh_size_value	The gear mesh size
mesh_size_min	If there are a range of gear mesh sizes, then this attribute represents the minimum mesh size
mesh_size_max	If there are a range of gear mesh sizes, then this attribute represents the maximum mesh size
mesh_size_units	The units associated with the mesh size; units are fully spelled and plural (e.g., millimeters instead of millimeter)
fishing_depth_value	The fishing depth; if fishing is reported to be at the surface then the depth value is assigned to 0
fishing_depth_min	If there are a range of fishing depths, then this attribute represents the minimum fishing depth; if fishing is reported to be at the surface then the depth value is assigned to 0

Column	Explanation
fishing_depth_max	If there are a range of fishing depths, then this attribute represents the maximum fishing depth
fishing_depth_units	The units associated with the fishing depth; units are fully spelled and plural (e.g., meters instead of meter)
tow_speed_value	The gear tow speed
tow_speed_min	If there are a range of gear tow speeds, then this attribute represents the minimum tow speed
tow_speed_max	If there are a range of gear tow speeds, then this attribute represents the maximum tow speed
tow_speed_units	The units associated with the tow speed; units are fully spelled and plural (e.g., knots instead of knot)
duration_deployment_value	The gear duration of deployment
duration_deployment_min	If there are a range of gear durations of deployment, then this attribute represents the minimum duration of deployment
duration_deployment_max	If there are a range of gear durations of deployment, then this attribute represents the maximum duration of deployment
duration_deployment_units	The units associated with the duration of deployment; units are fully spelled and plural (e.g., minutes instead of minute)
gear_notes	Any additional comments on the gear

Table A7. The associated prey biological data for each prey sample. This data could come from diet samples or from environmental samples of potential prey items.

Column	Explanation
prey_id	A unique number that is generated and assigned to each prey sample
predator_id	A unique number that is generated and assigned to each predator sample
source_id	This number corresponds with the source_id from the ‘sources.csv’ file
year_min	YYYY; if there is just one value for the year then it is found in this attribute; if there are a range of values for the year then the minimum value is found in this attribute
year_max	YYYY; if there are a range of values for the year then the maximum value is entered into this attribute
warm_cool_years	Either ‘warm’, ‘cool’ or NA; this attribute will only have a value if the samples are explicitly reported as being from a warm versus cool year(s) and can only be uniquely identified this way
odd_even_years	Either ‘odd, ‘even’ or NA; this attribute will only have a value if the samples are explicitly reported as being from an odd versus even year(s) and can only be uniquely identified this way

Column	Explanation
season_min	Either ‘spring’, ‘summer’, ‘autumn’, or ‘winter’; if there is just one value for the season then it is entered into this attribute; If there are a range of values for the season then the minimum value is entered into this attribute; this attribute will only have a value if there is no value for the month/date and the source explicitly defines the temporal sampling period by season
season_max	Either ‘spring’, ‘summer’, ‘autumn’, or ‘winter’; if there are a range of values for the season then the maximum value is entered into this attribute; this attribute will only have a value if there is no value for the month/date and the source explicitly defines the temporal sampling period by season
month_min	Month names are completely spelled out with the first letter capitalized; if there is just one value for the month then it is entered into this attribute; If there are a range of values for the month then the minimum value is found in this attribute
month_max	Month names are completely spelled out with the first letter capitalized; if there are a range of values for the month then the maximum value is found in this attribute
date_min	Expressed using year, month, and day; if there is just one value for the date then it is entered into this attribute; if there are a range of values for the date then the minimum value is found in this attribute
date_max	Expressed using year, month, and day; if there are a range of values for the date then the maximum value is found in this attribute
time_min	HH:MM:SS; if there is just one value for the time then it is found in this attribute; if there are a range of values for the time then the minimum value is found in this attribute
time_max	HH:MM:SS; if there are a range of values for the time then the maximum value is found in this attribute
lat_min	If there is just one value for the latitude then it is found in this attribute; if there are a range of values for the latitude then the minimum value is found in this attribute; values are in decimal degrees format
lat_max	If there are a range of values for the latitude then the maximum value is found in this attribute; values are in decimal degrees format
lon_min	If there is just one value for the longitude then it is entered into this attribute; if there are a range of values for the

Column	Explanation
	longitude then the minimum value is entered into this attribute; values are in decimal degrees format
lon_max	If there are a range of values for the longitude then the maximum value is found in this attribute; values are in decimal degrees format
predator_lowest_taxonomic_level	The lowest taxonomic level reported in the source; if a source reports to the species level then this attribute includes both the genus and species names (e.g., Oncorhynchus nerka); only scientific names are reported, not common names
predator_life_stage	Either ‘juvenile’, ‘adult’ or NA
predator_life_stage_min	If there are a mixture of juveniles and adults, then ‘juvenile’ is entered here
predator_life_stage_max	If there are a mixture of juveniles and adults, then ‘adult’ is entered here
predator_freshwater_age	An integer to indicate the number of years spent living in freshwater
predator_freshwater_age_min	If there are a mixture of freshwater ages, then this attribute represents the minimum age; an integer to indicate the number of years spent living in freshwater
predator_freshwater_age_max	If there are a mixture of freshwater ages, then this attribute represents the maximum age; an integer to indicate the number of years spent living in freshwater
predator_ocean_age	An integer to indicate the number of years spent living in the ocean
predator_ocean_age_min	If there are a mixture of ocean ages, then this attribute represents the minimum age; an integer to indicate the number of years spent living in the ocean
predator_ocean_age_max	If there are a mixture of ocean ages, then this attribute represents the maximum age; an integer to indicate the number of years spent living in the ocean
predator_maturity	Either ‘juvenile’, ‘immature’, ‘maturing’ ‘mature’, ‘kelt’ (for steelhead), or NA
predator_maturity_min	If there are a mixture of maturity levels, then the minimum maturity level is found here
predator_maturity_max	If there are a mixture of maturity levels, then the maximum maturity level is found here
predator_length_value_cm	The length of a predator in centimeters (could be either fork length or total length); only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source

Column	Explanation
predator_length_min_cm	The minimum length of a predator in centimeters (could be either fork length or total length) if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_length_max_cm	The maximum length of a predator in centimeters (could be either fork length or total length) if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_weight_value_g	The weight of a predator in grams; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_weight_min_g	The minimum weight of a predator in grams if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_weight_max_g	The maximum weight of a predator in grams if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of diet data from a source
predator_subsample_id	A unique number that is generated and assigned to predator samples if a source reports the diets of individual predators with no unique identifiers; values are assigned for each source starting from 1 and increasing by a value of 1 each time (e.g., 1,2,3…); if unique subsample_ids are not required then the default value is 0
predator_sex	Either 'male', 'female' or 'unspecified'
hatchery_wild	Either 'hatchery', 'wild' or 'unspecified'
predator_replicates	The total number of predator replicates per sample
predator_notes	Any additional comments on the predator
gear_type_predator_id1	This id number corresponds with the gear_type_predator_id from the 'gear_type_predator' csv file
gear_type_predator_id2	This id number corresponds with the gear_type_predator_id from the 'gear_type_predator' csv file; this attribute is required if there are at least 2 types of gear used to sample predators

Column	Explanation
gear_type_predator_id3	This id number corresponds with the gear_type_predator_id from the 'gear_type_predator' csv file; this attribute is required if there are at least 3 types of gear used to sample predators
gear_type_predator_id4	This id number corresponds with the gear_type_predator_id from the 'gear_type_predator' csv file; this attribute is required if there are at least 4 types of gear used to sample predators
gear_type_predator_id5	This id number corresponds with the gear_type_predator_id from the 'gear_type_predator' csv file; this attribute is required if there are at least 5 types of gear used to sample predators
prey_lowest_taxonomic_level	The lowest taxonomic level reported in the source; if a source reports to the species level then this attribute includes both the genus and species names (e.g., Calanus pacificus); in some cases the lowest taxonomic level is not a scientific name – like 'gelatinous' or 'zooplankton_collective' or 'miscellaneous'
prey_kingdom	The kingdom based on the lowest taxonomic level
prey_phylum	The phylum based on the lowest taxonomic level
prey_class	The class based on the lowest taxonomic level
prey_order	The order based on the lowest taxonomic level
prey_family	The family based on the lowest taxonomic level
prey_genus	The genus based on the lowest taxonomic level
prey_species	The species based on the lowest taxonomic level
prey_life_stage	The prey life stage
prey_life_stage_min	If there are a mixture of life stages, then this attribute represents the minimum life stage
prey_life_stage_max	If there are a mixture of life stages, then this attribute represents the maximum life stage
prey_length_value_mm	The length of prey in millimeters; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of prey data from a source
prey_length_min_mm	The minimum length of prey in millimeters if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of prey data from a source
prey_length_max_mm	The maximum length of prey in millimeters if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are

Column	Explanation
	the only way to uniquely identify samples of prey data from a source
prey_weight_value_mg	The weight of prey in milligrams; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of prey data from a source
prey_weight_min_mg	The minimum weight of prey in milligrams if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of prey data from a source
prey_weight_max_mg	The maximum weight of prey in milligrams if there are a range of sizes; only reported if there is no other way to determine life stage, or if length or weight categories are the only way to uniquely identify samples of prey data from a source
prey_sex	Either 'male', 'female' or 'unspecified'
prey_subsample_id	A unique number that is generated and assigned to prey samples if a source reports the biological parameters of individual prey with no unique identifiers; values are assigned for each source starting from 1 and increasing by a value of 1 each time (e.g., 1,2,3…)
prey_replicates	The total number of prey replicates per sample
prey_notes	Any additional comments on the prey
gear_type_prey_id1	This id number corresponds with the gear_type_prey_id from the 'gear_type_prey' csv file; if the prey is part of a diet data sample then the id should be 1 which corresponds to the 'predator' gear type (i.e. sample came from a predator stomach)
gear_type_prey_id2	This id number corresponds with the gear_type_prey_id from the 'gear_type_prey' csv file; this attribute is required if there are at least 2 types of gear used to sample predators
gear_type_prey_id3	This id number corresponds with the gear_type_prey_id from the 'gear_type_prey' csv file; this attribute is required if there are at least 3 types of gear used to sample predators
gear_type_prey_id4	This id number corresponds with the gear_type_prey_id from the 'gear_type_prey' csv file; this attribute is required if there are at least 4 types of gear used to sample predators
gear_type_prey_id5	This id number corresponds with the gear_type_prey_id from the 'gear_type_prey' csv file; this attribute is

Column	Explanation
	required if there are at least 5 types of gear used to sample predators
biological_parameter	The prey biological parameter reported in the source (e.g., body length, body weight)
prey_bio_notes	Any additional comments on the prey biological parameters
value	The biological parameter value
mean	The biological parameter mean
error	The error associated with the biological parameter mean
min	If there are a range of values for the biological parameter this attribute represents the minimum value
max	If there are a range of values for the biological parameter this attribute represents the maximum value
units	The units associated with the biological parameter; units are fully spelled and plural (e.g., centimeters instead of centimeter)

Table A8. The associated environmental data for each salmon or prey sample.

Column	Explanation
environmental_data_id	A unique number that is generated and assigned to each environmental data point
source_id	This number corresponds with the source_id from the ‘sources’ csv file
year_min	YYYY; if there is just one value for the year then it is found in this attribute; if there are a range of values for the year then the minimum value is found in this attribute
year_max	YYYY; if there are a range of values for the year then the maximum value is entered into this attribute
warm_cool_years	Either ‘warm’, ‘cool’ or NA; this attribute will only have a value if the samples are explicitly reported as being from a warm versus cool year(s) and can only be uniquely identified this way
odd_even_years	Either ‘odd, ‘even’ or NA; this attribute will only have a value if the samples are explicitly reported as being from an odd versus even year(s) and can only be uniquely identified this way
season_min	Either ‘spring’, ‘summer’, ‘autumn’, or ‘winter’; if there is just one value for the season then it is entered into this attribute; If there are a range of values for the season then the minimum value is entered into this attribute; this attribute will only have a value if there is no value for the month/date and the source explicitly defines the temporal sampling period by season

Column	Explanation
season_max	Either ‘spring’, ‘summer’, ‘autumn’, or ‘winter’; if there are a range of values for the season then the maximum value is entered into this attribute; this attribute will only have a value if there is no value for the month/date and the source explicitly defines the temporal sampling period by season
month_min	Month names are completely spelled out with the first letter capitalized; if there is just one value for the month then it is entered into this attribute; If there are a range of values for the month then the minimum value is found in this attribute
month_max	Month names are completely spelled out with the first letter capitalized; if there are a range of values for the month then the maximum value is found in this attribute
date_min	Expressed using year, month, and day; if there is just one value for the date then it is entered into this attribute; if there are a range of values for the date then the minimum value is found in this attribute
date_max	Expressed using year, month, and day; if there are a range of values for the date then the maximum value is found in this attribute
time_min	HH:MM:SS; if there is just one value for the time then it is found in this attribute; if there are a range of values for the time then the minimum value is found in this attribute
time_max	HH:MM:SS; if there are a range of values for the time then the maximum value is found in this attribute
lat_min	If there is just one value for the latitude then it is found in this attribute; if there are a range of values for the latitude then the minimum value is found in this attribute; values are in decimal degrees format
lat_max	If there are a range of values for the latitude then the maximum value is found in this attribute; values are in decimal degrees format
lon_min	If there is just one value for the longitude then it is entered into this attribute; if there are a range of values for the longitude then the minimum value is entered into this attribute; values are in decimal degrees format
lon_max	If there are a range of values for the longitude then the maximum value is found in this attribute; values are in decimal degrees format
environmental_data_type	The environmental data type reported in the source (e.g., temperature, salinity)
measurement_depth	The depth associated with the environmental parameter measurement; if the measurement in reported to be at the

Column	Explanation
	surface (e.g., sea surface temperature) then the measurement depth value is assigned to 0
depth_units	The units associated with the measurement depth; units are fully spelled and plural (e.g., meters instead of meter)
environmental_subsample_id	A unique number that is generated and assigned to environmental samples if there are no other unique identifiers; values are assigned for each source starting from 1 and increasing by a value of 1 each time (e.g., 1,2,3…)
environmental_notes	Any additional comments on the environmental parameter measurement
value	The value of the environmental parameter
mean	The mean of the environmental parameters
error	The error associated with the environmental parameter mean
min	If there are a range of values for the environmental parameter this attribute represents the minimum value
max	If there are a range of values for the environmental parameter this attribute represents the maximum value
environmental_units	The units associated with the environmental parameter; units are fully spelled and plural (e.g., micrograms per liter instead of microgram per liter)